Periodic solutions for a pair of delay-coupled active theta neurons

Carlo R. Laing *

October 31, 2024

Abstract

We consider a pair of identical theta neurons in the active regime, each coupled to the other via a delayed Dirac delta function. The network can support periodic solutions and we concentrate on solutions for which the neurons are half a period out of phase with one another, and also solutions for which the neurons are perfectly synchronous. The dynamics are analytically solvable, so we can derive explicit expressions for the existence and stability of both types of solutions. We find two branches of solutions, connected by symmetry-broken solutions which arise when the period of a solution as a function of delay is at a maximum or a minimum. *2020 MSC codes:* 92B20, 92B25, 34K24; *keywords:* neuron dynamics, delay differential equations, bifurcation.

1 Introduction

Many physical entities such as neurons and lasers can be modelled as oscillators [5, 19]. Coupling them together results in a network of coupled oscillators. The effect of one oscillator on others in a network may be delayed due to, for example, the finite speed of light, or of action potentials propagating along axons [3, 5].

One of the simplest model oscillators is the theta neuron [4], which is the normal form of the saddle-node-on-invariant-circle (SNIC) bifurcation [7]. A

*School of Mathematical and Computational Sciences, Massey University (Albany), Private Bag 102-904 North Shore Mail Centre, Auckland, New Zealand. `mailto:c.r.laing@massey.ac.nz` , `https://orcid.org/0000-0002-6086-2978`

theta neuron has a single parameter, I, which can be chosen so that the neuron is either excitable or active (periodically firing). It has the advantage that its state can be found explicitly as a function of time for constant I [14]. In a previous paper [14] we considered a single theta neuron with delayed self-coupling (an autapse [21]) in the form of a Dirac delta function of time. The action of a delta function on a theta neuron can be easily calculated, so we were able to analytically describe periodic solutions of this model and determine their stability, giving a complete description of the types of periodic solutions, where they occur in parameter space and their stability.

More recently we considered a pair of theta neurons, each coupled to the other through delayed delta functions [15]. We considered the case of excitable neurons and found two types of periodic solutions: those for which the neurons were perfectly synchronous, and those for which the neurons were half a period out of phase with one another. Extending the analysis in [14] we derived explicit expressions for the existence and stability of both types of solutions. We also described symmetry-broken solutions and analytically determined their stability. We found disconnected branches of solutions, all of which lose stability when the period of a solution as a function of delay is at a minimum.

This paper considers a pair of theta neurons, each coupled to the other through delayed delta functions, but when the uncoupled neurons are active. We perform similar analysis to that in [15], finding two continuous branches of periodic solutions, one for which the neurons are perfectly synchronous, and one for which they alternate firing. These branches undergo symmetry-breaking bifurcations whenever the period as a function of delay is either a maximum or a minimum. The model is presented in Sec. 2, synchronous solutions are studied in Sec. 3, and alternating ones in Sec. 4. Symmetry-broken solutions are studied in Sec. 5, we consider the case of smooth feedback in Sec. 6 and conclude in Sec. 7.

2 Model

We first consider a single theta neuron [4] governed by

$$\frac{d\theta}{dt} = 1 - \cos\theta + (1 + \cos\theta)I, \tag{1}$$

where $\theta \in [0, 2\pi)$ and I is a positive constant. The solution of (1) is

$$\theta(t) = 2\tan^{-1}\left[\sqrt{I}\tan\left(\sqrt{I}t + \tan^{-1}\left(\frac{\tan[\theta(0)/2]}{\sqrt{I}}\right)\right)\right]. \tag{2}$$

In what follows we set $I = 1$, and thus a single theta neuron satisfies $d\theta/dt = 2$ and thus $\theta(t) = \theta(0) + 2t$. (While this may seem to be a drastic assumption, if $I \neq 1$ letting $\tan(\theta/2) = \sqrt{I}\tan(\phi/2)$ we find that $d\phi/dt = 2$ [18].)

In this paper we consider a pair of such neurons coupled to one another via delayed Dirac delta functions, described by

$$\frac{d\theta_1}{dt} = 1 - \cos\theta_1 + (1 + \cos\theta_1)\left(1 + \kappa \sum_{i:t-\tau<s_i<t} \delta(t - s_i - \tau)\right) \tag{3}$$

$$\frac{d\theta_2}{dt} = 1 - \cos\theta_2 + (1 + \cos\theta_2)\left(1 + \kappa \sum_{i:t-\tau<t_i<t} \delta(t - t_i - \tau)\right), \tag{4}$$

where τ is the (constant) delay and firing times in the past of neuron 1 can be written $\{\dots, t_{-3}, t_{-2}, t_{-1}, t_0\}$ and those of neuron 2 can be written $\{\dots, s_{-3}, s_{-2}, s_{-1}, s_0\}$. The constant κ is the strength of coupling between the neurons. The influence of the delta function is to increment θ using

$$\tan(\theta^+/2) = \tan(\theta^-/2) + \kappa, \tag{5}$$

where θ^- is the value of θ before the delta function acts and θ^+ is the value after [14]. Such a network with $I = -1$ (i.e., when both neurons are excitable rather than active) and $0 < \kappa$ was considered in [15].

