# Delays in activity based neural networks

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In this paper we study the effect of two distinct discrete delays on the dynamics of a Wilson-Cowan neural network. This activity based model describes the dynamics of synaptically interacting excitatory and inhibitory neuronal populations. We discuss the interpretation of the delays in the language of neurobiology and show how they can contribute to the generation of network rhythms. First we focus on the use of linear stability theory to show how to destabilise a fixed point, leading to the onset of oscillatory behaviour. Next we show for the choice of a Heaviside nonlinearity for the firing rate that such emergent oscillations can be either synchronous or anti-synchronous depending on whether inhibition or excitation dominates the network architecture. To probe the behaviour of smooth (sigmoidal) nonlinear firing rates we use a mixture of numerical bifurcation analysis and direct simulations, and uncover parameter windows that support chaotic behaviour. Finally we comment on the role of delays in the generation of *bursting* oscillations, and discuss natural extensions of the work in this paper.

**Keywords: Wilson-Cowan networks, multiple-delays, phase-locking, chaos**

## 1. Introduction

Delays arise naturally in models of neurobiological systems. For example the finite speed of an action potential (AP) propagating along an axon means that spike-signalling between neurons depends upon how far apart they are. Hence, the interest in understanding network models with *space-dependent* delays, as in (Laing & Coombes 2006). Upon arrival at a synaptic contact point the transduction of an electrical signal into a biochemical signal and back again, to a post-synaptic potential (PSP), gives rise to a further delay. Yet another delay is associated with the spread of the PSP through the dendritic tree of the neuron to the cell body, where further APs can be initiated. It is now quite common to model both these forms of signal processing using either a form of *distributed* delay, as in (Laing & Longtin 2003), or as a simple fixed or *discrete* delay. For an excellent review of the role of time delays in neural systems we refer the reader to the article by Campbell (2007). The effects of such delays can be quite varied. Although commonly associated with the generation of oscillations (Plant 1981), delays can also lead to oscillator death (Reddy *et al.* 1998), control phase-locking (Coombes & Lord 1997), and underlie multi-stability (Shayer & Campbell 2000).

In this paper we focus on the dynamics of two-population neural models with the incorporation of two discrete delays. In particular we will work with the well known Wilson & Cowan model (1972). Such activity based models are expected to provide a caricature of the behaviour of more realistic spiking networks when the time-scale of synaptic processing is much longer than the membrane time constant of a typical cell (Ermentrout 1986). This is perhaps most clearly demonstrated by recent work of Roxin *et al.* (2005), which further emphasises that a single delay in the activity based representation can further improve the match with spiking networks. The delay in the activity based model is interpreted by them as describing the time course of AP initiation. However, an alternative interpretation of this delay is that it is necessary to adequately model the time-lag involved in generating a rate based representation of a spiking network. In particular single neuron firing rates (for slow synapses) will be largely determined by the steady state values of non-spiking currents, and thus the delay may be more naturally interpreted as the time for these currents to relax. In any case, this paper will show how to analyse a delayed neural network with a hybrid approach, combining linear stability theory, the construction of periodic orbits (for piece-wise constant nonlinear firing rate functions) and numerical techniques.

## 2. The model

As discussed above, under certain approximations spiking network models can be reduced to just a few variables. One famous example is the Wilson & Cowan (1972) model, which describes the evolution of a network of synaptically interacting neuronal populations (typically one being excitatory and the other inhibitory). In the presence of delays this model takes the form

$$\begin{aligned} \dot{u} &= -u + f(\theta_u + au(t-\tau_1) + bv(t-\tau_2)), \\ \frac{1}{\alpha}\dot{v} &= -v + f(\theta_v + cu(t-\tau_2) + dv(t-\tau_1)). \end{aligned} \tag{2.1}$$

Here, $u$ and $v$ represent the synaptic activity of the two populations, with a relative time-scale for response set by $\alpha^{-1}$. The architecture of the network is fixed by the *weights* $a, b, c, d$, whilst $\theta_{u,v}$ describe background drives (biases). The *firing rate* function $f$ is commonly chosen as a sigmoid:

$$f(z) = \frac{1}{1+\mathrm{e}^{-\beta z}}, \tag{2.2}$$

which satisfies the (Ricatti) equation $f' = \beta f(1-f)$, with $\beta > 0$. The fixed delays $\tau_1$ and $\tau_2$ distinguish between delayed self-interactions and delayed cross-interactions. The delay differential equation (DDE) model (2.1) is similar, though not equivalent, to *voltage* based models, which have linear combinations of sigmoidal functions of the different variables on the right hand side (Marcus & Westervelt 1989; Olien & Bélair 1997; Shayer & Campbell 2000; Wei & Ruan, 1997). Restrictions of the parameter choices recover a number of models already considered in the literature, such as that of i) Glass *et al.* (1988), when $a < 0$, $b = 0$, ii) Chen & Wu (1999), when $\alpha = 1$, $a = d = 0$ and $b = c > 0$, iii) Battaglia *et al.* (2007), when $\alpha = 1$, $a = d < 0$, $b = c > 0$ and $f(z)$ is a threshold-linear firing rate.

