

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

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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

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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

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

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

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

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 $d\theta/dt = 2$ [18].)

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

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

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

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

$$\tan(\theta^+ / 2) = \tan(\theta^- / 2) + \tau, \quad (5)$$

where θ^- is the value of θ just before the spike and θ^+ is the value just after.

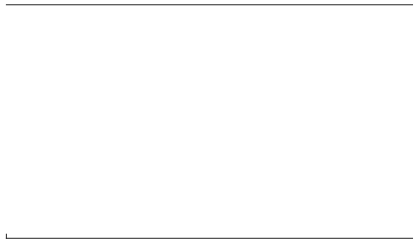


Figure 1: Example periodic solutions of (3)-(4). The top row shows synchronised solutions while the bottom shows alternating solutions. The left column has $\tau = 2$ while the right has $\tau = -1$. All have $\omega = 2$.

3.1 Existence

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

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

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

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

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

$$(\tau, T) = (s + nT(s), T(s)), \quad (8)$$

where $0 \leq s \leq \pi$. 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 reset at time t_0 and neuron 2 last reset at s_0 where $s_0 \leq t_0$. The most distant past reset of neuron 1 in $(t_0 - \pi, t_0)$ is t_{-n} and the most distant past reset of neuron 2 in $(s_0 - \pi, s_0)$ is s_{-n} .

For neuron 1, from t_0 we wait $\pi - (t_0 - s_{-n})$ at which point neuron 1 has its phase incremented due to a reset of neuron 2. Before the reset, ϕ_1^- equals

$$\phi_1^- = \phi_1 + 2(\pi - (t_0 - s_{-n})),$$

and after reset it is ϕ_1^+ where

$$\tan(\phi_1^+ - 2) = \tan(\phi_1^- - 2) + \epsilon.$$

Neuron 1 will then fire after a further time τ_1 where

$$\tau_1 = \frac{\pi - \phi_1^+}{2}.$$

Thus

$$\begin{aligned} t_1 &= t_0 + \pi - (t_0 - s_{-n}) + \tau_1 \\ &= \pi + s_{-n} + \tau_1 - 2 - \tan^{-1}[\epsilon + \tan(\phi_1^- - 2 + \pi - (t_0 - s_{-n}))]. \end{aligned} \quad (9)$$

Similarly for neuron 2, from time s_0 we wait $\pi - (s_0 - t_{-n})$ until neuron 2 has its phase incremented as a result of the reset of neuron 1. Before the reset ϕ_2^- equals

$$\phi_2^- = \phi_2 + 2(\pi - (s_0 - t_{-n})),$$

and after the reset it equals ϕ_2^+ where

$$\tan(\phi_2^+ - 2) = \tan(\phi_2^- - 2) + \epsilon.$$

Neuron 2 will then fire after a further time τ_2 where

$$\tau_2 = \frac{\pi - \phi_2^+}{2}.$$

So

$$\begin{aligned} s_1 &= s_0 + \pi - (s_0 - t_{-n}) + \tau_2 \\ &= \pi + t_{-n} + \tau_2 - 2 - \tan^{-1}[\epsilon + \tan(\phi_2^- - 2 + \pi - (s_0 - t_{-n}))]. \end{aligned} \quad (10)$$