Example solutions of (3)-(4) are shown in Fig. 1. In this paper we focus on solutions of the form shown: either both neurons are perfectly synchronous, or they are half a period out of phase with one another. Since between the times at which a delta function acts we have $d\theta/dt = 2$, and we know the effect of the delta function, (5), we can analytically construct solutions such as those in Fig. 1 and determine their stability. In Sec. 3 we consider synchronous solutions and in Sec. 4 we consider alternating solutions.

3 Synchronous solutions

We first consider periodic solutions of (3)-(4) for which the neurons are perfectly synchronous, as shown in the top row of Fig. 1. The influence of one neuron on the other is thus the same as that of the neuron on itself. The existence of such solutions is governed by the same equation that governs the behaviour of a single neuron delay-coupled to itself [14].

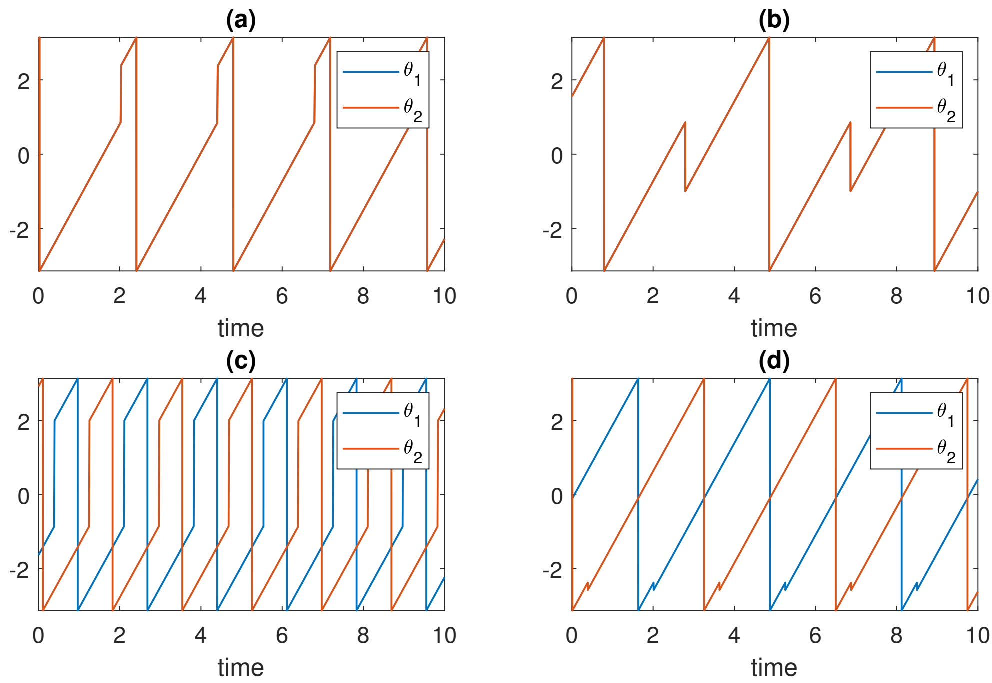

Figure 1: Example periodic solutions of (3)-(4). The top row shows synchronised solutions while the bottom shows alternating solutions. The left column has $\kappa = 2$ while the right has $\kappa = -1$. All have $\tau = 2$.

3.1 Existence

As shown in [14], perfectly synchronous periodic solutions of (3)-(4) with period T satisfy

$$(n+1)T = \tau + \frac{\pi}{2} - \tan^{-1}\left[\kappa + \tan\left(\tau - nT + \frac{\pi}{2}\right)\right], \tag{6}$$

where $\tan^{-1}$ is the arctangent function and n is the number of past firing times in the interval $(-\tau, 0)$, assuming that a neuron has just fired at time $t = 0$. The primary branch of solutions, corresponding to $n = 0$, is given explicitly by

$$T(\tau) = \tau + \frac{\pi}{2} - \tan^{-1}\left[\kappa + \tan\left(\tau + \frac{\pi}{2}\right)\right] \tag{7}$$

for $0 \leqslant \tau \leqslant \pi$, while secondary branches are given parametrically, using the reappearance of periodic solutions in delay differential equations with fixed delays [25], as

$$(\tau, T) = (s + nT(s), T(s)), \tag{8}$$

where $0 \leqslant s \leqslant \pi$. Several branches of such solutions are shown in blue in Fig. 2.

3.2 Stability

We now derive the stability of a synchronous periodic solution. Suppose neuron 1 last fired at time t_0 and neuron 2 last fired at s_0 where $s_0 \approx t_0$. The most distant past firing of neuron 1 in $(t_0 - \tau, t_0)$ is t_{-n} and the most distant past firing of neuron 2 in $(s_0 - \tau, s_0)$ is s_{-n}.

