PHASE OSCILLATOR NETWORK MODELS OF BRAIN DYNAMICS

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ABSTRACT. Networks of periodically firing neurons can be modelled as networks of coupled phase oscillators, each oscillator being described by a single angular variable. Networks of two types of neural phase oscillators are analysed here: the theta neuron and the Winfree oscillator. By taking the limit of an infinite number of neurons and using the Ott/Antonsen ansatz, we derive and then numerically analyse "neural field" type differential equations which govern the evolution of macroscopic order parameter-like quantities. The mathematical framework presented here allows one efficiently simulate such networks, and to investigate the effects of changing the structure of a network of neurons, or the parameters of such networks.

1. INTRODUCTION

It is well established that a single neuron can fire a periodic train of action potentials when given a constant stimulus [3, 19, 21] and thus, under some circumstances, be regarded as an oscillator. Neurons are coupled in networks, so in order to understand neural systems (of which the largest is a complete brain) it is of interest to study coupled networks of oscillators. Such oscillators are idealisations of single neurons, and their connections only approximate the myriad of dynamic processes going on in an actual neural network, but by studying simplified models we hope to gain some understanding of real systems.

One simplification often made when studying networks of oscillators is to represent the state of an oscillator by a single angular variable, its phase. The phase is a periodic variable and increases by 2π during each period of oscillation. Such a simplification can drastically reduce the number of variables needed to describe the state of oscillator (since only one is now needed) and a principled reduction of a general network of oscillators to a network of coupled phase oscillators can be performed in some circumstances [44, 19, 3].

In this chapter we consider networks of two types of neural phase oscillators, namely the theta neuron and the Winfree oscillator. The theta neuron is perhaps better known, as it is the canonical model for a Type I neuron [23], but the Winfree oscillator has a long history [58]. Both types of phase oscillator are of a particular form which makes them amenable to the use of the Ott/Antonsen ansatz [47, 46]. This ansatz can be used to simplify the dynamics of an infinite number of coupled, heterogeneous phase oscillators. Given the extremely large number of neurons in the brain (or in any significant part of it), we expect the behaviour of infinite networks to closely match that of large but finite

ones. The study of oscillations in neuroscience is a large topic [55, 56, 20, 10, 54] and we point the interested reader to a recent comprehensive review [3].

We consider theta neurons in Sec. 2 and Winfree oscillators in Sec. 3. Some of the analysis and results have been presented elsewhere (particularly in [37, 35, 49, 39]) but some results are new, and the possible dynamics of the networks presented here are by no means completely known.

2. Theta neurons

2.1. **Model network.** The theta neuron is the canonical model for a Type I neuron for which the onset of firing is through a saddle-node on an invariant circle bifurcation [15, 18]. It can be derived by a nonlinear coordinate transformation from the quadratic integrate-and-fire neuron model [37, 14]. A theta neuron receiving an input current $I(t)$ satisfies

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

where $\theta \in [0, 2\pi)$. If $I(t)$ is constant and less than zero, (1) has two equilibria, $\theta_\pm = \pm\cos^{-1}[(I+1)/(1-I)]$, and θ_- is stable and θ_+ is unstable. If I is constant and greater than zero, θ increases motonically with time. Treating θ as a periodic variable, as we will do from now on, it then has period $\pi/\sqrt{I}$. When θ increases through π the neuron is said to "fire", i.e. produce an action potential.

If a theta neuron is part of a network, its current input $I(t)$ will generally be time-dependent, and result from the dynamics of the neurons which are connected to it. For simplicity we start with a fully-connected network of N neurons, where each neuron is synaptically connected to each other one with the same strength g. Thus the network is described by

$$(2) \qquad \frac{d\theta_j}{dt} = 1 - \cos\theta_j + (1 + \cos\theta_j)(I_j + g\bar{s}); \qquad j = 1, 2 \ldots N$$

where

$$(3) \qquad \bar{s} = \frac{1}{N}\sum_{k=1}^{N} s_k$$

and each s_k satisfies the equation

$$(4) \qquad \tau\frac{ds_k}{dt} = a_n(1 - \cos\theta_k)^n - s_k; \qquad n \in \mathbb{N}^+$$

