

Rodica Curtu · Bard Ermentrout

Oscillations in a refractory neural net

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Abstract. A functional differential equation that arises from the classic theory of neural networks is considered. As the length of the absolute refractory period is varied, there is, as shown here, a super-critical Hopf bifurcation. As the ratio of the refractory period to the time constant of the network increases, a novel relaxation oscillation occurs. Some approximations are made and the period of this oscillation is computed.

1. Introduction

Wilson and Cowan [10] introduced a class of neural network equations modeling the excitatory and inhibitory interactions between two populations of cells. Each population obeys a functional-differential equation of the form:

$$\tau \frac{du(t)}{dt} = -u(t) + \left(1 - \int_{t-R}^t u(s) ds\right) f(I(t))$$

where τ is the time constant, $I(t)$ represents inputs to the population, f is the firing rate curve, and R is the absolute refractory period of the neurons. The function $u(t)$ is the fraction of the population of neurons which is firing. It can also be regarded as the actual firing rate of the population. The refractory term premultiplying the firing rate was approximated (by assuming that R is small) as

$$1 - \int_{t-R}^t u(s) ds \approx 1 - Ru(t).$$

All subsequent analyses of these equations either make this assumption or set $R = 0$.

There have been numerous analyses of neural networks with delays. Castelfranco and Stech [2] prove the existence of oscillatory solutions to a two-dimensional model due to Plant which has delayed negative feedback. Similar results are described by Campbell et al. in a model for pupillary control [1]. Marcus and Westervelt [9] linearize a Hopfield symmetrically coupled network

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R. Curtu, B. Ermentrout (for correspondence): Department of Mathematics, University of Pittsburgh, Pittsburgh PA 15260, USA. e-mail: bard@pitt.edu

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and show that the fixed points are asymptotically stable. Ye et al. [11] improve on this result by rigorously showing global stability of fixed points for the Hopfield network with delay.

The purpose of this note is to explore the consequences of keeping the original form of the Wilson-Cowan equations. In particular, we will look at a self-excited population of cells. We consider the functional-differential equation

$$\tau \frac{du}{dt} = -u + \left(1 - \frac{1}{R} \int_{t-R}^t u(s) ds \right) f(u)$$

where f is a smooth monotonically increasing function ($f' > 0$) which takes values between 0 and 1. We have normalized the integral term in order to study the temporal effects of altering this absolute refractory period.

By rescaling the time $t \mapsto t/R$ and letting $r = R/\tau$ denote the ratio of the absolute refractory period to the time constant of the network, the equation becomes

$$\frac{du}{dt} = r \left[-u + \left(1 - \int_{t-1}^t u(s) ds \right) f(u) \right] \quad (1)$$

We can alternatively rescale time as $t \mapsto t/\tau$ and obtain:

$$\frac{du}{dt} = -u + \left(1 - \frac{1}{r} \int_{t-r}^t u(s) ds \right) f(u).$$

In this rescaling, it is clear that this is a “delayed negative-feedback” system and that in the limit as $r \rightarrow 0$ we obtain the original Wilson-Cowan equations

$$\frac{du}{dt} = -u + (1 - u)f(u).$$

Because the calculations are simpler, we will use the first rescaling, (1) in the remainder of the paper.

Figure 1 shows a simulation of (1) for a variety of values of the parameter r . The horizontal line corresponds to a fixed point. For the choice of parameters in the figure, solutions converge to the fixed point for $r < 4.7$ and for $r > 4.8$ all solutions numerically converge to a periodic orbit. Thus, it appears that as the refractoriness r increases, the constant solution loses stability through a Hopf bifurcation. For all larger values of r , solutions converge to a family of periodic orbits whose amplitude increases. Our goal in the subsequent sections is to show that this is in fact the correct picture. Section 2 is devoted to the analysis of fixed points and their stability. In section 3, we find the normal form for the Hopf bifurcation and show that the bifurcation is supercritical. We then look at the limit as r gets large. We show that the resulting equation behaves like a relaxation oscillator and compute the period for this system. We close with some simulations of waves and related phenomena in a locally connected network.

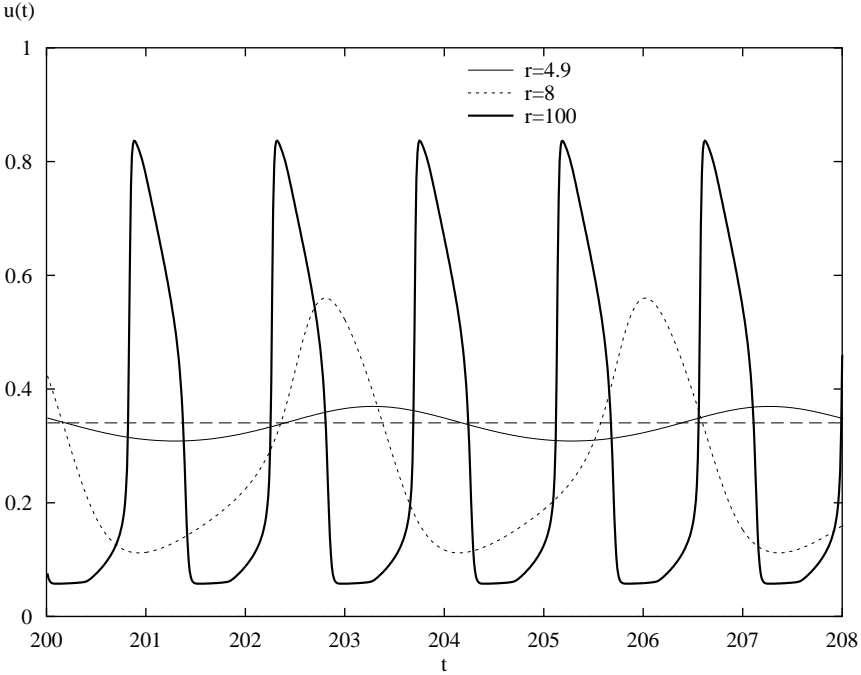


Fig. 1. The behavior of (1) for different values of the parameter $r = R/\tau$ with $f(u) = 1/(1 + \exp(-8(u - .333)))$. The period of the smallest oscillation is 4 and that of the largest is 1.43.

2. Fixed points and stability

The fixed points for (1) are $u = \bar{u}$ for all t and \bar{u} satisfies

$$-\bar{u} + (1 - \bar{u})f(\bar{u}) = 0 \tag{2}$$

It is easy to check that because $0 < f < 1$ there is no equilibrium point in $(-\infty, 0] \cup [\frac{1}{2}, \infty)$, but there is at least one in $(0, \frac{1}{2})$, say \bar{u} .

For such an equilibrium we can rewrite the equation (1), by defining $u := \bar{u} + y$ and using the Taylor expansion for the function f about \bar{u} , as

$$\begin{aligned} \frac{dy}{dt} = r & \left[-y + y(1 - \bar{u})f'(\bar{u}) - f(\bar{u}) \int_{t-1}^t y(s) ds \right] \\ & + r \left[-y f'(\bar{u}) \int_{t-1}^t y(s) ds + y^2(1 - \bar{u}) \frac{f''(\bar{u})}{2} \right] \\ & + r \left[-y^2 \frac{f''(\bar{u})}{2} \int_{t-1}^t y(s) ds + y^3(1 - \bar{u}) \frac{f'''(\bar{u})}{6} \right] + \mathcal{O}(y^4) \end{aligned} \tag{3}$$

As a first step in our analysis we will consider only the linearized part of the equation (3), *i.e.*

$$\frac{dy}{dt} = r \left(-A y - b \int_{t-1}^t y(s) ds \right)$$

where the coefficients A and b are given by $A = 1 - (1 - \bar{u}) f'(\bar{u}) < 1$ and $b = f(\bar{u}) \in (0, 1)$.