For neuron 1, from t_0 we wait $\tau - (t_0 - s_{-n})$ at which point neuron 1 has its phase incremented due to a past firing of neuron 2. Before the reset, θ_1 equals

$$\theta_1^- = \pi + 2(\tau - (t_0 - s_{-n})),$$

and after reset it is θ_1^+ where

$$\tan(\theta_1^+/2) = \tan(\theta_1^-/2) + \kappa.$$

Neuron 1 will then fire after a further time Δ_1 where

$$\Delta_1 = \frac{\pi - \theta_1^+}{2}.$$

Thus

$$\begin{aligned} t_1 &= t_0 + \tau - (t_0 - s_{-n}) + \Delta_1 \\ &= \tau + s_{-n} + \pi/2 - \tan^{-1}[\kappa + \tan(\pi/2 + \tau - (t_0 - s_{-n}))]. \end{aligned} \tag{9}$$

Similarly for neuron 2, from time s_0 we wait $\tau - (s_0 - t_{-n})$ until neuron 2 has its phase incremented as a result of the past firing of neuron 1. Before the reset θ_2 equals

$$\theta_2^- = \pi + 2(\tau - (s_0 - t_{-n})),$$

and after the reset it equals θ_2^+ where

$$\tan(\theta_2^+/2) = \tan(\theta_2^-/2) + \kappa.$$

Neuron 2 will then fire after a further time Δ_2 where

$$\Delta_2 = \frac{\pi - \theta_2^+}{2}.$$

So

$$\begin{aligned} s_1 &= s_0 + \tau - (s_0 - t_{-n}) + \Delta_2 \\ &= \tau + t_{-n} + \pi/2 - \tan^{-1}[\kappa + \tan(\pi/2 + \tau - (s_0 - t_{-n}))]. \end{aligned} \tag{10}$$

Equations (9) and (10) give t_1 and s_1 in terms of previous firing times, but in general we have

$$s_{i+1} = \tau + t_{i-n} + \pi/2 - \tan^{-1}[\kappa - \cot(\tau - (s_i - t_{i-n}))] \tag{11}$$
$$t_{i+1} = \tau + s_{i-n} + \pi/2 - \tan^{-1}[\kappa - \cot(\tau - (t_i - s_{i-n}))], \tag{12}$$

where we used $\tan(\pi/2 + x) = -\cot x$. We write (11)-(12) as

$$F(s_{i+1}, t_{i-n}, s_i) = 0 \tag{13}$$
$$G(t_{i+1}, s_{i-n}, t_i) = 0. \tag{14}$$

To find the stability of a solution we perturb $t_i \to t_i + \eta_i$ and $s_i \to s_i + \mu_i$. Then to linear order we have

$$\frac{\partial F}{\partial s_{i+1}}\mu_{i+1} + \frac{\partial F}{\partial t_{i-n}}\eta_{i-n} + \frac{\partial F}{\partial s_i}\mu_i = 0 \tag{15}$$
$$\frac{\partial G}{\partial t_{i+1}}\eta_{i+1} + \frac{\partial G}{\partial s_{i-n}}\mu_{i-n} + \frac{\partial G}{\partial t_i}\eta_i = 0, \tag{16}$$

which, after evaluating the partial derivatives at a periodic solution with period T, we write as

$$-\mu_{i+1} + (1-\gamma)\eta_{i-n} + \gamma\mu_i = 0 \tag{17}$$
$$-\eta_{i+1} + (1-\gamma)\mu_{i-n} + \gamma\eta_i = 0, \tag{18}$$

where

$$\gamma = \frac{\csc^2(\tau - nT)}{1 + [\kappa - \cot(\tau - nT)]^2}. \tag{19}$$

This is the same quantity as was found in [14] when studying the stability of a periodic solution of a self-coupled theta neuron. Assuming solutions of the linear equations (17)-(18) of the form $\mu_i = A\lambda^i$ and $\eta_i = B\lambda^i$ for some constants A and B, as in [15], we obtain the characteristic equation for the multipliers, λ:

$$F_a(\lambda) \equiv \lambda^{2n+2} - 2\gamma\lambda^{2n+1} + \gamma^2\lambda^{2n} - (1-\gamma)^2 = 0. \tag{20}$$

This is the same equation as was found in [15], where two excitable neurons were studied, the only difference being the definition of γ. The magnitudes of the roots of $F_a(\lambda)$ determine the stability of the perfectly synchronous periodic solution. If all roots have $|\lambda| \leqslant 1$ the periodic solution is not unstable, but if one or more roots have $|\lambda| > 1$ the periodic solution is unstable.

We first consider the case $n = 0$. Then $F_a(\lambda) = (\lambda - 1)(\lambda + 1 - 2\gamma)$. The root $\lambda = 1$ reflects the invariance of the system to uniform time translation, and since $0 < \gamma$ the only instability that can occur is when $\gamma = 1$. This point corresponds to $dT/d\tau = 0$ on the primary branch. To see that this is the case, differentiating (7) with respect to τ we find that $dT/d\tau = 1 - \gamma$ where γ is given by (19) with $n = 0$. Thus $dT/d\tau = 0$ when $\gamma = 1$.

Summarising the results in [15] for $0 < n$, we find that such a synchronous solution undergoes two types of bifurcations, one when $dT/d\tau = 0$ and the other at a saddle-node bifurcation (i.e. when the curve of period, T, as a function of delay, τ, is either vertical or horizontal) on each branch, indexed by n.