and a_n is chosen so that

$$(5) \qquad \int_0^{2\pi} a_n(1 - \cos\theta)^n d\theta = 2\pi$$

i.e. $a_n = 2^n(n!)^2/(2n)!$. The function $a_n(1 - \cos\theta)^n$ mimics the action potential created as θ passes through π; it is plotted for $n = 2$ and 10 in Fig. 1. This function then drives s_k on the synaptic timescale of τ, contributing to the input current $\bar{s}$ which is the mean of the s_k. I_j is the constant input current to neuron j in the absence of any other input
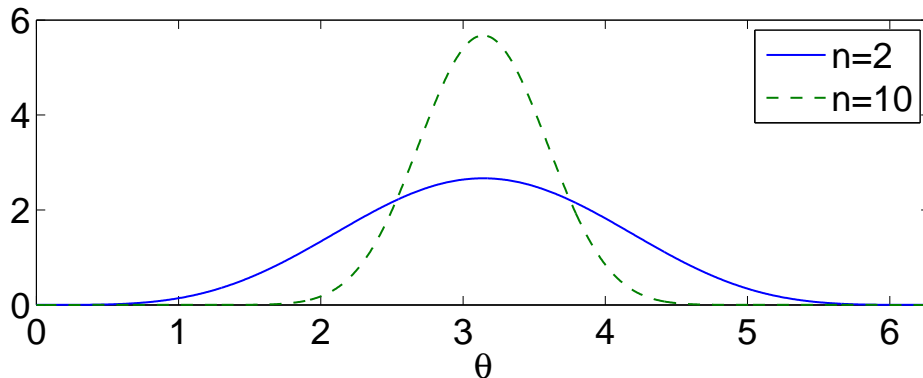
FIGURE 1. The function $a_n(1 - \cos\theta)^n$ for $n = 2$ (solid) and $n = 10$ (dashed).

and is randomly chosen from a distribution $h(I)$ to be specified below. Note that if $g > 0$ the synaptic connections are excitatory, whereas if $g < 0$ they are inhibitory. The case of $\tau = 0$ was studied by [39]. They found that for some parameter regimes, the system can exhibit bistability between two "macroscopic" steady states (where the average activity of the network is approximately constant) and also between a macroscopic steady state and macroscopic oscillations, in which the average activity varies periodically.

Rather than investigate the network (2), (4) directly we pass to the continuum limit, letting $N \to \infty$, in the expectation that analysis of this case will provide insights into the dynamics of large but finite networks. The system is then described by a probability density function $F(I, \theta, t)$ which satisfies [45, 53, 1]

$$(6) \qquad \frac{\partial F}{\partial t} + \frac{\partial}{\partial \theta}(Fv) = 0$$

where

$$(7) \qquad v(I, \theta, t) \equiv 1 - \cos\theta + (1 + \cos\theta)(I + gS(t)),$$

where $S(t)$ satisfies

$$(8) \qquad \tau \frac{dS}{dt} = \int_{-\infty}^{\infty} \int_0^{2\pi} F(I, \theta, t) a_n (1 - \cos\theta)^n \, d\theta \, dI - S.$$

(Note that S is real.) The form of (7) means that (6) is amenable to the use of the Ott/Antonsen ansatz [47, 46], and thus we write

$$(9) \qquad F(I, \theta, t) = \frac{h(I)}{2\pi} \left\{ 1 + \sum_{j=1}^{\infty} [\alpha(I, t)]^j e^{ji\theta} + \text{c.c.} \right\}$$

for some function α, where "c.c." means the complex conjugate of the previous term. In (9) we have expanded the θ dependence of F in a Fourier series, but of a particular form: one in which the jth coefficient is not arbitrary, but is some function, α, to the jth power. Ott and Antonsen [47, 46] showed that solutions of (6), where v is of a particular form, exponentially decay to a state described by (9) provided the oscillators are not

identical. Thus we can determine the asymptotic dynamics of (6) by assuming that F is given by (9). It is helpful to introduce the complex order parameter, as considered by Kuramoto in the context of coupled phase oscillators [30, 53]

$$(10) \qquad z(t) \equiv \int_{-\infty}^{\infty} \int_{0}^{2\pi} F(I, \theta, t) e^{i\theta} \, d\theta \, dI.$$