Before analysing the full DDE system it is first useful to describe the dynamics in the absence of delays, where we recover the basic Wilson & Cowan model. For $\tau_1 = \tau_2 = 0$ it is straight-forward to find values of $\theta_u$ and $\theta_v$ corresponding to

Hopf and saddle-node bifurcations. The point $(u^*, v^*)$ is an equilibrium if there is a solution to the pair of equations

$$\theta_u = f^{-1}(u^*) - au^* - bv^*, \qquad \theta_v = f^{-1}(v^*) - cu^* - dv^*, \tag{2.3}$$

where $f^{-1}(z) = \beta^{-1}\ln(z/(1-z))$. The Jacobian matrix is therefore

$$L = \begin{bmatrix} -1 + a\beta u^*(1-u^*) & b\beta u^*(1-u^*) \\ \alpha c\beta v^*(1-v^*) & \alpha[-1 + d\beta v^*(1-v^*)] \end{bmatrix}. \tag{2.4}$$

Thus the conditions for a Hopf bifurcation (HB) are

$$\mathrm{Tr}L = -(1+\alpha) + a\beta u^*(1-u^*) + \alpha d\beta v^*(1-v^*) = 0 \quad \text{and} \ \det L > 0. \tag{2.5}$$

Eliminating $v^*$ as

$$v^*_\pm(u) = \frac{1 \pm \sqrt{1 - 4[(1+\alpha)/\beta - au^*(1-u^*)]/(\alpha d)}}{2}, \tag{2.6}$$

we can then plot the fixed point equation (parametrically) in the $(\theta_u, \theta_v)$ plane, as in Fig. 1. A similar procedure can be used to determine the locus of saddle-node (SN) bifurcations defined by $\det L = 0$, as well as the Bogdanov-Takens bifurcation defined by $\det L = 0$ and $\mathrm{Tr}L = 0$ (when the SN and HB curves intersect). Indeed the Wilson & Cowan model also supports a saddle-node on an invariant circle bifurcation (when the SN curve lies between the two HB curves), and can also support a saddle-separatrix loop and a double limit cycle. See (Hoppensteadt & Izhikevich 1997, Ch 2) for a detailed discussion.

## 3. Linear stability analysis of fixed point

The existence of an equilibrium is, of course, independent of any delays. Many authors have described in detail how the presence of delays affects the stability of an equilibrium, and here we follow the spirit of work by (Marcus & Westervelt 1989; Wei & Ruan 1999; Giannakopoulos & Zapp 2001). In the presence of delays the linearised equations of motion have solutions of the form $(u, v) = (\overline{u}, \overline{v})\mathrm{e}^{\lambda t}$. Demanding that the amplitudes $(\overline{u}, \overline{v})$ be non-trivial gives a condition on $\lambda$ that may be written in the form $\mathcal{E}(\lambda) = 0$, where

$$\mathcal{E}(\lambda) = \det \begin{bmatrix} \lambda + 1 - a\beta u^*(1-u^*)\mathrm{e}^{-\lambda\tau_1} & -b\beta u^*(1-u^*)\mathrm{e}^{-\lambda\tau_2} \\ -c\beta v^*(1-v^*)\mathrm{e}^{-\lambda\tau_2} & \lambda/\alpha + 1 - d\beta v^*(1-v^*)\mathrm{e}^{-\lambda\tau_1} \end{bmatrix}, \tag{3.1}$$

and the equilibrium $(u^*, v^*)$ is given by the simultaneous solution of (2.3). For $\lambda \in \mathbb{R}$ we see that $\lambda = 0$ when

$$(1-\kappa_1)(1-\kappa_2) - \kappa_3 = 0, \tag{3.2}$$

where $\kappa_1 = a\beta u^*(1-u^*)$, $\kappa_2 = d\beta v^*(1-v^*)$ and $\kappa_3 = bc\beta^2 u^* v^*(1-u^*)(1-v^*)$. Thus a *real* instability of a fixed point is defined by (3.2) and is independent of $(\tau_1, \tau_2)$. Referring back to the analysis of §2, we see that this is identical to the condition for a saddle-node bifurcation. In contrast a *dynamic* instability will occur whenever

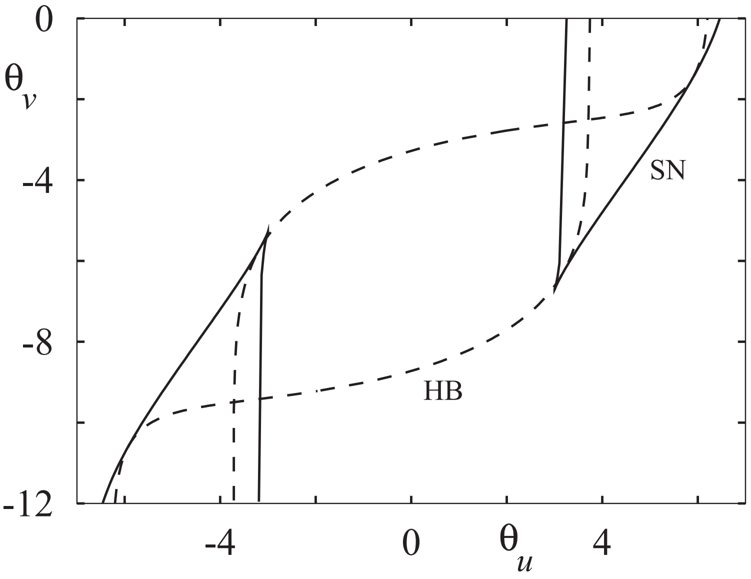

Figure 1. Hopf (HB – dashed line) and saddle-node (SN – solid line) bifurcation set in the Wilson-Cowan network (no delays) with a mixture of excitatory and inhibitory connections for $\alpha = 1$, $a = -b = c = 10$, $d = 2$ and $\beta = 1$.