The stability of this equation is determined by studying the roots of the characteristic equation obtained by substituting $y(t) = \exp \lambda t$ into the linearized equation. This results in

$$\lambda + Ar + br \frac{1 - e^{-\lambda}}{\lambda}. \quad (4)$$

A very similar equation to this is studied in Diekmann et al., Chapter XI.4.3. We summarize the main points as they apply to the present equations. First, $\lambda = 0$ if and only if $A + b = 0$ and furthermore as long as $b \neq 0$, $\lambda = 0$ is a simple root. All roots with positive real part are bounded by the following inequality:

$$|\lambda| < r(|A| + |b|).$$

Thus, the only way that roots can enter the right-half plane is to go through the imaginary axis. Clearly if $b = 0$ and $A > 0$, then all roots have negative real parts. Furthermore, as we just noted, roots can cross 0 only if $A + b = 0$. Thus, we are interested in when there are roots of the form $\lambda = i\omega$. Substituting this into (4) we see that

$$Ar = -\frac{\omega \sin \omega}{1 - \cos \omega}, \quad (5)$$

$$br = \frac{\omega^2}{1 - \cos \omega}. \quad (6)$$

Since there are singularities at $\omega = 2k\pi$, these equations define a series of parametric curves defined in the regions $\omega \in (2k\pi, 2(k+1)\pi)$ for k an integer. The first two of these curves are plotted in Figure 2. Crossing these curves results in new complex eigenvalues with positive real parts. To study stability as a function of the parameter r , we note that (Ar, br) defines a line through the origin with slope b/A as r varies in the (Ar, br) plane shown in the figure. If this line crosses the lower emphasized curve then stability is lost through a pair of complex eigenvalues as the parameter r increases. Taking the ratio of the two above equations, we see that there will be such a root if and only if:

$$\frac{A}{b} = -\frac{\sin \omega}{\omega}. \quad (7)$$

The minimum of this function is -1 and the maximum is $M = -\sin(\xi)/\xi$ where ξ is the smallest root of $\tan(x) = x$ greater than π . Thus, the slope of the line b/A must lie between $1/M \approx 4.60334$ and -1 . These two lines are illustrated in Figure 2. If b/A lies between -1 and $4.6033 \dots$, then starting at small values of r

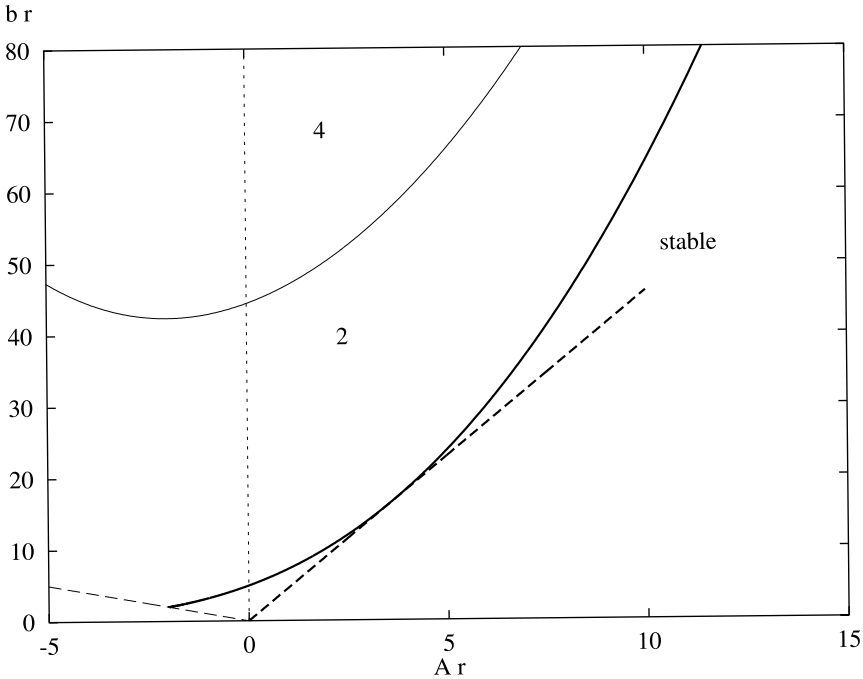


Fig. 2. Stability diagram for (4) as a function of Ar and br . Straight lines depicts the curve $b = -A$ and $b = A/M$ where M is defined in the text. The remaining curves depict lines along which there are purely imaginary roots. Numbers denote the number of eigenvalues with positive real parts.

as r increases, it pierces the lower stability curve and a pair of complex conjugate eigenvalues cross the imaginary axis resulting in a loss of stability. Clearly, if b/A is within these bounds, then we can solve (7) for a value of ω between 0 and 2π . Then we can use (6) to find

$$\tilde{r}_0 = \frac{1}{b} \frac{\omega^2}{1 - \cos \omega}$$

the critical value of r (which is always positive). If b/A is positive and less than $1/M$ then no increases in r can ever lead to a loss of stability. If the slope b/A is negative and shallower than -1 , then for all positive values of r there is a real positive root to (4). To see this, note that we can rewrite (4) as

$$br \frac{1 - e^{-\lambda}}{\lambda} = -(\lambda + Ar).$$

The left-hand side is monotonically decreasing, positive, and starts at br at $\lambda = 0$. Suppose that $-Ar > br$. Then $-(\lambda + Ar)$ is larger than br at $\lambda = 0$ and crosses the x -axis when $\lambda = -Ar > 0$. Thus, there is an intersection of the two for a positive value of λ between 0 and $-Ar$.

We summarize these calculations in the following theorem.

Theorem 1. *Suppose \bar{u} is a fixed point of the equation (1). Let $A = 1 - (1 - \bar{u}) f'(\bar{u})$ and $b = f(\bar{u})$.*

- *Suppose that $-b < A < bM$ where $M = -\sin(\xi)/\xi \approx 1/4.60334 = 0.2172336$ with ξ the smallest root greater than π to $\tan(x) = x$. Then for r small enough, the fixed point is stable. As r increases, stability is lost when r crosses \tilde{r}_0 where*

$$\tilde{r}_0 = \frac{1}{b} \frac{\omega_0^2}{1 - \cos \omega_0}$$

and ω_0 is the unique root to

$$\frac{A}{b} = -\frac{\sin \omega}{\omega}$$

between 0 and 2π .

- *If $A > Mb$ then the fixed point is stable for all values of r .*
- *If $A < -b$ then the fixed point is unstable for all positive r .*

3. Normal form

The numerical simulations in figure 1 indicate that there exist oscillatory solutions for large enough r . Because of the above stability analysis we suspect the presence of an Andronov-Hopf bifurcation point for certain values of the parameter r . The next reasonable step would be the construction of the corresponding normal form and this is exactly what we do in this section. The Hopf bifurcation theorem has been rigorously proven for (1) and related equations in Diekmann, et al.[3] Indeed, the authors compute the normal form for a related equation in Chapter XI4.3. Faria and Magalhães [4] describe a method to compute normal forms using the adjoint for equations of the form:

$$\frac{dz}{dt} = L(p)z_t + F(z_t, p)$$

where p represents parameters. Our approach is similar to theirs. With minor modifications, we could apply the formula in Theorem 3.9 Diekmann, et al. [3] (page 298), but for completeness, we derive the coefficients for the normal form here.