The quantity z can be thought of as the expected value of $e^{i\theta}$. Substituting the ansatz (9) into (10) and integrating over θ we have

$$(11) \qquad z(t) = \int_{-\infty}^{\infty} h(I)\bar{\alpha}(I, t) \, dI$$

where overbar indicates complex conjugate. If $h(I)$ is the Lorentzian centered at $I = I_0$, with width Δ, i.e.

$$(12) \qquad h(I) = \frac{\Delta/\pi}{(I - I_0)^2 + \Delta^2}$$

then contour integration can be used to evaluate the integral in (11) to obtain $z(t) = \bar{\alpha}(I_0 + i\Delta, t)$ [46]. The parameter Δ gives the level of heterogeneity of the neurons, and if $I_0 < 0$ most neurons are quiescent with no input whereas if $I_0 > 0$ most neurons periodically fire in the absence of input. Substituting (9) into (8) and performing both integrals we find [52, 35] that S satisfies

$$(13) \qquad \tau\frac{dS}{dt} = H(z(t); n) - S$$

where

$$(14) \qquad H(z; n) = a_n \left[C_0 + \sum_{j=1}^{n} C_j(z^j + \bar{z}^j) \right]$$

and

$$(15) \qquad C_j = \sum_{k=0}^{n} \sum_{m=0}^{k} \frac{n!(-1)^k \delta_{k-2m,j}}{2^k(n-k)!m!(k-m)!}$$

It can be shown that for impulsive coupling, i.e. $n \to \infty$, $H(z; \infty) = (1-|z|^2)/(1+z+\bar{z}+|z|^2)$. We will set $n = 2$ in all following calculations, giving $a_2 = 2/3, C_0 = 3/2, C_1 = -1$ and $C_2 = 1/4$. Substituting (9) into (6) we find that α satisfies

$$(16) \qquad \frac{\partial \alpha}{\partial t} = -i\left[\frac{I + gS - 1}{2} + (1 + I + gS)\alpha + \left(\frac{I + gS - 1}{2}\right)\alpha^2 \right]$$

and evaluating this at $I = I_0 + i\Delta$ we obtain

$$(17) \qquad \frac{dz}{dt} = \frac{(iI_0 - \Delta)(1 + z)^2 - i(1 - z)^2}{2} + \frac{ig(1 + z)^2 S}{2}$$

The first term in (17) describes the dynamics of the uncoupled network, and the second, the influence of synaptic coupling. Equations (17) and (13) form a complete description

of the infinite network. This pair of equations was studied with $\tau = 0$, i.e. instantaneous synapses, by [39]. For a physical interpretation of $z \in \mathbb{C}$, write $z(t) = r(t)e^{i\psi(t)}$. Integrating (9) over I we obtain the probability density function

$$(18) \qquad p(\theta, t) = \frac{1 - r^2(t)}{2\pi\{1 - 2r(t)\cos[\theta - \psi(t)] + r^2(t)\}}$$

which is a unimodal function of θ with maximum at $\theta = \psi$, and whose sharpness is governed by the value of r [35, 34]. Alternatively, we follow [42] and define

$$(19) \qquad w \equiv \frac{1 - \bar{z}}{1 + \bar{z}} = \frac{1 + 2ir\sin\psi - r^2}{1 + 2r\cos\psi + r^2}.$$

In the continuum limit, the firing rate of (2), f, is equal to the flux through $\theta = \pi$, i.e.

$$(20) \qquad f = v(I, \pi, t)p(\pi, t) = \frac{\text{Re}(w)}{\pi}.$$

Writing (17) in terms of w we obtain

$$(21) \qquad \frac{dw}{dt} = iI_0 + \Delta - iw^2 + igS$$

where S can be determined as a function of w by writing $z = (1 - \bar{w})/(1 + \bar{w})$.

2.2. **Results.** We now show some of the types of behavior exhibited by the system (17) and (13) and its generalisations.