$\lambda = i\omega$ for $\omega \neq 0$, where $\omega \in \mathbb{R}$. The bifurcation condition in this case is defined by the simultaneous solution of the equations Re $\mathcal{E}(i\omega) = 0$ and Im $\mathcal{E}(i\omega) = 0$, namely

$$\begin{aligned} 0 &= (1 - \kappa_1 \cos(\omega\tau_1))(1 - \kappa_2 \cos(\omega\tau_1)) - (\omega + \kappa_1 \sin(\omega\tau_1))(\omega/\alpha + \kappa_2 \sin(\omega\tau_1)) \\ &\quad - \kappa_3 \cos(2\omega\tau_2), \qquad (3.3) \\ 0 &= (1 - \kappa_1 \cos(\omega\tau_1))(\omega/\alpha + \kappa_2 \sin(\omega\tau_1)) + (\omega + \kappa_1 \sin(\omega\tau_1))(1 - \kappa_2 \cos(\omega\tau_1)) \\ &\quad + \kappa_3 \sin(2\omega\tau_2). \qquad (3.4) \end{aligned}$$

For parameters that ensure $\omega \neq 0$ we shall say that the simultaneous solution of equations (3.3) and (3.4) defines a Hopf bifurcation at $(\tau_1, \tau_2) = (\tau_1^c, \tau_2^c)$. More correctly we should also ensure that as the delays pass through this critical point that the rate of change of Re $\lambda$ is non-zero (transversality) and that there are no other eigenvalues with zero real part (non-degeneracy).

Interestingly models with two delays can lead to an interference effect whereby although either delay, if long enough, can bring about instability, there is a window of $(\tau_1, \tau_2)$ where solutions are stable to Hopf bifurcations. This is nicely discussed in Chapter six of the book by MacDonald (1989); see also Chapter 3 of the book by Stépán (1989). An example of this effect, obtained by computing the locus of Hopf bifurcations according to the above prescription, is shown in Fig. 2. A similar figure, showing a band of stability that lies between two broad regions of instability, is found in the work of Murdoch *et al.* (1987).

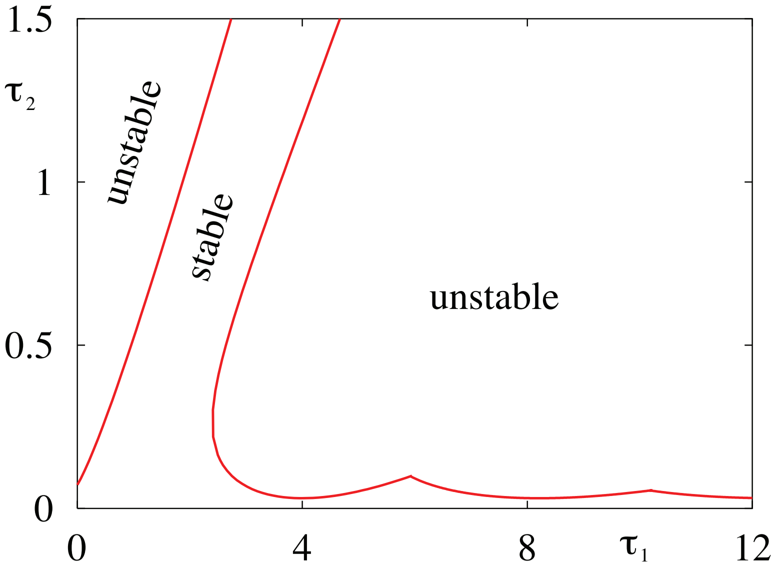

Figure 2. A bifurcation diagram showing the stability of the equilibrium in the Wilson & Cowan model with two delays. Parameters as in Fig. 1 with $(\theta_u, \theta_v) = (-2, -4)$.

## 4. Synchronous and anti-synchronous solutions

In general, despite linear stability analysis showing where to look, it is a challenge to find periodic solutions in closed form. Moreover, determining their stability is a problem that, in general, is best examined with numerical tools. However, some results are known about the phase relationship between the two populations during an oscillation. In particular Chen *et al.* (2000) have shown that for $\alpha = 1$, $\theta_u = \theta_v$, $a = d = 0$ and $b = c$ that every non-constant solution of (2.1) is either synchronous or phase-locked. Here we explore the explicit construction of such solutions in the limit of high gain ($\beta \to \infty$), so that $f(z) = H(z)$, with $H$ the Heaviside step function. Such equations are commonly encountered in physiological control systems (Glass *et al.* 1998; Longtin & Milton 1998). For example in Fig. 3 we show a coexisting synchronous and anti-synchronous stable periodic orbit in a network with purely inhibitory connections. Previous work on the analysis of periodic orbits in delayed neural networks with Heaviside nonlinearity can be found in (Guo *et al.* 2005).

### (*a*) *Inhibitory network*

We first consider a purely inhibitory network with $a, b, c, d < 0$, with some bias $\theta_u = \theta_v$ and $\alpha = 1$. Regarding a synchronous $T$-periodic solution, $u(t) = v(t)$ with $u(t + T) = u(t)$, like that shown in the top panel of Fig. 3, we parametrise such a solution in terms of two fundamental times $T_{1,2}$ and the maxima and minima $A_\pm$ of the orbit. Here $T_1$ denotes the time spent on the decreasing part of the trajectory, and $T_2$ that spent on the rising phase. Exploiting the piece-wise linear nature of

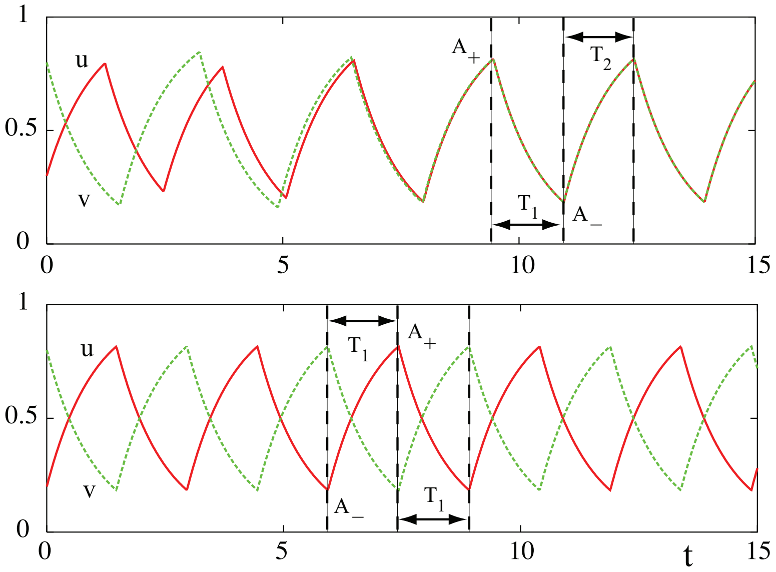

Figure 3. Co-existing synchronous (top) and anti-synchronous (bottom) solutions for $f(z) = H(z)$. Parameters are $\alpha = 1$, $a = d = -1$, $b = c = -0.4$, $\theta_u = \theta_v = 0.7$, $\tau_1 = 1$ and $\tau_2 = 1.4$.