Let us consider the equation (3) and define the linear operators

$$Ly := \frac{dy}{dt} + A r_0 y + b r_0 \int_{t-1}^t y(s) ds$$

$$\Lambda y := -A y - b \int_{t-1}^t y(s) ds$$

as well as the quadratic and cubic forms

$$B(y_1, y_2) := r_0 \left[\frac{(1 - \bar{u})f''(\bar{u})}{2} y_1 y_2 - \frac{f'(\bar{u})}{2} y_1 \int_{t-1}^t y_2(s) ds \right. \\ \left. - \frac{f'(\bar{u})}{2} y_2 \int_{t-1}^t y_1(s) ds \right]$$

$$C(y_1, y_2, y_3) := r_0 \left[\frac{(1 - \bar{u})f'''(\bar{u})}{6} y_1 y_2 y_3 - \frac{f''(\bar{u})}{6} y_1 y_2 \int_{t-1}^t y_3(s) ds \right. \\ \left. - \frac{f''(\bar{u})}{6} y_2 y_3 \int_{t-1}^t y_1(s) ds - \frac{f''(\bar{u})}{6} y_3 y_1 \int_{t-1}^t y_2(s) ds \right]$$

Taking a small perturbation of the parameter ($r = r_0 + \alpha$), the equation (3) can be rewritten as

$$Ly = \alpha \Lambda y + B(y, y) + C(y, y, y) + \alpha B(y, y) + \mathcal{O}(y^4) \quad (8)$$

Since we are interested in finding small oscillatory solutions we can consider the following asymptotic expansion for (small) y and α

$$\alpha = \epsilon \alpha_1 + \epsilon^2 \alpha_2 + \epsilon^3 \alpha_3 + \dots \\ y(t) = \epsilon u_0(t) + \epsilon^2 u_1(t) + \epsilon^3 u_2(t) + \dots \quad \epsilon \rightarrow 0$$

and obtain, instead of (8),

$$\epsilon Lu_0 + \epsilon^2 Lu_1 + \epsilon^3 Lu_2 + \mathcal{O}(\epsilon^4) \\ = [\epsilon \alpha_1 + \epsilon^2 \alpha_2 + \epsilon^3 \alpha_3 + \dots] \cdot [\epsilon \Lambda u_0 + \epsilon^2 \Lambda u_1 + \epsilon^3 \Lambda u_2 + \dots] \\ + [1 + \epsilon \alpha_1 + \dots] \cdot B(\epsilon u_0 + \epsilon^2 u_1 + \epsilon^3 u_2 + \dots, \epsilon u_0 + \epsilon^2 u_1 + \epsilon^3 u_2 + \dots) \\ + C(\epsilon u_0 + \epsilon^2 u_1 + \epsilon^3 u_2 + \dots, \epsilon u_0 + \epsilon^2 u_1 + \epsilon^3 u_2 + \dots, \epsilon u_0 + \epsilon^2 u_1 \\ + \epsilon^3 u_2 + \dots) + \mathcal{O}(\epsilon^4) \quad \text{as } \epsilon \rightarrow 0$$

or, equivalently,

$$\epsilon Lu_0 + \epsilon^2 Lu_1 + \epsilon^3 Lu_2 + \mathcal{O}(\epsilon^4) \\ = \epsilon^2 [\alpha_1 \Lambda u_0 + B(u_0, u_0)] + \epsilon^3 [\alpha_1 \Lambda u_1 + \alpha_2 \Lambda u_0 + 2B(u_0, u_1) \\ + C(u_0, u_0, u_0) + \alpha_1 B(u_0, u_0)] + \mathcal{O}(\epsilon^4). \quad (9)$$

Based on the fact that the equation $Ly = 0$ has two independent solutions ($e^{\pm i\omega_0 t}$) on the center manifold and by the asymptotic expansion

$$Lu_0 = \epsilon [\alpha_1 \Lambda u_0 + B(u_0, u_0) - Lu_1] + \dots$$

we can choose

$$u_0(t) = z(t)e^{i\omega_0 t} + \bar{z}(t)e^{-i\omega_0 t}$$

with z depending on ϵ (e.g. $z = z(\epsilon^2 t)$). The expansion with respect to ϵ gives $z = z(0) + \epsilon^2 t z'(0) + \mathcal{O}(\epsilon^4)$ as ϵ tends to 0. We then use z and the properties of the defined operators and obtain

$$\begin{aligned} 0 = & \epsilon [\alpha_1 z(0) \Lambda(e^{i\omega_0 t}) + \alpha_1 \bar{z}(0) \Lambda(e^{-i\omega_0 t}) + 2z(0)\bar{z}(0) B(e^{i\omega_0 t}, e^{-i\omega_0 t}) \\ & + z(0)^2 B(e^{i\omega_0 t}, e^{i\omega_0 t}) + \bar{z}(0)^2 B(e^{-i\omega_0 t}, e^{-i\omega_0 t}) - Lu_1] \\ & + \epsilon^2 [-Lu_2 - z'(0) L(te^{i\omega_0 t}) - \bar{z}'(0) L(te^{-i\omega_0 t}) + \alpha_1 \Lambda u_1 \\ & + \alpha_2 z(0) \Lambda(e^{i\omega_0 t}) + \alpha_2 \bar{z}(0) \Lambda(e^{-i\omega_0 t}) + 2B(u_0, u_1) + \alpha_1 B(u_0, u_0) \\ & + C(u_0, u_0, u_0)] + \mathcal{O}(\epsilon^3). \end{aligned} \quad (10)$$

The coefficient of ϵ should be zero on the center manifold. This implies that at $\epsilon = 0$ we must solve $Lu_1 = g$, with the given function g ,

$$\begin{aligned} g(t) = & \alpha_1 z(0) \Lambda(e^{i\omega_0 t}) + \alpha_1 \bar{z}(0) \Lambda(e^{-i\omega_0 t}) + 2z(0)\bar{z}(0) B(e^{i\omega_0 t}, e^{-i\omega_0 t}) \\ & + z(0)^2 B(e^{i\omega_0 t}, e^{i\omega_0 t}) + \bar{z}(0)^2 B(e^{-i\omega_0 t}, e^{-i\omega_0 t}). \end{aligned}$$

In order to ensure the existence of a solution for the equation $Lu_1 = g$ we need the inhomogeneous term $g(t)$ to be orthogonal to the solutions of the adjoint homogeneous equation. The adjoint operator of L (see appendix A) is $L^*y := -\frac{dy}{dt} + Ar_0 y + br_0 \int_t^{t+1} y(s) ds$, and on the two-dimensional center manifold $e^{i\omega_0 t}$ and $e^{-i\omega_0 t}$ are independent solutions for L^* . The inner product is the usual one: $\langle \phi, \psi \rangle = \int_0^{\frac{2\pi}{\omega_0}} \phi(t) \bar{\psi}(t) dt$, so we need

$$\int_0^{\frac{2\pi}{\omega_0}} g(t) e^{\pm i\omega_0 t} dt = 0.$$

Using the identities which are proven in appendix B,

$$\begin{aligned} L(e^{\lambda t}) &= \tilde{L}(\lambda) e^{\lambda t} \\ \Lambda(e^{\lambda t}) &= \tilde{\Lambda}(\lambda) e^{\lambda t} \\ B(e^{\lambda_1 t}, e^{\lambda_2 t}) &= \tilde{B}(\lambda_1, \lambda_2) e^{(\lambda_1 + \lambda_2)t} \\ C(e^{\lambda_1 t}, e^{\lambda_2 t}, e^{\lambda_3 t}) &= \tilde{C}(\lambda_1, \lambda_2, \lambda_3) e^{(\lambda_1 + \lambda_2 + \lambda_3)t} \end{aligned}$$

for certain functions \tilde{L} , $\tilde{\Lambda}$, \tilde{B} and \tilde{C} , the function g can be expressed as a linear combination of powers of $e^{i\omega_0 t}$ and $e^{-i\omega_0 t}$. The orthogonality condition becomes

$$\begin{cases} \alpha_1 \bar{z}(0) \frac{2\pi}{\omega_0} \tilde{\Lambda}(-i\omega_0) = 0 \\ \alpha_1 z(0) \frac{2\pi}{\omega_0} \tilde{\Lambda}(i\omega_0) = 0 \end{cases}$$