3.3 Branches of solutions

Plotting branches of solutions as given by (7)-(8) for $\kappa = 2$, and indicating their stability, we obtain the blue curve in Fig. 2. Note that these curves are the same as shown in Fig. 7 of [14], but their stability is different, due to the possibility of losing stability to a solution which is not synchronous. These symmetry broken states are shown in black in Fig. 2, and they are analysed in Sec. 5.1. Note: if on an unstable section of a branch there are two saddle-node bifurcations (marked with filled circles in Fig. 2) there are *two* unstable multipliers between the bifurcations. Stable solutions lose stability in symmetry-breaking bifurcations when $dT/d\tau = 0$, and between a symmetry-breaking and a saddle-node bifurcation a solution has one unstable multiplier.

4 Alternating solutions

We now consider solutions for which the neurons take turns firing, half a period out of phase with one another, as shown in the bottom row of Fig. 1.

4.1 Existence

As shown in [15], the existence of alternating solutions of (3)-(4) is given by (6) under the replacement of τ by $\tau + T/2$:

$$(n + 1/2)T = \tau + \frac{\pi}{2} - \tan^{-1}\left[\kappa + \tan\left(\tau - (n - 1/2)T + \frac{\pi}{2}\right)\right]. \qquad (21)$$

The meaning of n in (21) is that if neuron 1 fires at time 0, there are n past firing times of neuron 2 in $(-\tau, 0)$; n could be zero.

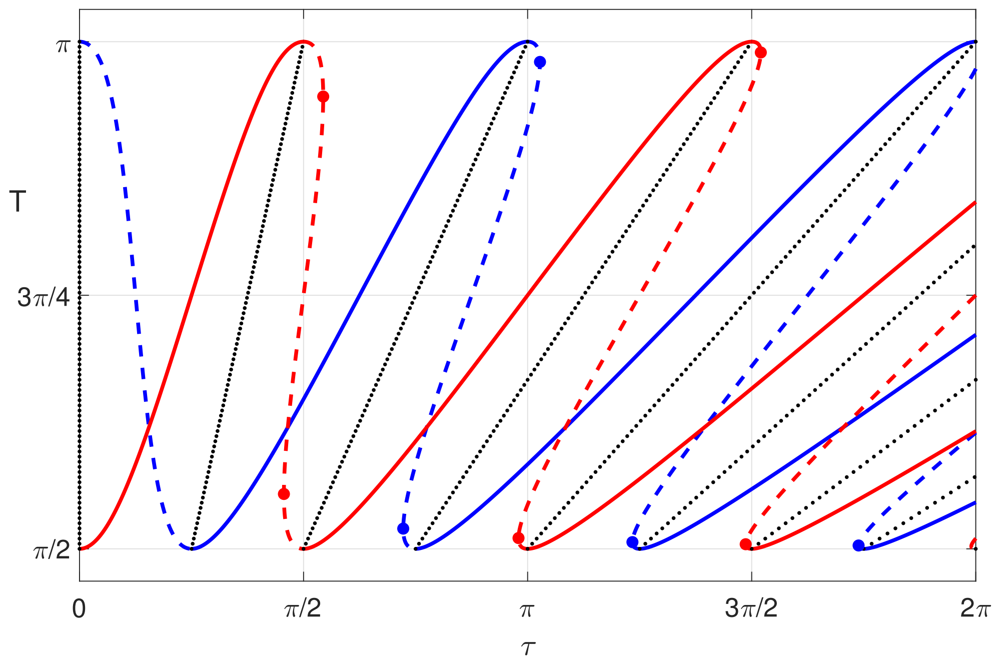

Figure 2: Blue: synchronous periodic solutions (solid stable, dashed unstable). The nth branch goes from $(n\pi, \pi)$ to $((n+1)\pi, \pi)$. Red: alternating periodic solutions (solid stable, dashed unstable). The nth branch goes from $((n-1/2)\pi, \pi)$ to $((n+1/2)\pi, \pi)$. Black: symmetry-broken periodic solutions (all unstable, except the branch at $\tau = 0$ which is neutrally stable). The filled circles indicate saddle-node bifurcations. $\kappa = 2$.

4.2 Stability

Performing a similar analysis as in Sec. 3.2 or [15] we obtain the firing time maps, valid when the oscillators are approximately half a period out of phase:

$$t_{i+1} = \tau + s_{i+1-n} + \pi/2 - \tan^{-1}\left[\kappa + \tan\left(\pi/2 + \tau - (t_i - s_{i+1-n})\right)\right] \quad (22)$$

$$s_{i+1} = \tau + t_{i-n} + \pi/2 - \tan^{-1}\left[\kappa + \tan\left(\pi/2 + \tau - (s_i - t_{i-n})\right)\right] \quad (23)$$

for $i = 0, 1, 2, \ldots$.