the dynamics we then have that

$$A_- = A_+ \mathrm{e}^{-T_1}, \tag{4.1}$$

$$A_+ = 1 + (A_- - 1)\mathrm{e}^{-T_2}, \tag{4.2}$$

$$\theta_u = -aA_+ \mathrm{e}^{-(T_1-\tau_1)} - bA_+ \mathrm{e}^{-(T_1-\tau_2)}, \tag{4.3}$$

$$\theta_u = -a\left[1 + (A_- - 1)\mathrm{e}^{-(T_2-\tau_1)}\right] - b\left[1 + (A_- - 1)\mathrm{e}^{-(T_2-\tau_2)}\right]. \tag{4.4}$$

Solving these we obtain the period of oscillation $T = T_1 + T_2$, where

$$T_1 = \ln\left(\frac{s + \theta_u + a + b}{\theta_u}\right), \qquad T_2 = \ln\left(\frac{\theta_u - s}{\theta_u + a + b}\right), \tag{4.5}$$

and $s = -(ae^{\tau_1} + be^{\tau_2})$. The amplitude of the oscillation is $A = A_+ - A_- = (a + b + s)/s$.

Similarly, to analyse an anti-synchronous solution, $u(t) = v(t+T/2)$ with $u(t) = u(t + T)$, as in the bottom panel of Fig. 3, we note that by symmetry, the rising and falling phases have the same duration, say $T_1$. For the parameters considered we find that $\tau_1 < T_1 < \tau_2$, and we obtain the relations

$$A_- = A_+ \mathrm{e}^{-T_1} \tag{4.6}$$

$$A_+ = 1 + (A_- - 1)\mathrm{e}^{-T_1} \tag{4.7}$$

$$\theta_u = -a\left[1 + (A_- - 1)\mathrm{e}^{-(T_1-\tau_1)}\right] - b\left[1 + (A_- - 1)\mathrm{e}^{-(2T_1-\tau_2)}\right]. \tag{4.8}$$

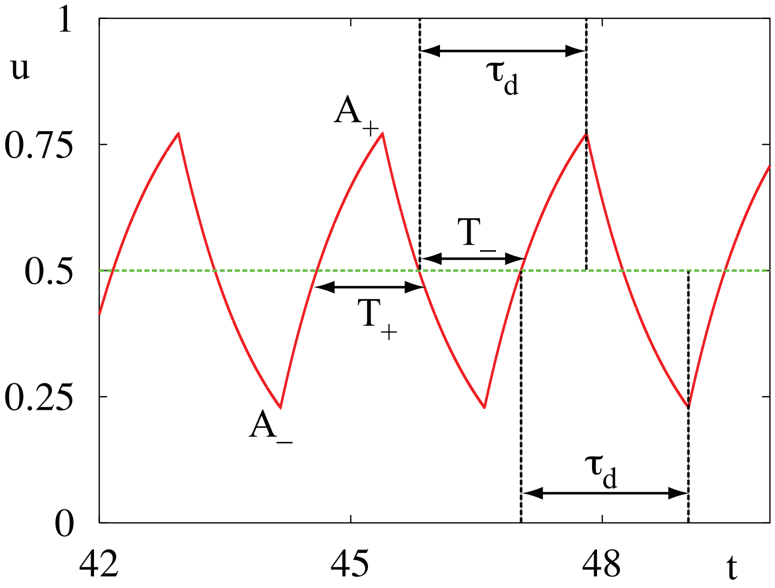

Figure 4. A periodic solution in a single population model with excitatory self-feedback. In this example $a = 1$, $b = 0$, $-\theta_u = h = 0.5$ and $\tau_1 = \tau_d = 2$.

Solving the above we find that $T_1$ satisfies the transcendental equation

$$\theta_u = -a\left[1 + \frac{e^{\tau_1}(e^{-T_1} - 1)}{e^{T_1} - e^{-T_1}}\right] - b\left[1 + \frac{e^{\tau_2}e^{-2T_1}(1 - e^{T_1})}{e^{T_1} - e^{-T_1}}\right]. \tag{4.9}$$

The period $T$ is $2T_1$ and the absolute amplitude of oscillation, $A = A_+ - A_-$, is given by

$$A = \frac{\left(1 - e^{-T_1}\right)^2}{1 - e^{-2T_1}}. \tag{4.10}$$

### (*b*) *Excitatory self-feedback*

For a single population with self-feedback it is also possible to construct periodic solutions (for a Heaviside firing rate). Here we consider just the evolution of $u$ with $a = 1$, $b = 0$, $\theta_u = -h$, $h > 0$ and $\tau_1 = \tau_d$, a fixed delay. An example of a periodic trajectory is shown in Fig. 4. It is natural to parametrise the solution in terms of the four unknowns $A_\pm$ and $T_\pm$, which denote the largest ($A_+$) and smallest ($A_-$) values of the trajectory and the times spent above ($T_+$) and below ($T_-$) the threshold $h$. The trajectory increases from $A_-$ for a duration $T_+$ and decreases from $A_+$ for a duration $T_-$. The values for these four unknowns are found by enforcing periodicity of the solution and requiring it to cross threshold twice, giving us four simultaneous equations:

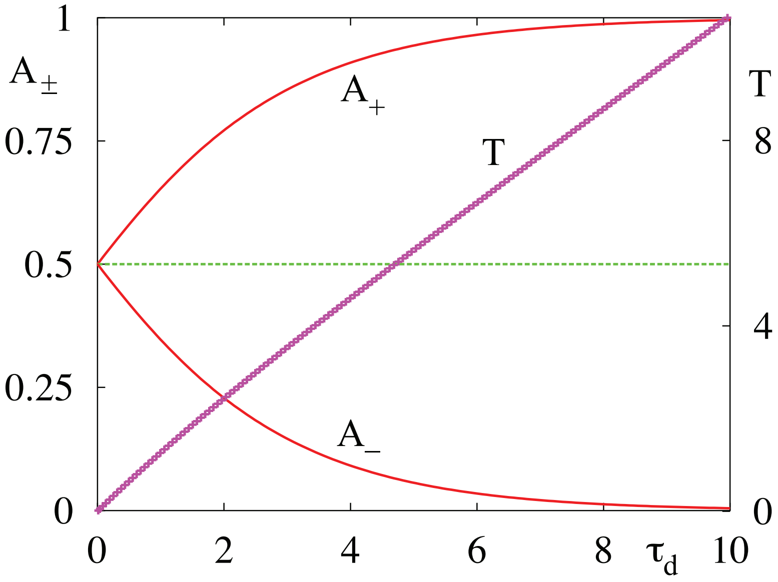

Figure 5. Period and amplitude of an oscillatory solution in a single population with excitatory self-feedback as a function of the delay $\tau_d$. Other parameters as in Fig. 4.

$$A_+ = A_- \mathrm{e}^{-T_+} + 1 - \mathrm{e}^{-T_+}, \tag{4.11}$$

$$A_- = A_+ \mathrm{e}^{-T_-}, \tag{4.12}$$

$$A_+ = h\mathrm{e}^{-(\tau_d - T_-)} + 1 - \mathrm{e}^{-(\tau_d - T_-)}, \tag{4.13}$$

$$A_- = h\mathrm{e}^{-(\tau_d - T_+)}. \tag{4.14}$$

We solve these to find

$$T_+ = \ln \frac{1 - A_-}{1 - A_+} = \tau_d + \ln \frac{A_-}{h}, \qquad T_- = \ln \frac{A_+}{A_-} = \tau_d + \ln \frac{1 - A_+}{1 - h}, \tag{4.15}$$

assuming $1 > h$ (so that threshold can be reached). The amplitudes $A_\pm$ satisfy

$$A_- = 1 + (1 - 1/h)A_+, \qquad A_+ = A_- + [\mathrm{e}^{(T - \tau_d)} - 1], \tag{4.16}$$

where $T = T_+ + T_-$ is the period of oscillation. We thus find that $T$ satisfies the transcendental equation

$$T = 2\tau_d + \left( \ln \left[ \frac{R - \mathrm{e}^{(T-\tau_d)}}{R - 1} \right] + \ln \left[ R + (1 - R)\mathrm{e}^{(T-\tau_d)} \right] \right), \tag{4.17}$$

where $R = 1/h$. The absolute amplitude $A = A_+ - A_-$ is given by $A = [\mathrm{e}^{(T-\tau_d)} - 1]$. A plot of the period and amplitude as a function of $\tau_d$ is shown in Fig. 5. By linearising about the periodic orbit shown in Fig. 4 and finding its Floquet exponents, one can show that this orbit is actually unstable (Coombes & Laing, 2008).

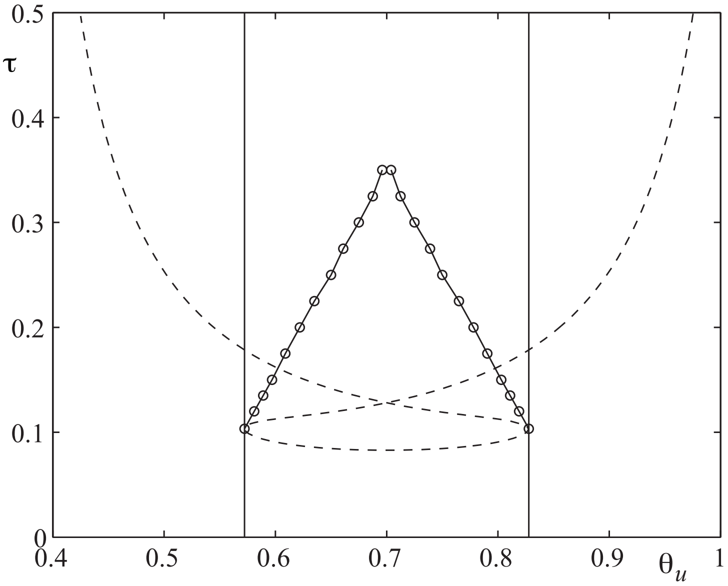

Figure 6. Bifurcation diagram. Solid line: saddle-node bifurcation of fixed points. Dashed line: Hopf bifurcation. Circles joined by a line: saddle-node bifurcation of periodic orbits. Parameter values are $\alpha = 1$, $\theta_v = 0.5$, $\tau_1 = \tau_2 = \tau$, $\beta = 60$, $a = -1$, $b = -0.4$, $c = -1$ and $d = 0$.