Obviously in this case α_1 is zero, and the equation corresponding to u_1 is on the center manifold

$$\begin{aligned} Lu_1 = & z(0)^2 \tilde{B}(i\omega_0, i\omega_0) e^{2i\omega_0 t} + \bar{z}(0)^2 \tilde{B}(-i\omega_0, -i\omega_0) e^{-2i\omega_0 t} \\ & + 2z(0)\bar{z}(0) \tilde{B}(i\omega_0, -i\omega_0) \end{aligned} \quad (11)$$

Choose

$$u_1 = a_1 z^2 e^{2i\omega_0 t} + 2a_2 z \bar{z} + a_3 \bar{z}^2 e^{-2i\omega_0 t}$$

↓

$$u_1 = a_1 z^2(0) e^{2i\omega_0 t} + 2a_2 z(0) \bar{z}(0) + a_3 \bar{z}^2(0) e^{-2i\omega_0 t} + \mathcal{O}(\epsilon^2 t) \quad \text{as } \epsilon \rightarrow 0$$

and introduce in L and compare with (11). We get the coefficients a_1, a_2, a_3 ,

$$\begin{aligned} a_1 &= \frac{\tilde{B}(i\omega_0, i\omega_0)}{\tilde{L}(2i\omega_0)} \\ a_2 &= \frac{\tilde{B}(i\omega_0, -i\omega_0)}{\tilde{L}(0)} \\ a_3 &= \frac{\tilde{B}(-i\omega_0, -i\omega_0)}{\tilde{L}(-2i\omega_0)} \end{aligned}$$

with $a_2 \in \mathbf{R}$ and $\bar{a}_1 = a_3$.

So far we have calculated u_0, u_1, α_1 . We can now conclude that in the equation (10), u_2 should satisfy

$$\begin{aligned} Lu_2 &= -z'(0) L(te^{i\omega_0 t}) - \bar{z}'(0) L(te^{-i\omega_0 t}) \\ &\quad + \alpha_2 z(0) \tilde{\Lambda}(i\omega_0) e^{i\omega_0 t} + \alpha_2 \bar{z}(0) \tilde{\Lambda}(-i\omega_0) e^{-i\omega_0 t} \\ &\quad + 2a_1 z^3(0) B(e^{i\omega_0 t}, e^{2i\omega_0 t}) + 4a_2 z^2(0) \bar{z}(0) B(e^{i\omega_0 t}, 1) \\ &\quad + 2a_3 \bar{z}^3(0) B(e^{-i\omega_0 t}, e^{-2i\omega_0 t}) + 4a_2 z(0) \bar{z}^2(0) B(e^{-i\omega_0 t}, 1) \\ &\quad + 2a_1 z^2(0) \bar{z}(0) B(e^{-i\omega_0 t}, e^{2i\omega_0 t}) + 2a_3 z(0) \bar{z}^2(0) B(e^{i\omega_0 t}, e^{-2i\omega_0 t}) \\ &\quad + z^3(0) C(e^{i\omega_0 t}, e^{i\omega_0 t}, e^{i\omega_0 t}) + 3z^2(0) \bar{z}(0) C(e^{i\omega_0 t}, e^{i\omega_0 t}, e^{-i\omega_0 t}) \\ &\quad + \bar{z}^3(0) C(e^{-i\omega_0 t}, e^{-i\omega_0 t}, e^{-i\omega_0 t}) + 3z(0) \bar{z}^2(0) C(e^{i\omega_0 t}, e^{-i\omega_0 t}, e^{-i\omega_0 t}) \end{aligned}$$

Similar to what we have already seen for u_1 , in order to have solutions, we need the right hand side to be orthogonal on $e^{\pm i\omega_0 t}, i, e$

$$\begin{aligned} z'(0) \int_0^{\frac{2\pi}{\omega_0}} e^{-i\omega_0 t} L(te^{i\omega_0 t}) dt + \bar{z}'(0) \int_0^{\frac{2\pi}{\omega_0}} e^{-i\omega_0 t} L(te^{-i\omega_0 t}) dt \\ = \alpha_2 z(0) \tilde{\Lambda}(i\omega_0) \frac{2\pi}{\omega_0} + 2a_1 z^2(0) \bar{z}(0) \tilde{B}(-i\omega_0, 2i\omega_0) \frac{2\pi}{\omega_0} \\ + 4a_2 z^2(0) \bar{z}(0) \tilde{B}(i\omega_0, 0) \frac{2\pi}{\omega_0} + 3z^2(0) \bar{z}(0) \tilde{C}(i\omega_0, i\omega_0, -i\omega_0) \frac{2\pi}{\omega_0} \end{aligned}$$

and, finally,

$$\begin{aligned} z'(0) &= \frac{i\omega_0 \alpha_2}{r_0 \left[2 + A r_0 + i(\omega_0 - \frac{A r_0 + b r_0}{\omega_0}) \right]} z(0) \\ &\quad + \frac{4a_2 \tilde{B}(i\omega_0, 0) + 2a_1 \tilde{B}(-i\omega_0, 2i\omega_0) + 3\tilde{C}(i\omega_0, i\omega_0, -i\omega_0)}{2 + A r_0 + i(\omega_0 - \frac{A r_0 + b r_0}{\omega_0})} z^2(0) \bar{z}(0) \end{aligned} \tag{12}$$

with specific values for \tilde{B} and \tilde{C} calculated in Appendix B.

We have just proven the following theorem.

Theorem 2. *Suppose that \bar{u} is an equilibrium point of the equation (1) and that A, b satisfy $-b < A < Mb$ where M is as in Theorem 1. Take \tilde{r}_0 and ω_0 as in Theorem 1 and denote by δ the coefficient of $z^2(0)\bar{z}(0)$ in (12).*

Then the normal form on the center manifold at $r = \tilde{r}_0$ is given by (12). If $Re(\delta) < 0$ ($Re(\delta) > 0$) then at $r = \tilde{r}_0$ the system passes through a supercritical (subcritical) Andronov-Hopf bifurcation which proves the existence of a small amplitude periodic stable (unstable) solution in the vicinity of the steady state near the bifurcation point.