We want to linearise around an alternating periodic solution of (22)-(23). To do that, write (22)-(23) as

$$R(t_{i+1}, s_{i-n+1}, t_i) = 0 \quad (24)$$

$$S(s_{i+1}, t_{i-n}, s_i) = 0, \quad (25)$$

then perturb the firing times and assume that these perturbations either grow or decay exponentially with index. The calculations are similar to those in

Sec. 3.2 and we obtain the characteristic equation governing the stability of these solutions:

$$F_b(\lambda) \equiv \lambda^{2n+1} - 2\gamma\lambda^{2n} + \gamma^2\lambda^{2n-1} - (1-\gamma)^2 = 0, \tag{26}$$

where

$$\gamma = \frac{\csc^2(\tau - (n-1/2)T)}{1 + [\kappa - \cot(\tau - (n-1/2)T)]^2}. \tag{27}$$

This characteristic equation was found in [15] for the case of two excitable neurons, but in that paper γ referred to a different quantity, not that in (27). Using the results in [15] for the roots of (26) we have that the alternating periodic solution with $n = 0$ is stable for $0 < \gamma < 1$ and unstable for $1 < \gamma$. For $0 < n$ each branch of alternating periodic solutions undergoes two bifurcations when the curve of T as a function of τ is either vertical or horizontal, just as for the synchronous solutions. Branches of these solutions are shown in red in Fig. 2, with stability indicated. Saddle-node bifurcations are also shown.

5 Symmetry-broken solutions

As mentioned, both types of solutions analysed above undergo bifurcations when $dT/d\tau = 0$. These are symmetry-breaking bifurcations and we now analyse the resulting solutions.

5.1 Symmetry-breaking from synchronous solutions

We start with (11)-(12) and break the symmetry so that $s_i - t_{i-n} = (n - \phi)T$ and $t_i - s_{i-n} = (n + \phi)T$; thus $\phi = 0$ corresponds to the perfectly synchronous case. Substituting these into (11)-(12) we obtain equations for the existence of such states:

$$\tan(\pi/2 + \tau - (n+1-\phi)T) = \kappa + \tan(\pi/2 + \tau - (n-\phi)T) \tag{28}$$

$$\tan(\pi/2 + \tau - (n+1+\phi)T) = \kappa + \tan(\pi/2 + \tau - (n+\phi)T). \tag{29}$$

Using the identity $\tan a - \tan b = \sin(a-b)/(\cos a \cos b)$ on first (28) and then on (29), and the fact that cosine is an even function, we find that solutions of (28)-(29) satisfy $T = 2\tau/(2n+1)$. In this case both (28) and (29) reduce to

$$\cot((1/2 - \phi)T) = \kappa - \cot((1/2 + \phi)T). \tag{30}$$

For fixed κ, solutions of (30) lie on a curve in (T, ϕ) space, as shown in Fig. 3. The curves terminate at $\phi = \pm 1/2$, and these values correspond to alternating solutions. When $\phi = \pm 1/2$ we see from (30) that $T = \pi$, independent

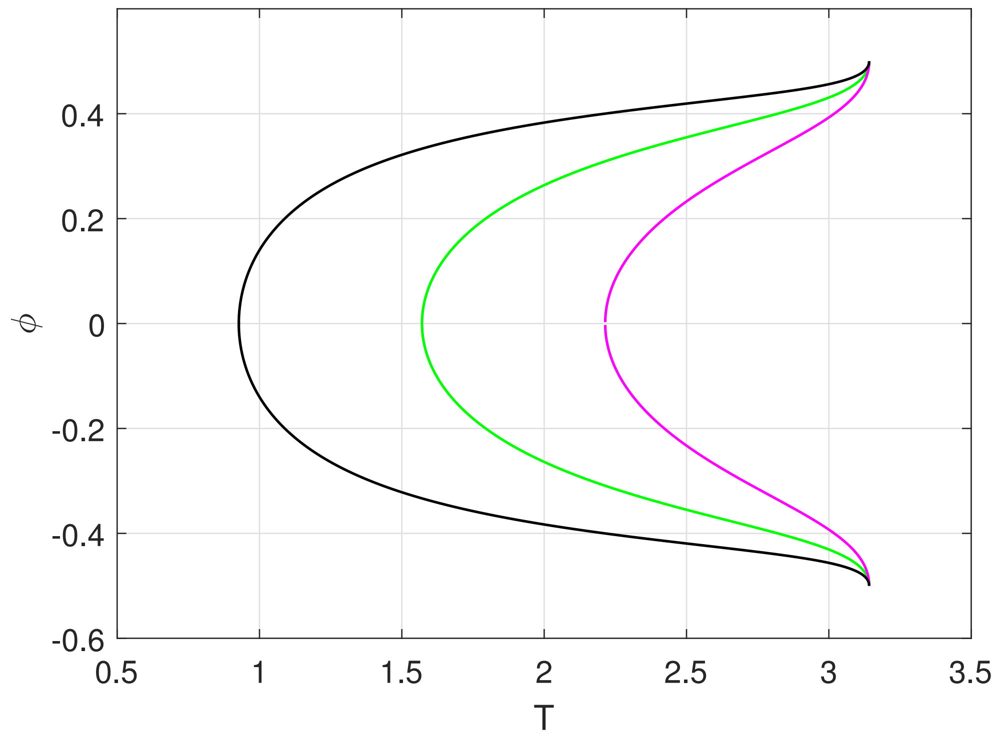

Figure 3: Solutions of (30), describing symmetry-broken solutions, for $\kappa = 4, 2, 1$ (left to right).