## 5. Numerical bifurcation analysis

In the high-gain limit (when $f$ is the Heaviside) explicit solutions of (2.1) can be constructed, as in the previous section. For a general firing rate function solutions cannot normally be explicitly constructed, but bifurcations of fixed points can be detected and followed in parameter space, as in §3. DDE-BIFTOOL (Engelborghs 2001, 2002) is a software package for the numerical bifurcation analysis of systems of delay differential equations which can not only detect bifurcations of fixed points, but can also follow branches of stable and unstable periodic orbits, and homoclinic and heteroclinic orbits. In this section we demonstrate its capabilities by analysing (2.1) as $\theta_u$ and $\tau_1 = \tau_2 \equiv \tau$ are varied. Typical results are shown in Fig. 6, where curves of saddle-node and Hopf bifurcations of fixed points are shown, along with saddle-node bifurcations of periodic orbits. Here, as expected from §3, varying $\tau$ does not change the fixed points, but it does affect their stability. Figure 7 shows horizontal slices through Fig. 6 at $\tau = 0.5$, 0.2 and 0.09. For $\tau = 0.5$, there is a branch of stable periodic orbits joining Hopf bifurcations on the upper and lower branches of fixed points. Between $\tau = 0.5$ and $\tau = 0.2$, a pair of saddle-node bifurcations of periodic orbits is created, resulting in the creation of a branch of unstable periodic orbits. For $\tau = 0.09$, an unstable periodic orbit is created from Hopf bifurcations on the unstable middle branch of fixed points.

Brute force numerical simulation can also be used to explore small systems of delay differential equations. For example, Battaglia *et al.* (2007) studied a system very similar to ours, setting $a = d < 0$ and $b = c > 0$, but using a threshold linear

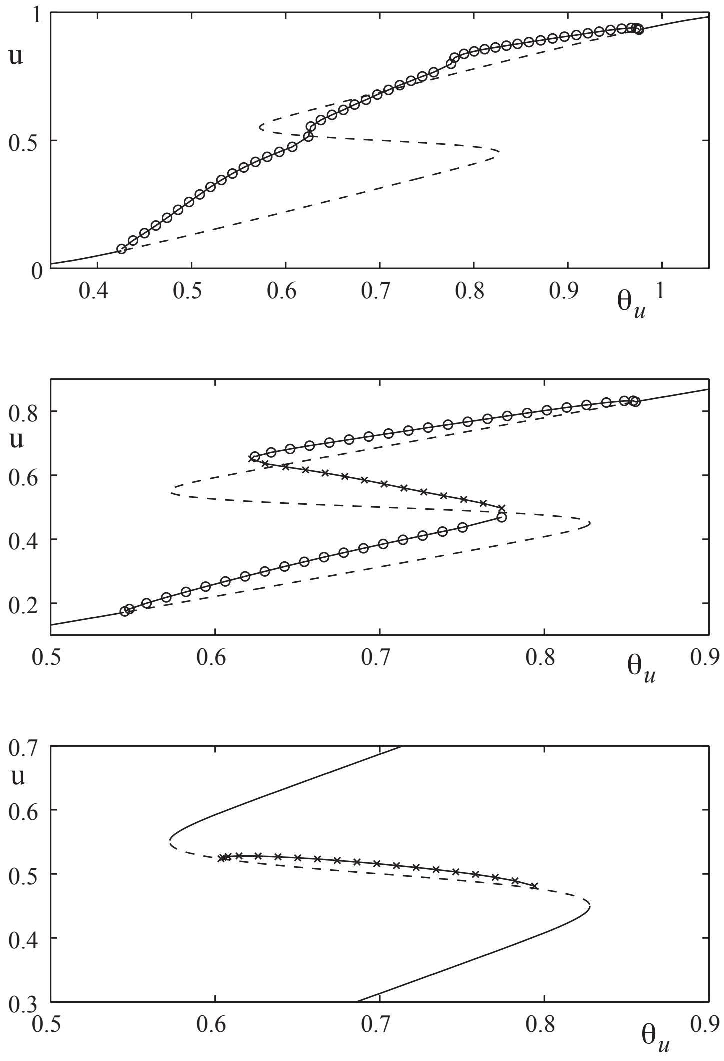

Figure 7. Horizontal cuts through Fig. 6 at $\tau = 0.5$ (top), $\tau = 0.2$ (middle) and $\tau = 0.09$ (bottom). Solid/dashed line: stable/unstable fixed points; circles/crosses: stable/unstable periodic orbit (the maximum of $u$ over one oscillation is plotted). Parameter values are as in Fig. 6. Note the different axis scales.

firing rate function: $f(z) = z$ if $z > 0$, and zero otherwise. They varied both local and long-range interaction strengths ($a$ and $b$ in our notation) and found various types of chaotic and periodic behaviour. We have performed a similar calculation, with results shown in Fig. 8. For these parameter values the system appears to have only one fixed point, and this undergoes a Hopf bifurcation on the curve shown. The most positive Lyapunov exponent can be found in the same way as for a system of ordinary differential equations (ODEs), by numerically integrating the variational equation in parallel with the underlying system. (Note that only one