Proof. The nondegeneracy condition requires the real part of the coefficient of $z(0)$ to be nonzero. The real part of the coefficient is

$$\frac{\omega_0^2 - (A + b)r_0}{r_0[(2 + Ar_0)^2 + (\omega_0 - (A + b)r_0/\omega_0)^2]}.$$

Substitution of $r_0 = \omega_0^2/[b(1 - \cos \omega_0)]$ into the numerator and using the fact that $A/b = -\sin(\omega_0)/\omega_0$ we find that the numerator is

$$\frac{\omega_0^2}{1 - \cos \omega_0} \left(\frac{\sin \omega_0}{\omega_0} - \cos \omega_0 \right).$$

The first term cannot vanish since $\omega_0 \in (0, 2\pi)$. Thus, the coefficient will be zero if and only if

$$\frac{\sin \omega_0}{\omega_0} = \cos \omega_0.$$

Recall that the extrema of $\sin(\omega)/\omega = -A/b$ can occur only when $\sin(\omega)/\omega = \cos \omega$ so that the numerator will vanish only along the lines $A = -b$ and $A = Mb$. Since $-b < A < bM$ this is impossible. \square

3.1. Example

We consider the function

$$f(x) = \frac{1}{1 + e^{-a(x+\theta)}} \quad \text{with } a = 8, \quad \theta = -0.333.$$

There is only one equilibrium point \bar{u} . We compute A, b and the values for the first three derivatives

$$\begin{aligned} \bar{u} &= 0.335909 \\ A &= -0.328002 \\ b &= 0.505818 \\ f'(\bar{u}) &= 1.99973 \\ f''(\bar{u}) &= -0.186145 \\ f'''(\bar{u}) &= -63.9653 \end{aligned}$$

and solve for ω and r . There is a unique solution

$$\begin{aligned}\omega_0 &= 1.541455 & \text{and} \\ r_0 &= 4.839469881\end{aligned}$$

By immediate calculation $\sin(\omega_0)/\omega_0 - \cos \omega_0 = 0.619121$, so the linear coefficient in the normal form is positive and the rest state loses stability when the value of r increases through $r = r_0$. At $r = r_0$ a stable periodic orbit is born. In this example the quantities which appear in the formula for the coefficient of $z^2\bar{z}$ in the normal form are

$$\begin{aligned}2 + Ar_0 + i(\omega_0 - \frac{r_0(A+b)}{\omega_0}) &= 0.4126442001 + 0.9831933729i \\ \tilde{L}(0) &= 0.8605351764 \\ \tilde{L}(2i\omega_0) &= -1.54079164 + 1.496237313i \\ \tilde{B}(i\omega_0, 0) &= -8.275709357 + 3.047038468i \\ \tilde{B}(-i\omega_0, 2i\omega_0) &= -3.52893752 + 0.0893831027i \\ \tilde{B}(i\omega_0, -i\omega_0) &= -6.574664704 \\ \tilde{B}(i\omega_0, i\omega_0) &= -6.574664704 + 6.094076935i \\ \tilde{C}(i\omega_0, i\omega_0, -i\omega_0) &= -33.97038306 - 0.0945445928i \\ a_1 &= 4.172849433 + 0.097025506i \\ a_2 &= -7.640204473 \\ \delta &= -36.6125 - 138.977i\end{aligned}$$

Obviously since $Re(\delta) < 0$ this is a supercritical Andronov-Hopf bifurcation.

We note that Figure 1 shows the numerical solutions for a variety of values of r . In particular, the fixed point is the only attractor for $r = 4.7$ but clearly, when $r = 4.9$ there is a stable periodic solution. The period computed analytically is $2\pi/\omega_0 = 4.08$ which agrees well with the numerically found period of 4.00. Thus, the numerical solutions and the Hopf calculations are consistent.

4. Relaxation oscillator

We now consider equation (1) for large values of the parameter r . By introducing $\epsilon = \frac{1}{r}$ and the function $z(t)$

$$z(t) := \int_{t-1}^t u(s) ds$$

equation (1) is equivalent to the two-dimensional delay-differential equation

$$\begin{cases} \epsilon du/dt &= -u + (1-z)f(u) \\ dz/dt &= u(t) - u(t-1) \end{cases} \quad (13)$$

We recall that (1) is obtained by rescaling time t with respect to the parameter r in the original equation, so t represents a *slow time*. We analyze the solution by

treating ϵ as a small positive parameter. We will first point out how to construct a singular periodic orbit for this system and then we will estimate the period T for the relaxation oscillator. Mallet-Paret and Nussbaum [8] have extensively and rigorously analyzed an equation similar to (13):

$$\epsilon \frac{dx(t)}{dt} = -x(t) + f(x(t - 1))$$

where f is an odd negative feedback function (that is, $xf(x) \leq 0$). In particular, they consider a step function for f . Hale and Huang [5] have studied the vector analogue:

$$\epsilon \frac{dx(t)}{dt} = -Ax(t) + Af(\lambda, x(t - 1))$$

where A is an invertible matrix and f is smoothly dependent on x and the free parameter λ . They assume that the map $x \rightarrow f(\lambda, x)$ undergoes a period-doubling bifurcation at $\lambda = 0$ and then prove that the delay-differential equation undergoes a similar bifurcation. More recent work by Hale and Huang [6] shows a similar behavior as well as a Hopf bifurcation. As far as we know, however, the rigorous analysis of equation (13) has not been done and remains an open problem. Our approach is formal and approximate.

By setting $\epsilon = 0$ in (13), we obtain the equations corresponding to the slow flow

$$\begin{cases} 0 &= -u + (1 - z) f(u) \\ dz/dt &= u(t) - u(t - 1) \end{cases} \tag{14}$$

For the fast flow we consider the original integro-differential equation. In this case the function z is $z(t) = \frac{1}{r} \int_{t-r}^t u(s) ds$ and it satisfies

$$dz/dt = (u(t) - u(t - r))/r.$$

When r tends to infinity (ϵ tends to zero), the system becomes

$$\begin{cases} du/dt &= -u + (1 - z) f(u) \\ dz/dt &= 0 \end{cases}$$

Thus, the two-dimensional system is decomposed in two one-dimensional equations, the solutions of which we now characterize.

Consider the graph for

$$0 = -u + (1 - z) f(u)$$

$$\text{with } f(x) = \frac{1}{1 + e^{-a(x+\theta)}}, a = 8, \theta = -0.333$$

The sign of $(-u + (1 - z) f(u))$ is negative above the graph and positive below it. Consider the points A, B, C, D on the graph with corresponding coordinates: $A(u_1, z_{\min}), B(u_{\max}, z_{\min}), C(u_2, z_{\max}), D(u_{\min}, z_{\max})$. (See Figure 3.) We