2.2.1. *Oscillations with inhibitory coupling.* Suppose we set $I_0 = 1$ (i.e. most neurons fire when uncoupled) and decrease g from zero, i.e. increase the strength of inhibitory coupling. Doing so we obtain Fig. 2. For g close to zero only one steady state exists, which is stable. As g is decreased this becomes unstable through a Hopf bifurcation which appears to be supercritical. Decreasing g further the periodic orbit created in the Hopf bifurcation is destroyed in a saddle-node-on-an-invariant-circle bifurcation, and a pair of fixed points (one stable and one unstable) are created. As a verification of the results of the continuum analysis, Fig. 3 shows behaviour of the original network of theta neurons (2)-(4) at three different values of g. S was measured for each of these simulations and the corresponding values are plotted in Fig. 2 (stars).

2.2.2. *Two populations.* Suppose now that we have two populations, one excitatory and one inhibitory, projecting to one another but with no within-population connections. (Slightly different but similar networks were proposed and studied by [40, 42].) Suppose that the intrinsic currents are randomly chosen from Lorentzian distributions each with width Δ, but means I_i (inhibitory population) and I_e (excitatory population). Taking the limit as the number of neurons in each population becomes infinite, as above, we
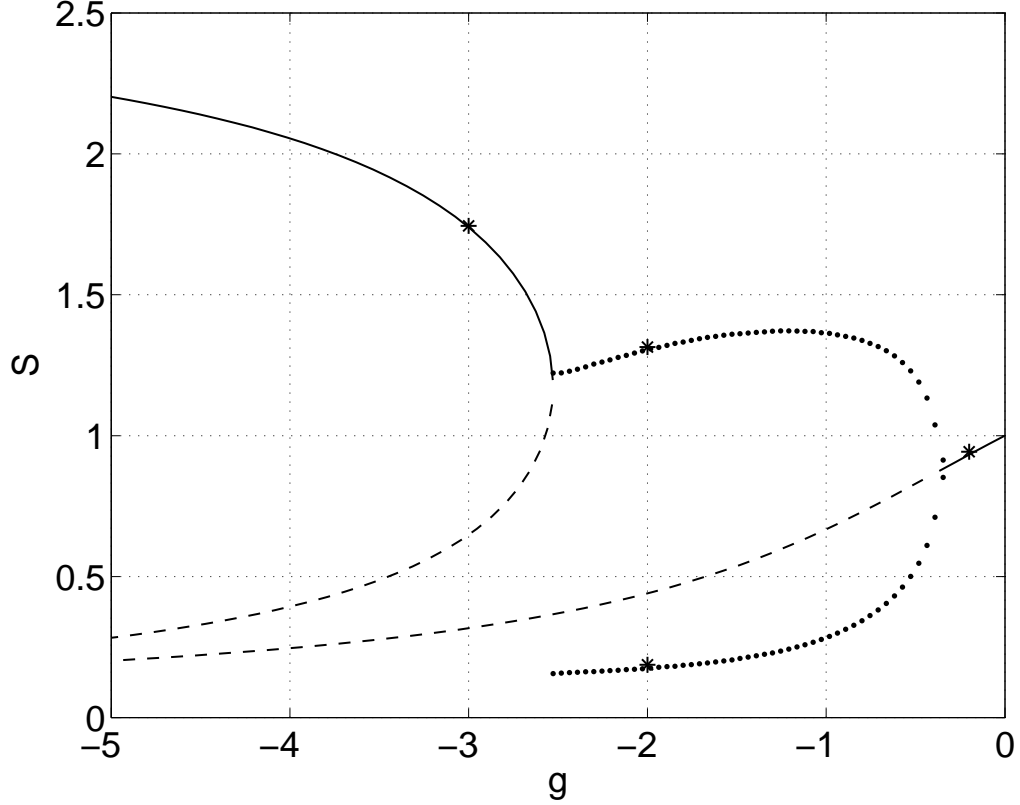
FIGURE 2. S at steady state of (17) and (13) (solid lines, stable; dashed lines: unstable). Dots show maximum and minimum values of S over one period of oscillation when no steady states are stable. Stars show values measured from the simulations in Fig. 3. Parameters: $I_0 = 1, \Delta = 0.05, \tau = 1$.