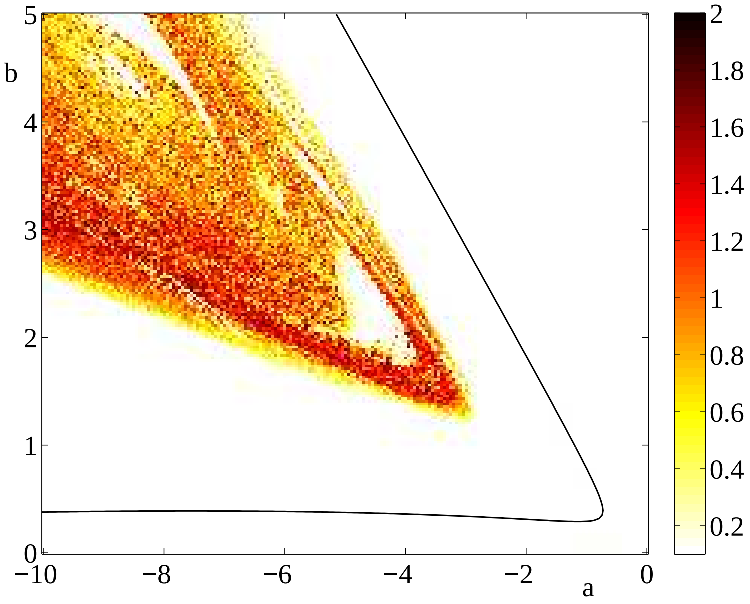

Figure 8. Maximal Lyapunov exponent. The black line marks a Hopf bifurcation, to the right of which there is a stable steady state. A positive exponent indicates chaotic behaviour. Parameter values are $\alpha = 1$, $\theta_u = \theta_v = 0.2$, $\tau_1 = \tau_2 = 0.1$, $\beta = 60$, $a = d$ and $b = c$.

initial condition was used for each point in the parameter space, so multistability is not detected.)

Figure 9 (left) shows a typical chaotic solution corresponding to the point $(a, b) = (-6, 2.5)$ in Fig. 8. The right panel of Fig. 9 shows a quasiperiodic orbit which was obtained using the parameter values in the left panel, but simply decreasing $\beta$ (the steepness of the firing rate function).

## 6. Discussion

Periodic and chaotic behaviour of the type seen above are of great interest in neural systems, as are “bursting” oscillations (Coombes & Bressloff 2005). Although the origins of bursting in low dimensional ODEs is quite well understood there has been very little work on bursting in delay differential equations. Here we briefly summarise the results of several groups. Destexhe & Gaspard (1993) studied a system of two coupled DDEs, meant to model interacting populations of excitatory and inhibitory neurons. By varying one parameter they found bursts containing different numbers of action potentials. The bursting could be understood as resulting from a homoclinic tangency to an unstable limit cycle, and did not require the usual “slow-fast” analysis (Coombes & Bressloff 2005). When the delays in their system were set to zero, the bursting could not exist, since the system was then two-dimensional. However, the general presence of a delay is not necessary to ob-

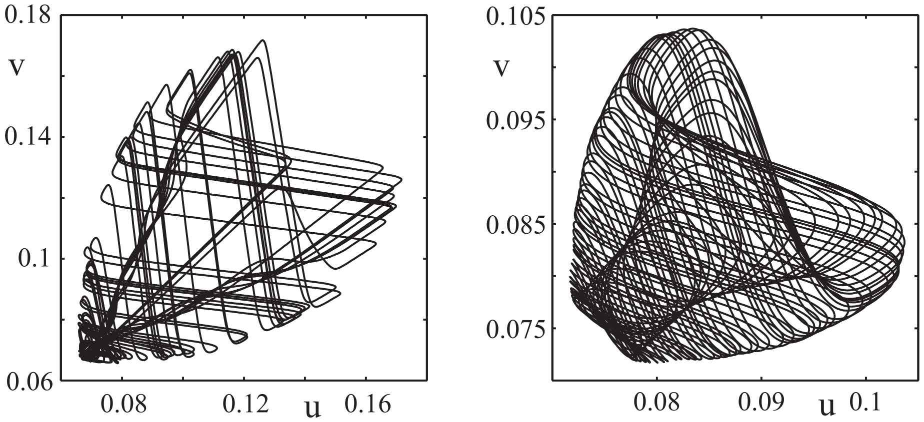

Figure 9. Left: a chaotic solution. Right: a quasiperiodic solution. Parameters are $\alpha = 1$, $a = d = -6$, $b = c = 2.5$, $\theta_u = \theta_v = 0.2$, $\tau_1 = \tau_2 = 0.1$, with $\beta = 60$ (left) and $\beta = 40$ (right).

serve this bifurcation, as it can appear in three-dimensional ODEs (Hirschberg & Laing, 1995).

Laing & Longtin (2003) studied the effects of paired delayed excitatory and inhibitory feedback on a single integrate-and-fire neuron, with and without noise. By assuming that the feedback was slow relative to the membrane time constant they derived a rate model for the dynamics. With either inhibitory or paired excitatory and inhibitory feedback these authors found periodic and chaotic oscillations in the firing rate of the neuron, i.e. bursting. They verified many of their results by simulating an actual integrate-and-fire neuron with appropriate delayed feedback.

Throughout this paper we have focused on discrete delays in neural population models without spatial extent. However, there is a large body of literature devoted to continuum models of neural tissue, particularly with regard to understanding the mechanisms of pattern and wave formation (see Coombes 2005 for a review). Many of the techniques we have touched upon here may be adapted for the treatment of such *neural field* equations (which are typically written as nonlocal evolution equations of integral type). Indeed work in this direction has already been pursued by Roxin *et al.* (2005) in the context of macroscopic pattern formation in the cortex, and by Golomb & Ermentrout (1999) and Bressloff (2000) for the analysis of travelling waves in synaptic networks of integrate-and-fire neurons. More recent work on space-dependent delays (induced by the finite conduction speeds of action potentials along axons) can be found in (Atay & Hutt 2006; Laing & Coombes 2006; Coombes *et al.* 2007).

In summary, delays are ubiquitous in neural systems and should therefore be included in any realistic neural model. Here we have briefly outlined the types of analysis available for small systems of neuronally-inspired delay differential equations. There remains much to be discovered about the role of delays in more realistic neural models.

## References

Atay, F. M. & Hutt, A. 2006 Neural fields with distributed transmission speeds and long-range feedback delays. *SIAM Journal on Applied Dynamical Systems* **5**, 670–698.

Battaglia, D., Brunel, N. & Hansel, D. 2007 Temporal decorrelation of collective oscillations in neural networks with local inhibition and long-range excitation. *Physical Review Letters* **99**, 238106(1–4).