of κ. When $\phi = 0$ we have $T = 2\cot^{-1}(\kappa/2)$. Thus the symmetry-broken solutions lie on the lines $T = 2\tau/(2n+1)$ where $(2n+1)\cot^{-1}(\kappa/2) \leqslant \tau \leqslant (n+1/2)\pi$ and are plotted in black in Fig. 2 emanating from each minimum on the curve of synchronous solutions (shown in blue). They each terminate at a maximum on the curve of alternating solutions (shown in red). Note that only every second of the black curves shown in Fig. 2 are described by this analysis; the other curves are analysed in Sec. 5.2. The stability of these types of solutions can be calculated as in [15] and they are all unstable.

5.2 Symmetry-breaking from alternating solutions

5.2.1 $\tau = 0$ solutions

We see from Fig. 2 that a symmetric alternating solution exists for $\tau = 0$. But a whole family of asymmetric solutions also exist, shown with the vertical black line at $\tau = 0$ in Fig. 2. We now analyse them.

Between firing times the flow is given by $d\theta_1/dt = 2$ and $d\theta_2/dt = 2$.

Assume that θ_2 has just fired (i.e., $\theta_2 = \pi$) and $\theta_1 = \alpha$ where $0 < \alpha < \pi$. Both θ_1 and θ_2 will increase until $\theta_1 = \pi$, which takes a time $\Delta_1 = (\pi - \alpha)/2$, at which point $\theta_2 = 2\pi - \alpha$. The phase θ_2 is then incremented to $\theta_2^+ = 2\tan^{-1}(\kappa + \tan(\pi - \alpha/2))$. Both phases then continue to increase until $\theta_2 = \pi$, which takes a further time $\Delta_2 = (\pi - \theta_2^+)/2$, at which point $\theta_1 = \pi + 2\Delta_2 = 2\pi - \theta_2^+$. The phase θ_1 is then incremented to $\theta_1^+ = 2\tan^{-1}(\kappa + \tan(\pi - \theta_2^+/2))$. For this process to describe a periodic solution we need $\theta_1^+ = \alpha$, which is true for all $0 < \alpha < \pi$. (A similar calculation can be done for $\pi < \alpha < 2\pi$.) Thus there is a continuum of such periodic solutions.

The period of such a solution is $T = \Delta_1 + \Delta_2$ and so we can write $\Delta_1 = (1/2 + \phi)T$ and $\Delta_2 = (1/2 - \phi)T$ for some $-1/2 < \phi < 1/2$, where $\phi = 0$ corresponds to the symmetric alternating solution. We find that $\cot(\Delta_1) = \tan(\alpha/2)$ and $\cot(\Delta_2) = \kappa - \tan(\alpha/2)$ and thus $\cot(\Delta_2) = \kappa - \cot(\Delta_1)$, or

$$\cot((1/2 - \phi)T) = \kappa - \cot((1/2 + \phi)T), \tag{31}$$

which is identical to (30), whose solutions are shown in Fig. 3. This family of asymmetric solutions lie on the T axis with $2\cot^{-1}(\kappa/2) < T \leqslant \pi$ and are shown in black in Fig. 2. These solutions are neutrally stable, as there is a continuum of them.

5.2.2 $\tau > 0$ solutions

The solutions in the previous section exist for $\tau = 0$. Using the reappearance of solutions of DDEs we see that a solution with a given ϕ and T which satisfies (31) is also a periodic solution with the same ϕ and T when the delay equals a multiple of T. Thus these symmetry-broken solutions lie on the lines $T = \tau/n$ with $2n\cot^{-1}(\kappa/2) < \tau \leqslant n\pi$; these are shown black in Fig. 2. These lines leave minima on the curves of alternating solutions (shown in red) when $\phi = 0$ and terminate at maxima on curves of synchronous solutions (shown in blue) when $\phi = \pm 1/2$. The stability of these solutions can be determined using calculations similar to those in [15], and they are unstable.

6 Smooth feedback

We now consider the case of smooth feedback, to see whether the results for Dirac delta function coupling persist. The equations we study are

$$\frac{d\theta_1}{dt} = 1 - \cos\theta_1 + (1 + \cos\theta_1)\{1 + \kappa P[\theta_2(t-\tau)]\} \tag{32}$$

$$\frac{d\theta_2}{dt} = 1 - \cos\theta_2 + (1 + \cos\theta_2)\{1 + \kappa P[\theta_1(t-\tau)]\}, \tag{33}$$

where

$$P(\theta) = a_m(1 - \cos\theta)^m,$$

with $a_m = 2^m(m!)^2/(2m)!$, is a pulsatile function centred at $\theta = \pi$ with $\int_0^{2\pi} P(\theta)d\theta = 2\pi$ for all m. Increasing m makes this function "sharper" and in the limit $m \to \infty$ we have $P(\theta) = 2\pi\delta(\theta - \pi)$ where δ is the Dirac delta function [13].