obtain

$$(22) \qquad \frac{dz_e}{dt} = \frac{(iI_e - \Delta)(1 + z_e)^2 - i(1 - z_e)^2}{2} - \frac{ig_i(1 + z_e)^2 S_i}{2}$$

$$(23) \qquad \tau_e \frac{dS_e}{dt} = H(z_e; n) - S_e$$

$$(24) \qquad \frac{dz_i}{dt} = \frac{(iI_i - \Delta)(1 + z_i)^2 - i(1 - z_i)^2}{2} + \frac{ig_e(1 + z_i)^2 S_e}{2}$$

$$(25) \qquad \tau_i \frac{dS_i}{dt} = H(z_i; n) - S_i$$

where $z_{e/i}$ is the order parameter for the excitatory/inhibitory population and $g_e, g_i \geq 0$. Typical periodic behaviour of such a coupled system is shown in Fig. 4 where we show the instantaneous firing rate as calculated using (19), (20). This rhythm is referred to as the "PING rhythm" [4, 5]. Note that for the parameters chosen, the inhibitory population only fires a volley of action potentials (i.e. a "spike" in frequency) as a result of input from the excitatory population. The authors [4, 5] describe a number of ways
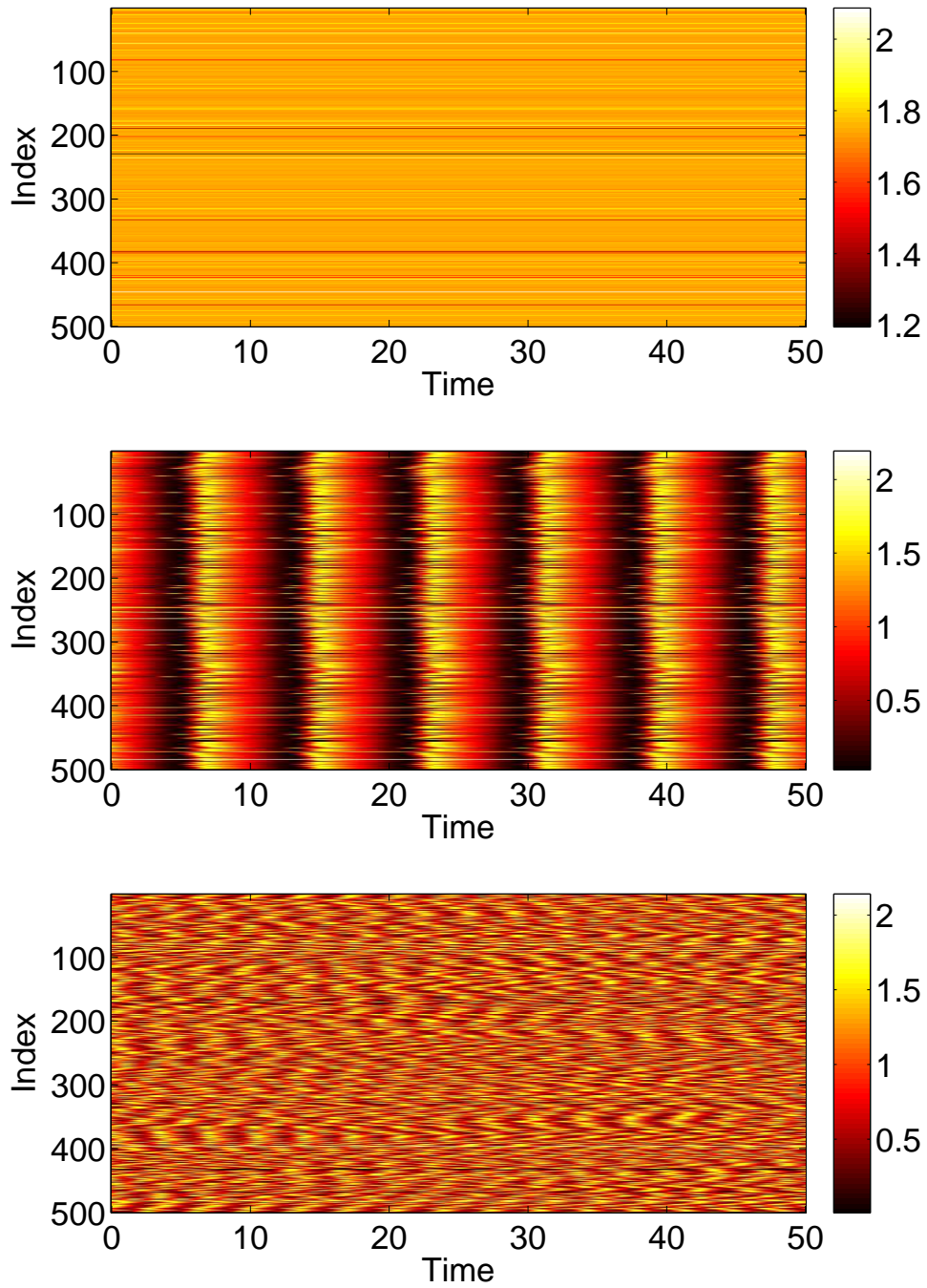