Bressloff, P. C. 2000 Traveling waves and pulses in a one-dimensional network of integrate-and-fire neurons. *Journal of Mathematical Biology* **40**, 169–183.

Campbell, S. A. 2007 Time delays in neural systems. In *Handbook of Brain Connectivity*, McIntosh, A. R. & Jirsa, V. K., ed. Springer-Verlag.

Chen, Y. & Wu, J. 1999 Minimal instability and unstable set of a phase-locked periodic orbit in a delayed neural network. *Physica D* **134**, 185–199.

Chen, Y. M., Wu, J. H. & Krisztin, T. 2000 Connecting orbits from synchronous periodic solutions to phase-locked periodic solutions in a delay differential system. *Journal of Differential Equations* **163**, 130–173.

Coombes, S. & Laing, C. R. 2008 Instabilities in threshold-diffusion equations with delay. *Physica D*, submitted.

Coombes, S. & Lord, G. J. 1997 Intrinsic modulation of pulse-coupled integrate-and-fire neurons. *Physical Review E* **56**, 5809–5818.

Coombes, S. 2005 Waves, bumps, and patterns in neural field theories *Biological Cybernetics* **93**, 91–108.

Coombes, S. & Bressloff, P. C. (Editors). 2005 Bursting: The Genesis of Rhythm in the Nervous System. World Scientific Press.

Coombes, S., Venkov, N. A., Shiau, L., Bojak, I., Liley, D. T. J. & Laing, C. R. 2007 Modeling electrocortical activity through improved local approximations of integral neural field equations. *Physical Review E* **76**, 051901.

Destexhe, A. & Gaspard,P. 1993 Bursting oscillations from a homoclinic tangency in a time-delay system. *Physics Letters A* **173**, 386–391.

Engelborghs, K., Luzyanina, T. & Samaey, G. 2001 DDE-BIFTOOL v. 2.00: a Matlab package for bifurcation analysis of delay differential equations. *Technical Report TW-330, Department of Computer Science, K. U. Leuven, Leuven, Belgium.*

Engelborghs, K., Luzyanina, T. & Roose, D. 2002 Numerical bifurcation analysis of delay differential equations using DDE-BIFTOOL. *ACM Transactions on Mathematical Software* **28**, 1–21.

Ermentrout, B. 1998 Neural networks as spatio-temporal pattern-forming systems. *Reports on Progress in Physics* **61**, 353–430.

Giannakapoulos, F. & Zapp, A. 2001 Bifurcations in a planar system of differential delay equations modeling neural activity. *Physica D* **159**, 215–232.

Glass, L., Beuter, A. & Larocque, D. 1998 Time delays, oscillations, and chaos in physiological control systems. *Mathematical Biosciences* **90**, 111–125.

Golomb, D. & Ermentrout, G. B. 1999 Continuous and lurching traveling pulses in neuronal networks with delay and spatially decaying connectivity. *Proceedings of the National Academy of Sciences USA* **96**, 13480–13485.

Guo, S., Huang, L. & Wu, J. 2005 Regular dynamics in a delayed network of two neurons with all-or-none activation functions. *Physica D* **206**, 32–48.

Hirschberg, P. & Laing, C. R. 1995 Successive homoclinic tangencies to a limit cycle. *Physica D* **89**, 1–14.

Hoppensteadt, F. C. & Izhikevich, E. M. 1997 Weakly Connected Neural Networks. Springer-Verlag, New York.

Laing, C. R. & Longtin, A. 2003 Dynamics of deterministic and stochastic paired excitatory-inhibitory delayed feedback. *Neural Computation* **15**, 2779–2822.

Laing, C. R. & Coombes, S. 2006 The importance of different timings of excitatory and inhibitory pathways in neural field models. *Network* **17**, 151–172.

Longtin, A. & Milton, J. G. 1998 Complex oscillations in the human pupil light reflex with mixed and delayed feedback. *Mathematical Biosciences* **90**, 183–199.

MacDonald, N. 1989 Biological delay systems: linear stability theory. Cambridge University Press.

Marcus, C. M. & Westervelt, R. M. 1989 Stability of analog neural networks with delay. *Physical Review A* **39**, 347–359.

Murdoch, W. W., Nisbet, R. M., Blyth, S. P., Gurney, W. S. C & Reeve, J. D. 1987 An invulnerable age class and stability in delay-differential parasitoid-host models. *The American Naturalist* **129**, 263–282.

Olien, L. & Bélair, J. 1997 Bifurcations, stability, and monotonicity properties of a delayed neural network model. *Physica D* **102**, 349–363.

Plant, R. E. 1981 A FitzHugh differential-difference equation modeling recurrent neural feedback. *SIAM Journal on Applied Mathematics* **40**, 150–162.

Reddy, R. D. V., Sen, A. & Johnston, G. L. 1998 Time delay induced death in coupled limit cycle oscillators. *Physical Review Letters* **80**, 5109–5112.

Roxin, A., Brunel, N. & Hansel, D. 2005 Role of delays in shaping spatiotemporal dynamics of neuronal activity in large networks. *Physical Review Letters* **94**, 238103(1–4).

Shayer, L. P. & Campbell, S. A. 2000 Stability, bifurcation, and multistability in a system of two coupled neurons with multiple time delays. *SIAM Journal on Applied Mathematics* **61**, 673–700.

Stépán, G. 1989 Retarded dynamical systems. Longman Scientific & Technical.

Wei, J. J. & Ruan, S. R. 1999 Stability and bifurcation in a neural network model with two delays. *Physica D* **130**, 255–272.

Wilson, H. R. & Cowan, J. D. 1972 Excitatory and inhibitory interactions in localized populations of model neurons. *Biophysical Journal* **12**, 1-24.