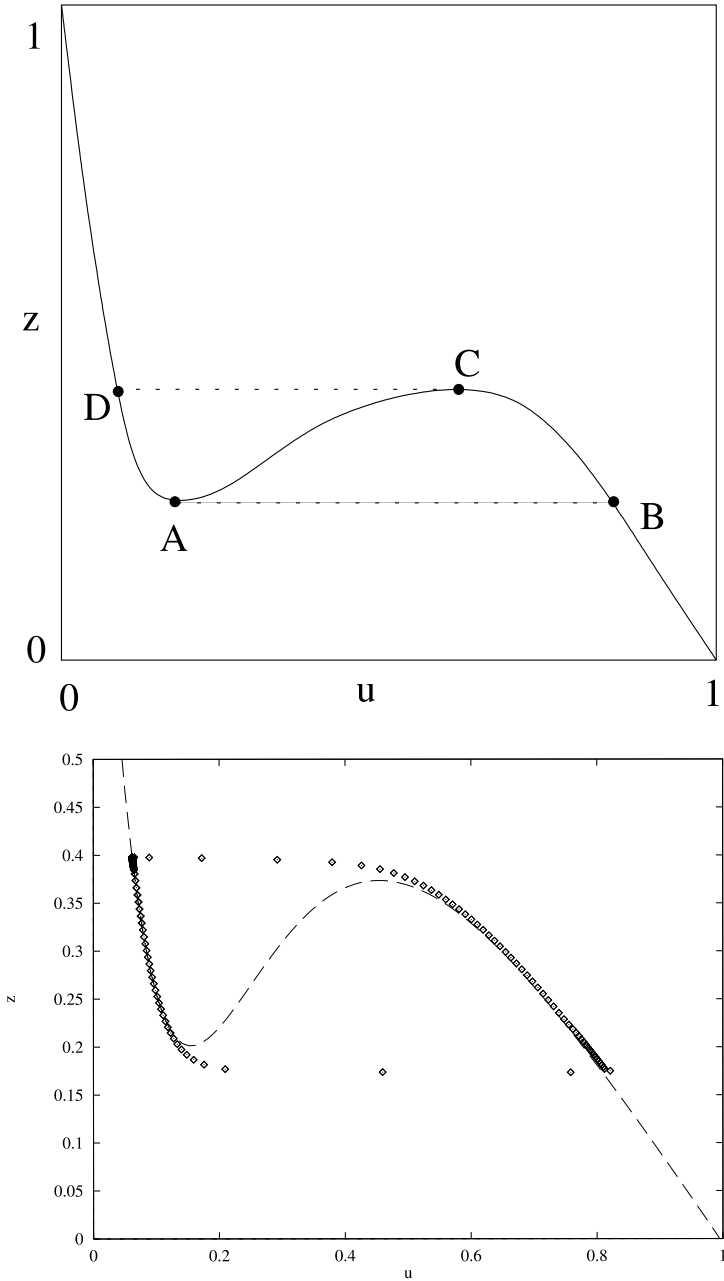


Fig. 3. Plot of $0 = -u + (1 - z)f(u)$ with points relevant to the relaxation oscillation labeled. Below is a numerically computed solution with $r = 300$ illustrating the relaxation character of the oscillation.

begin with the system at the point A at $t = 0$, where z cannot decrease anymore so a jump up takes place to the BC branch ($z = \text{constant}$ and u suddenly increases by the fast system). On this branch the system's law of motion is (14). Here $dz/dt > 0$ so z increases until the point reaches C . We remark that in order to have $dz/dt > 0$ on BC branch we need $u(t) > u(t - 1)$ all the time. This is obviously true at B since $u_B = u(t = 0+) = u_{\max} > u(t = -1)$. In order to have $u_C = u(t = T_d) > u(t = T_d - 1)$ we need $u(t = T_d - 1)$ to be on the DA branch. This implies that T_d must be less than 1.

At the point C since z cannot increase anymore there is a jump down to the branch DA ($z = \text{constant}$ and u decreases by the fast system). On the branch DA , z decreases from z_{\max} to z_{\min} . In order to have $dz/dt < 0$ we need $u(t) < u(t - 1)$, in particular $u_D = u(t = T_d+) = u_{\min} < u(t = T_d - 1)$ and $u_A = u(t = T) < u(t = T - 1)$, which means that it is necessary that $u(T - 1)$ be on the BC branch, *i.e.* $T - 1$ is positive and less than T_d .

Following these considerations we see that in order to construct a singular periodic solution it has to be true that

$$0 < T - 1 < T_d < 1 < T \quad (\Rightarrow T < 2)$$

where T is the period of oscillation and T_d is the time the system stays on the upper branch BC . We estimate T and T_d considering u constant: ($u = u_H$) on the branch BC and $u = u_L$ on the branch DA .

At $t = 0$, $z = z_{\min}$, $u = u_H$ and

$$dz/dt = u(t) - u(t - 1) = \begin{cases} 0 & , t \in [0, T_d + 1 - T] \\ u_H - u_L & , t \in [T_d + 1 - T, T_d] \\ 0 & , t \in [T_d, 1] \\ u_L - u_H & , t \in [1, T] \end{cases}$$

equivalently with

$$z(t) = \begin{cases} z_{\min} & , t \in [0, T_d + 1 - T] \\ (u_H - u_L)t + C_1 & , t \in [T_d + 1 - T, T_d] \\ C_2 & , t \in [T_d, 1] \\ (u_L - u_H)t & , t \in [1, T] \end{cases}$$

with $z(T) = z_{\min}$ and $z(T_d) = z_{\max}$. Using this and the identity $z(t = 0) = z_{\min} = \int_{-1}^0 u(s) ds$ we obtain an estimate for T and T_d

$$T = 1 + \frac{z_{\max} - z_{\min}}{u_H - u_L} \quad \text{and} \\ T_d = \frac{z_{\max} - u_L}{u_H - u_L}$$

For our example

$$\begin{aligned} u_{\min} &= 0.065 & u_1 &= 0.15957447 \\ u_{\max} &= 0.777 & u_2 &= 0.45106383 \\ z_{\min} &= 0.20141882 & z_{\max} &= 0.37353106 \end{aligned}$$

Choosing $u_H = u_{\min}$ and $u_L = u_{\min}$ we have

$$T = 1.2417 \quad T_d = 0.4333$$

The period for the oscillation shown in Figure 3 is 1.35. Given that u is not really constant on the branches, this is a pretty good estimate of the period. We can improve this estimate with just a minor change in the choice of u_L and u_H . Above, we chose u_{\max} and u_{\min} . A better estimate is to choose the mean value:

$$u_L = \frac{u_{\min} + u_1}{2}, \quad u_H = \frac{u_2 + u_{\max}}{2}.$$

For our example, this implies $u_L = 0.1122872$, $u_H = 0.6140319$ and

$$T = 1.3430, \quad T_d = 0.5206.$$

This is a considerably better estimate of the period without any extra work.

5. Discussion and further developments

We have analyzed the original Wilson-Cowan model for an excitatory population of neurons with an absolute refractory period. It is not surprising that there exist oscillations as the system is essentially a delayed negative feedback model. Curiously, however, as the effective delay increases, the oscillation converges to a relaxation-like pattern and the frequency goes to a nice limit. In terms of the original time, the actual oscillation period scales linearly with R the absolute refractory period.

We have looked only at oscillatory solutions of the scalar problem. What happens when two populations are coupled? Will the resulting oscillations synchronize? For example, what is the nature of solutions to

$$\frac{du_j}{dt} = r \left(1 - \int_{t-1}^t u(s) ds \right) f(u_j + gu_{3-j}) \quad j = 1, 2,$$

where g is the coupling coefficient? Numerical solutions of this indicate that all initial conditions tend to the synchronous state. We can use the results of section 3 to understand why this is true, at least near the Hopf bifurcation. Letting g be a small parameter, the normal form for the weakly coupled system is

$$z'_j = z_j N(|z_j|) + dz_{3-j} \quad j = 1, 2.$$

$N(v) = c(r - r_0) + \delta v^2$ where δ was calculated in section 4. The coefficient $d = (1 - \bar{u})f'(\bar{u})$ is real and positive. Thus, the synchronous solution is always a stable solution. (These results follow from Hoppensteadt and Izhikevich, [7]).