We set $m = 5$ and find branches of synchronous and alternating solutions using DDE-BIFTOOL [22]. They are plotted in Fig. 4, as are the symmetry-broken solutions, with stability indicated. We find perfect qualitative agreement with the results shown in Fig. 2, obtained for delta function coupling, showing the robustness of our results.

7 Discussion

We exactly described periodic solutions that occur in a pair of delay-coupled active theta neurons, and analytically found their stability. Our work is an extension of that in [15] where a pair of excitable theta neurons were studied. The results are similar, in that symmetry-breaking instabilities were found where $dT/d\tau = 0$. To obtain periodic solutions for excitable systems we needed excitatory coupling, i.e. $0 < \kappa$. The results in this paper also had $0 < \kappa$, but that is not necessary to see periodic solutions in networks of active neurons. The analysis performed here is equally valid for inhibitory coupling ($\kappa < 0$), the main difference being that all solutions will have periods greater than or equal to π (the period of an uncoupled neuron) as inhibition can only slow down oscillations.

We now briefly discuss similar work by others. A number of authors have considered delay-coupled phase oscillators which rotate at a constant speed when uncoupled, as we do. However, some choose the interactions between oscillators to be smooth, depending on sinusoidal functions of phase differences, for example [2, 3, 20, 26]. Others consider uniformly rotating oscillators with delayed delta function coupling [6, 8, 17, 24], but none have

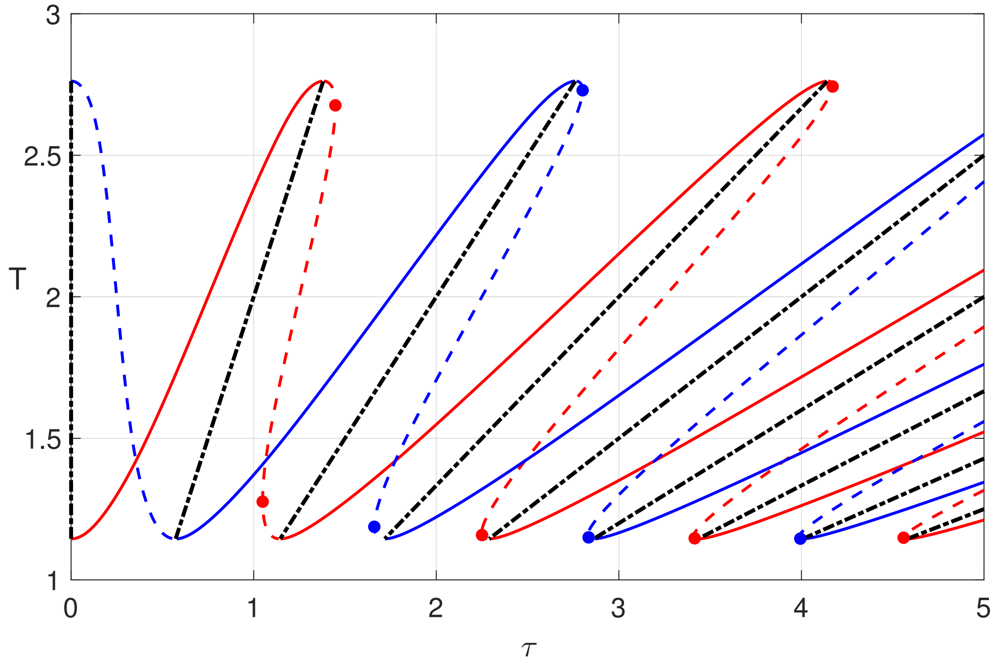

Figure 4: Periodic solutions of (32)-(33). Blue: synchronous solutions; red: alternating solutions. Solid: stable; dashed: unstable. The symmetry-broken solutions (all unstable) are shown in black. Filled circles show the points at which the number of unstable Floquet multipliers of a solution has changed from one to two; these are saddle-node bifurcations. $m = 5, \kappa = 2$.

used the update rule (5) specific to a theta neuron with pulsatile current input. As an example, Klinshov et al. [10] study a model containing a phase resetting curve $Z(\theta^-) = \theta^+ - \theta^-$ where θ^- is the value of θ before the delta function acts and θ^+ is the value after. For the update rule (5) we have

$$Z(\theta) = 2\tan^{-1}\left[\tan\left(\theta/2\right) + \kappa\right] - \theta.$$

One can show that $-1 < Z'(\theta)$ so neither a single self-coupled theta neuron nor a pair of them as considered here can undergo a "multijitter" bifurcation of the type seen in [9, 10, 11].

We note that a number of authors (including this one [16]) write $d\theta/dt = [\cdots] + f(\theta)\delta(t-\tau)$ to indicate that θ is incremented by the amount $f(\theta)$ at $t = \tau$. However, this interpretation of the impulsive differential equation is incorrect [1, 12]. Alternating and synchronous periodic solutions were found in a pair of delay-coupled FitzHugh-Nagumo systems [23], however this work and [15] are the most comprehensive studies of this phenomena so far, aided by the analytical solutions of the models under study.

Competing Interests: the author declares no competing interests.

References

[1] A. J. Catllá, D. G. Schaeffer, T. P. Witelski, E. E. Monson, and A. L. Lin. On spiking models for synaptic activity and impulsive differential equations. *SIAM Review*, 50(3):553–569, 2008.