and since $0 < \dots$ the only instability that can occur is when $\dots =$

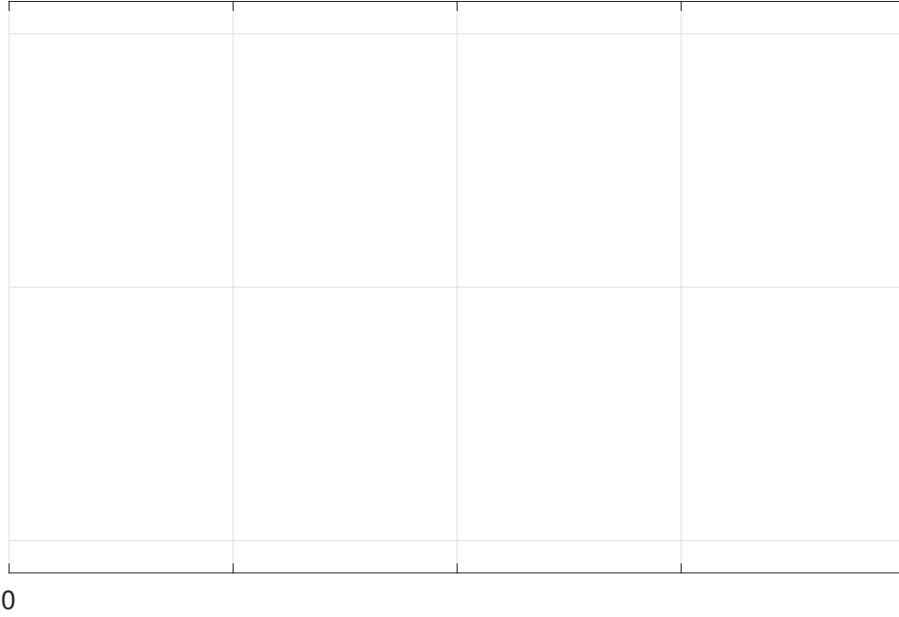


Figure 2: Blue: synchronous periodic solutions (solid stable, dashed unstable). The n th branch goes from (n, \dots) to $((n+1), \dots)$. Red: alternating periodic solutions (solid stable, dashed unstable). The n th branch goes from $((n-1=2), \dots)$ to $((n+1=2), \dots)$. Black: symmetry-broken periodic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

4.2 Stability

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

$$t_{i+1} = \dots + s_{i+1-n} + \dots = 2 - \tan^{-1} [\dots + \tan (\dots = 2 + \dots - (t_i - s_{i+1-n}))] \quad (22)$$

$$s_{i+1} = \dots + t_{i-n} + \dots = 2 - \tan^{-1} [\dots + \tan (\dots = 2 + \dots - (s_i - t_{i-n}))] \quad (23)$$

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

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 ring 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:

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

where

$$\lambda = \frac{\csc^2(\omega - (n-1)T)}{1 + [\cot(\omega - (n-1)T)]^2}. \quad (27)$$