If we let a be larger in the definition of the function f , then the system is not oscillatory but rather excitable. That is, a small initial condition decays back to 0 but a large value grows rapidly before decaying to rest. This suggests that a line of such units coupled locally can generate a traveling wave. Consider

$$u'_j = -u_j + \left(1 - \int_{t-1}^t u_j(s) ds \right) f\left(\frac{1}{3} \sum_k u_k\right)$$

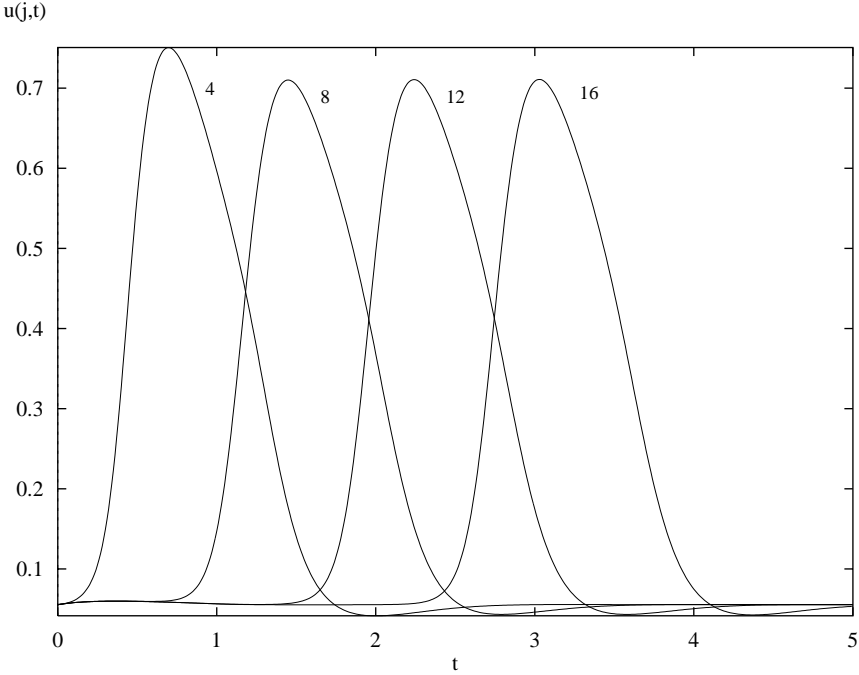


Fig. 4. The time evolution of cells 4,8,12,16, in a line of 20 cells for $f(u) = 1/(1 + \exp(-10(u - .333)))$ and $r = 10$.

where the sum is over the two neighbors. Figure 4 shows a simulation of this for 20 cells in which cell 1 is initially set to 1 and all the remaining cells are set to their resting state. The simulation suggests that the solution develops into a traveling wave. By letting $a \rightarrow \infty$, so that f approaches a step function, it may be possible to analytically construct the traveling wave for this model. This remains an open problem.

Appendix A

We construct the adjoint operator of L

$$Ly = \frac{dy}{dt} + Ar_0 y + br_0 \int_{t-1}^t y(s) ds$$

in the space of solutions spanned by $\{e^{i\omega_0 t}, e^{-i\omega_0 t}, e^{2i\omega_0 t}, e^{-2i\omega_0 t}, \dots\}$, which means we work with functions $x = x(t)$ which satisfy $x(0) = x(\frac{2\pi}{\omega_0})$ and have zero mean. We notice that the primitive $X(t) := \int_0^t x(s) ds$ is also periodic with period $\frac{2\pi}{\omega_0}$ and furthermore, it is true that $X(0) = X(\frac{2\pi}{\omega_0}) = 0$. We define the inner product as

$$\langle \phi, \psi \rangle = \int_0^{\frac{2\pi}{\omega_0}} \phi(t)\bar{\psi}(t) dt$$

Now for any two functions x, y in this space $\langle x, Ly \rangle = \langle L^*x, y \rangle$, where L^* is the adjoint of the operator L .

Compute $\langle x, Ly \rangle$:

$$\begin{aligned}
 \langle x, Ly \rangle &= \int_0^{\frac{2\pi}{\omega_0}} x(t) \left[\overline{\frac{dy}{dt} + A r_0 y + b r_0 \int_{t-1}^t y(s) ds} \right] \\
 &= x(t) \bar{y}(t) \Big|_0^{\frac{2\pi}{\omega_0}} - \int_0^{\frac{2\pi}{\omega_0}} \frac{dx}{dt} \bar{y}(t) dt + A r_0 \int_0^{\frac{2\pi}{\omega_0}} x(t) \bar{y}(t) dt \\
 &\quad + b r_0 \int_0^{\frac{2\pi}{\omega_0}} \left[\overline{x(t) \int_{t-1}^t y(s) ds} \right] \\
 &= - \int_0^{\frac{2\pi}{\omega_0}} \frac{dx}{dt} \bar{y}(t) dt + A r_0 \int_0^{\frac{2\pi}{\omega_0}} x(t) \bar{y}(t) dt \\
 &\quad + b r_0 \int_0^{\frac{2\pi}{\omega_0}} \left[\overline{x(t) \int_0^t y(s) ds} - \overline{x(t) \int_0^{t-1} y(s) ds} \right] \\
 &= \int_0^{\frac{2\pi}{\omega_0}} \left[A r_0 x(t) - \frac{dx}{dt} \right] \bar{y}(t) dt \\
 &\quad + b r_0 \left[\int_0^{\frac{2\pi}{\omega_0}} x(t) \bar{Y}(t) dt - \int_0^{\frac{2\pi}{\omega_0}} x(t) \bar{Y}(t-1) dt \right]
 \end{aligned}$$

Since $x = \frac{dX}{dt}$ and $y = \frac{dY}{dt}$ we use integration by parts and the properties of the functions X and Y to get

$$\begin{aligned}
 \langle x, Ly \rangle &= \int_0^{\frac{2\pi}{\omega_0}} \left[A r_0 x(t) - \frac{dx}{dt} \right] \bar{y}(t) dt - b r_0 \int_0^{\frac{2\pi}{\omega_0}} \left(\int_0^t x(s) ds \right) \bar{y}(t) dt \\
 &\quad + b r_0 \int_{-1}^{\frac{2\pi}{\omega_0}-1} X(t+1) \bar{y}(t) dt \\
 &= \int_0^{\frac{2\pi}{\omega_0}} \left[A r_0 x(t) - \frac{dx}{dt} - b r_0 \int_0^t x(s) ds + b r_0 \int_0^{t+1} x(s) ds \right] \bar{y}(t) dt \\
 &\quad + b r_0 \int_{-1}^0 X(t+1) \bar{y}(t) dt - b r_0 \int_{\frac{2\pi}{\omega_0}-1}^{\frac{2\pi}{\omega_0}} X(t+1) \bar{y}(t) dt
 \end{aligned}$$

After a change of dummy variables in the last integral we get

$$\langle x, Ly \rangle = \int_0^{\frac{2\pi}{\omega_0}} \left[A r_0 x(t) - \frac{dx}{dt} + b r_0 \int_t^{t+1} x(s) ds \right] \bar{y}(t) dt$$

The adjoint operator is

$$L^*x = -\frac{dx}{dt} + A r_0 x + b r_0 \int_t^{t+1} x(s) ds$$

By direct calculation we see that $L^*(e^{\pm i\omega_0 t}) = 0$. We use for this both $\lambda_0 = \pm i\omega_0$ and the characteristic equation (4).