[2] M. G. Earl and S. H. Strogatz. Synchronization in oscillator networks with delayed coupling: A stability criterion. *Physical Review E*, 67(3): 036204, 2003.

[3] B. Ermentrout and T.-W. Ko. Delays and weakly coupled neuronal oscillators. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 367(1891):1097–1115, 2009.

[4] G. B. Ermentrout and N. Kopell. Parabolic bursting in an excitable system coupled with a slow oscillation. *SIAM Journal on Applied Mathematics*, 46(2):233–253, 1986.

[5] G. B. Ermentrout and D. H. Terman. *Mathematical Foundations of Neuroscience*. Springer, New York, NY, 2010.

[6] U. Ernst, K. Pawelzik, and T. Geisel. Synchronization induced by temporal delays in pulse-coupled oscillators. *Physical Review Letters*, 74: 1570–1573, Feb 1995.

[7] B. Gutkin. Theta neuron model. In *Encyclopedia of Computational Neuroscience*, pages 3412–3419. Springer, 2022.

[8] V. Klinshov and V. Nekorkin. Synchronization of time-delay coupled pulse oscillators. *Chaos, Solitons & Fractals*, 44(1-3):98–107, 2011.

[9] V. Klinshov, L. Lücken, D. Shchapin, V. Nekorkin, and S. Yanchuk. Emergence and combinatorial accumulation of jittering regimes in spiking oscillators with delayed feedback. *Physical Review E*, 92(4):042914, 2015.

[10] V. Klinshov, L. Lücken, D. Shchapin, V. Nekorkin, and S. Yanchuk. Multistable jittering in oscillators with pulsatile delayed feedback. *Physical Review Letters*, 114(17):178103, 2015.

[11] V. Klinshov, L. Lücken, S. Yanchuk, and V. Nekorkin. Multi-jittering instability in oscillatory systems with pulse coupling. In M. Edelman, E. E. N. Macau, and M. A. F. Sanjuan, editors, *Chaotic, Fractional, and Complex Dynamics: New Insights and Perspectives*, pages 261–285. Springer, 2018.

[12] V. Klinshov, L. Lücken, and P. Feketa. On the interpretation of Dirac δ pulses in differential equations for phase oscillators. *Chaos: An Interdisciplinary Journal of Nonlinear Science*, 31(3), 2021.

[13] C. R. Laing. Derivation of a neural field model from a network of theta neurons. *Physical Review E*, 90(1):010901, 2014.

[14] C. R. Laing and B. Krauskopf. Theta neuron subject to delayed feedback: a prototypical model for self-sustained pulsing. *Proc. R. Soc. A*, 478:20220292, 2022.

[15] C. R. Laing and B. Krauskopf. Periodic solutions for a pair of delay-coupled excitable theta neurons. *Submitted to Proc. R. Soc. A*, 2024.

[16] C. R. Laing and A. Longtin. A two-variable model of somatic–dendritic interactions in a bursting neuron. *Bulletin of Mathematical Biology*, 64 (5):829–860, 2002.

[17] P. Li, W. Lin, and K. Efstathiou. Isochronous dynamics in pulse coupled oscillator networks with delay. *Chaos*, 27(5):053103, 2017. doi:10.1063/1.4982794.

[18] M. Monteforte and F. Wolf. Dynamical entropy production in spiking neuron networks in the balanced state. *Physical Review Letters*, 105 (26):268104, 2010.

[19] A. Pikovsky, M. Rosenblum, and J. Kurths. *Synchronization: A universal concept in nonlinear sciences.* Cambridge University Press, 2001.

[20] H. G. Schuster and P. Wagner. Mutual entrainment of two limit cycle oscillators with time delayed coupling. *Progress of Theoretical Physics*, 81(5):939–945, 1989.

[21] H. S. Seung, D. D. Lee, B. Y. Reis, and D. W. Tank. The autapse: a simple illustration of short-term analog memory storage by tuned synaptic feedback. *Journal of Computational Neuroscience*, 9(2):171–185, 2000.

[22] J. Sieber, K. Engelborghs, T. Luzyanina, G. Samaey, and D. Roose. *DDE-BIFTOOL Manual — Bifurcation analysis of delay differential equations.* 2015. arXiv preprint arXiv:1406.7144; available at: `https://sourceforge.net/projects/ddebiftool`.

[23] Y. Song and J. Xu. Inphase and antiphase synchronization in a delay-coupled system with applications to a delay-coupled FitzHugh–Nagumo system. *IEEE Transactions on Neural Networks and Learning Systems*, 23(10):1659–1670, 2012.

[24] M. M. Woodman and C. C. Canavier. Effects of conduction delays on the existence and stability of one to one phase locking between two pulse-coupled oscillators. *Journal of Computational Neuroscience*, 31: 401–418, 2011.

[25] S. Yanchuk and P. Perlikowski. Delay and periodicity. *Physical Review E*, 79(4):046221, 2009.

[26] M. S. Yeung and S. H. Strogatz. Time delay in the Kuramoto model of coupled oscillators. *Physical Review Letters*, 82(3):648, 1999.