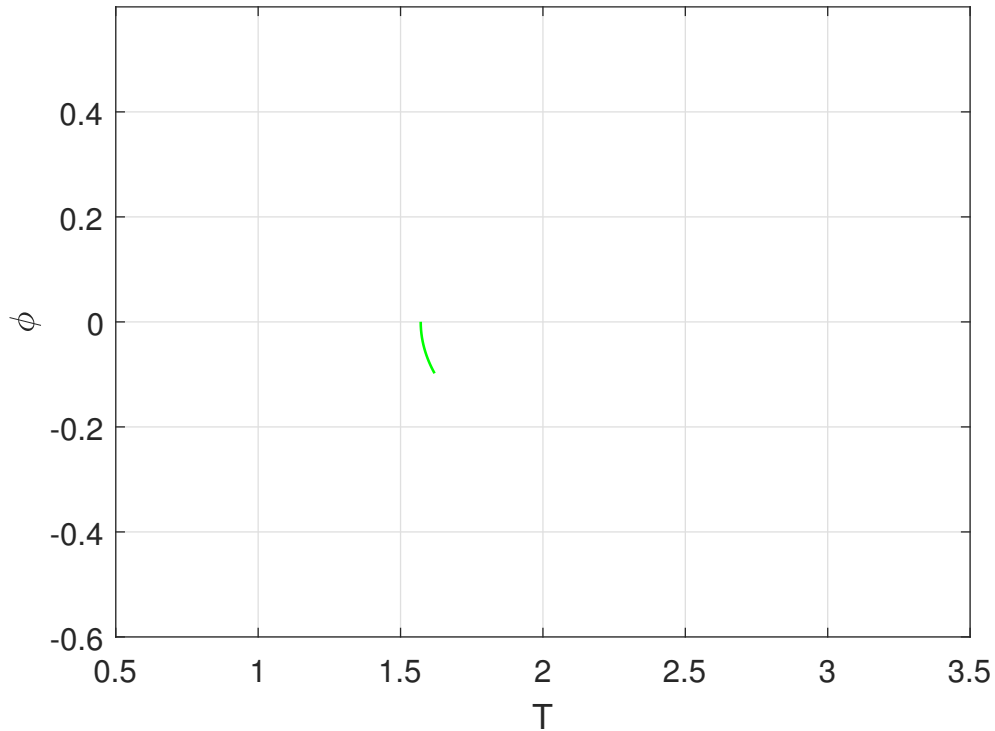


Figure 3: Solutions of (30), describing symmetry-broken solutions, for $\alpha = 4, 2, 1$ (left to right).

of ϕ . When $\alpha = 0$ we have $T = 2 \cot^{-1}(\alpha/2)$. Thus the symmetry-broken solutions lie on the lines $T = 2\alpha/(2n+1)$ where $(2n+1) \cot^{-1}(\alpha/2) \in (\pi/2, \pi)$ 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 $\alpha = 0$ solutions

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

Between firing times the flow is given by $d\phi_1/dt = 2$ and $d\phi_2/dt = 2$.

Assume that ϕ_2 has just reached (i.e., $\phi_2 = \pi$) and $\phi_1 = \alpha$ where $0 < \alpha < \pi$. Both ϕ_1 and ϕ_2 will increase until $\phi_1 = \pi$, which takes a time $\tau_1 = (\pi - \alpha)/\omega$, at which point $\phi_2 = 2\pi - \alpha$. The phase ϕ_2 is then incremented to $\phi_2^+ = 2\pi - \alpha + 2\pi = 4\pi - \alpha$. Both phases then continue to increase until $\phi_2 = \pi$, which takes a further time $\tau_2 = (\pi - \phi_2^+)/\omega = (\pi - (4\pi - \alpha))/\omega = (\alpha - 3\pi)/\omega$, at which point $\phi_1 = \pi + 2\tau_2\omega = \pi + 2(\alpha - 3\pi) = 2\alpha - 5\pi$. The phase ϕ_1 is then incremented to $\phi_1^+ = 2\pi + 2\alpha - 5\pi = 2\alpha - 3\pi$. For this process to describe a periodic solution we need $\phi_1^+ = \alpha$, 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 $T = \tau_1 + \tau_2$ and so we can write $\phi_1 = (1 + 2\tau_2/T)T$ and $\phi_2 = (1 - 2\tau_2/T)T$ for some $-1/2 < \tau_2/T < 1/2$, where $\tau_2/T = 0$ corresponds to the symmetric alternating solution. We find that $\cot(\phi_1) = \tan(\pi - 2\tau_2\omega)$ and $\cot(\phi_2) = -\tan(\pi - 2\tau_2\omega)$ and thus $\cot(\phi_2) = -\cot(\phi_1)$, or

$$\cot((1 - 2\tau_2/T)T) = -\cot((1 + 2\tau_2/T)T), \quad (31)$$

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

5.2.2 $\omega > 0$ solutions

The solutions in the previous section exist for $\omega = 0$. The solutions in the previous section exist for

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

$$\frac{d\theta_1}{dt} = 1 - \cos\theta_1 + (1 + \cos\theta_1)f_1 + P[\theta_2(t - \tau)]g \quad (32)$$

$$\frac{d\theta_2}{dt} = 1 - \cos\theta_2 + (1 + \cos\theta_2)f_1 + P[\theta_1(t - \tau)]g, \quad (33)$$

where

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

with $a_m = 2^m(m!)^2/(2m)!$

Figure 4: Periodic solutions of (32)-(33). Blue: synchronous solutions; red:

Competing Interests: the author declares no competing interests.

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