Appendix B

Directly from the definition of the operators L , Λ , B , C we can prove that $L(e^{\lambda t}) = \tilde{L}(\lambda)e^{\lambda t}$ where the function \tilde{L} is defined as follows:

$$\tilde{L}(\lambda) = \begin{cases} \lambda + A r_0 + \frac{(1-e^{-\lambda})b r_0}{\lambda} & , \lambda \neq 0 \\ (A+b)r_0 & , \lambda = 0 \end{cases}$$

Similarly,

$$\Lambda(e^{\lambda t}) = \tilde{\Lambda}(\lambda)e^{\lambda t} \quad \text{with} \quad \tilde{\Lambda}(\lambda) = \begin{cases} -A - \frac{1-e^{-\lambda}}{\lambda} b & , \lambda \neq 0 \\ -(A+b) & , \lambda = 0 \end{cases}$$

and

$$B(e^{\lambda_1 t}, e^{\lambda_2 t}) = \tilde{B}(\lambda_1, \lambda_2)e^{\lambda_1 t} e^{\lambda_2 t} \quad \text{with}$$

$$\tilde{B}(\lambda_1, \lambda_2) = \begin{cases} r_0 \frac{1-\bar{u}}{2} f''(\bar{u}) - \frac{1}{2} \left[\frac{1-e^{-\lambda_1}}{\lambda_1} + \frac{1-e^{-\lambda_2}}{\lambda_2} \right] f'(\bar{u}) r_0 & , \lambda_1 \neq 0, \lambda_2 \neq 0 \\ r_0 \frac{1-\bar{u}}{2} f''(\bar{u}) - \frac{1}{2} \left[1 + \frac{1-e^{-\lambda_1}}{\lambda_1} \right] f'(\bar{u}) r_0 & , \lambda_1 \neq 0, \lambda_2 = 0 \\ r_0 \frac{1-\bar{u}}{2} f''(\bar{u}) - \frac{1}{2} \left[1 + \frac{1-e^{-\lambda_2}}{\lambda_2} \right] f'(\bar{u}) r_0 & , \lambda_1 = 0, \lambda_2 \neq 0 \\ r_0 \frac{1-\bar{u}}{2} f''(\bar{u}) - f'(\bar{u}) r_0 & , \lambda_1 = 0, \lambda_2 = 0 \end{cases}$$

and

$$C(e^{\lambda_1 t}, e^{\lambda_2 t}, e^{\lambda_3 t}) = \tilde{C}(\lambda_1, \lambda_2, \lambda_3)e^{\lambda_1 t} e^{\lambda_2 t} e^{\lambda_3 t}$$

In our problem we are interested only in the case when all $\lambda_1, \lambda_2, \lambda_3$ are nonzero. Then $\tilde{C}(\lambda_1, \lambda_2, \lambda_3)$ is

$$\begin{aligned} \tilde{C}(\lambda_1, \lambda_2, \lambda_3) &= r_0 \frac{1-\bar{u}}{6} f'''(\bar{u}) \\ &\quad - \frac{1}{6} \left[\frac{1-e^{-\lambda_1}}{\lambda_1} + \frac{1-e^{-\lambda_2}}{\lambda_2} + \frac{1-e^{-\lambda_3}}{\lambda_3} \right] f''(\bar{u}) r_0 \end{aligned}$$

We make the remark that $\tilde{L}(\bar{\lambda}) = \overline{\tilde{L}(\lambda)}$, $\tilde{\Lambda}(\bar{\lambda}) = \overline{\tilde{\Lambda}(\lambda)}$, $\tilde{B}(\lambda_1, \lambda_2) = \tilde{B}(\lambda_2, \lambda_1)$, $\tilde{B}(\bar{\lambda}_1, \bar{\lambda}_2) = \overline{\tilde{B}(\lambda_1, \lambda_2)}$ and $\tilde{C}(\bar{\lambda}_1, \bar{\lambda}_2, \bar{\lambda}_3) = \overline{\tilde{C}(\lambda_1, \lambda_2, \lambda_3)}$

In order to find the coefficient of $z^2(0)\bar{z}(0)$ in the normal form (12) we compute

$$L(te^{i\omega_0 t}) = e^{i\omega_0 t} \left[2 + A r_0 + i \left(\omega_0 - \frac{A r_0 + b r_0}{\omega_0} \right) \right]$$

and

$$L(te^{-i\omega_0 t}) = e^{-i\omega_0 t} \left[2 + A r_0 + i \left(-\omega_0 + \frac{A r_0 + b r_0}{\omega_0} \right) \right]$$

Finally we have

$$\begin{aligned}\tilde{\Lambda}(i\omega_0) &= \frac{i\omega_0}{r_0} \\ \tilde{L}(0) &= (A + b)r_0 \\ \tilde{L}(2i\omega_0) &= \frac{A\omega_0^2}{b} + i \left[\omega_0 - \frac{\omega_0 r_0 A^2}{2b} + \frac{\omega_0^3}{2br_0} \right] \\ \tilde{B}(i\omega_0, -i\omega_0) &= r_0 \frac{1 - \bar{u}}{2} f''(\bar{u}) + \frac{A}{b} f'(\bar{u}) r_0 \\ \tilde{B}(i\omega_0, i\omega_0) &= \left[r_0 \frac{1 - \bar{u}}{2} f''(\bar{u}) + \frac{A}{b} f'(\bar{u}) r_0 \right] + i \frac{\omega_0}{b} f'(\bar{u}) \\ \tilde{B}(-i\omega_0, 2i\omega_0) &= \left[r_0 \frac{1 - \bar{u}}{2} f''(\bar{u}) + \left(\frac{Ar_0}{b} - \frac{A\omega_0^2}{2b^2} \right) f'(\bar{u}) \right] \\ &\quad + i \frac{r_0 \omega_0}{4b^2} \left[A^2 - \frac{\omega_0^2}{r_0^2} \right] f'(\bar{u}) \\ \tilde{B}(i\omega_0, 0) &= \left[r_0 \frac{1 - \bar{u}}{2} f''(\bar{u}) + \frac{A}{2b} f'(\bar{u}) r_0 - \frac{1}{2} f'(\bar{u}) r_0 \right] + i \frac{\omega_0}{2b} f'(\bar{u}) \\ \tilde{C}(i\omega_0, i\omega_0, -i\omega_0) &= \left[r_0 \frac{1 - \bar{u}}{6} f'''(\bar{u}) + \frac{A}{2b} f''(\bar{u}) r_0 \right] + i \frac{\omega_0}{6b} f''(\bar{u})\end{aligned}$$

References

- [1] Campbell, S.A., Belair, J., Ohira, T., Milton, J.: Complex dynamics and multistability in a damped harmonic oscillator with delayed negative feedback, *Chaos*, **5**, 640–645 (1995)
- [2] Castelfranco, A.M., Stech, H.W.: Periodic solutions in a model of recurrent neural feedback, *SIAM J. Appl. Math.*, **47**, 573–588, (1987)
- [3] Diekmann, O., van Gils, S.A., Verduyn Lunel, S.M., Walther, H.O.: *Delay Equations: Functional-, Complex-, and Nonlinear Analysis*, Springer-Verlag, New York, Applied Mathematical Sciences., Vol. 110 (1995)
- [4] Faria, T., Magalhães, L.: Normal forms for retarded functional-differential equations with parameters and applications to Hopf bifurcation, *J. Differential Equations*, **122**, 182–200 (1995)
- [5] Hale, J., Huang, W.: Square and pulse waves in matrix delay differential equations, *Dynamic Systems Appl.*, **1**, 51–70 (1992)
- [6] Hale, J., Huang, W.: Periodic solutions to singularly perturbed delay equations, *Z. Angew. Math. Phys.*, **47**, 57–88 (1996)
- [7] Hoppensteadt, F., Izhikevich, E.: *Weakly Connected Neural Nets*, Springer-Verlag Berlin (1998)
- [8] Mallet-Paret, J., Nussbaum, R.D.: Multiple transition layers in a singularly perturbed differential delay equation, *Proc. Roy. Soc. Edinburgh, Sect. A.*, **123**, 1119–1134 (1993)
- [9] Marcus, C.M., Westervelt, R.M.: Stability of analog neural networks with delay, *Phys. Rev. A.*, **39**, 347–359 (1989)

-
- [10] Wilson H.R., Cowan, J.D.: Excitatory and inhibitory interactions in localized populations of model neurons, *Biophys. J.*, **12**, 1–24 (1972)
 - [11] Ye, H., Michel, A.N., Wang, K.: Global stability and local stability of Hopfield neural networks with delays, *Phys. Rev. E*, **50**, 4206–4213 (1994)