FIGURE 3. Simulations of (2)-(4) at three different values of g. The s_k are shown colour-coded. $g = -3$ (top); $g = -2$ (middle) and $g = -0.2$ (bottom). S was measured for each simulation and average values over the simulation (or maximum and minimum over one oscillation in the case of $g = -2$) are show in Fig. 2. Parameters: $N = 500, I_0 = 1, \Delta = 0.05, \tau = 1$.
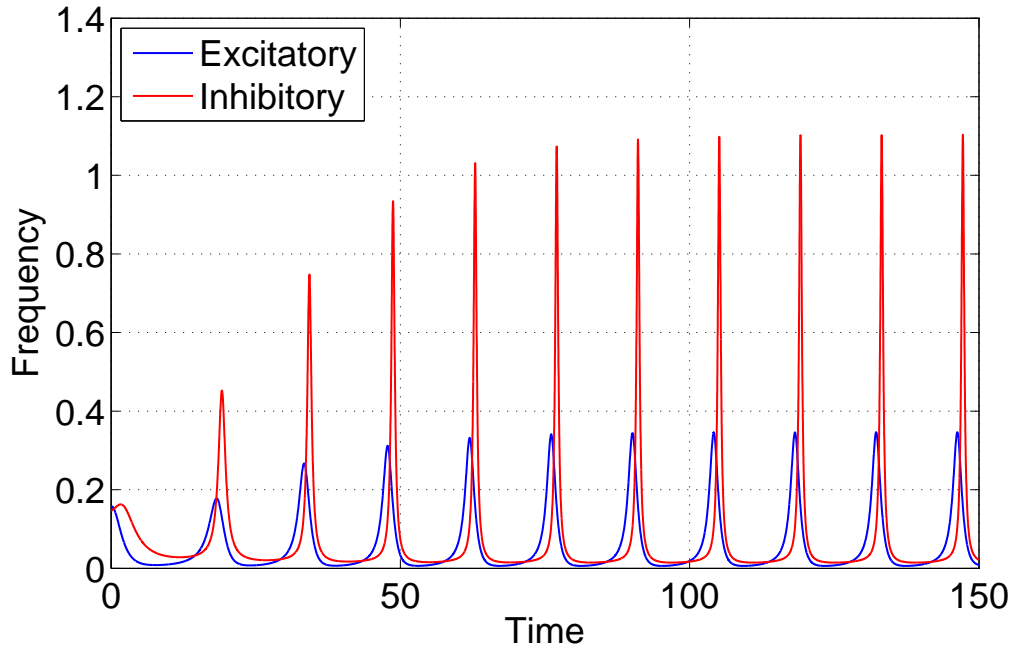
FIGURE 4. PING rhythm generated by (22)-(25). Parameters: $I_i = 0, I_e = 0.1, g_e = 0.4, g_i = 0.4, \Delta = 0.01, \tau_e = 0.2, \tau_i = 1, n = 2$.

in which the PING rhythm can be destroyed and we now demonstrate several of them and show that these scenarios can be understood in terms of generic bifurcations of the differential equations (22)-(25).

- In the first scenario the excitatory to inhibitory synapses become too weak, i.e. g_e is decreased. The corresponding bifurcation diagram is shown in Fig. 5. We see that the periodic behaviour is destroyed in a supercritical Hopf bifurcation as g_e is decreased.

- In the second scenario the inhibitory to excitatory synapses become too weak, i.e. g_i is decreased. The corresponding bifurcation diagram is shown in Fig. 6 where we show just the excitatory population for simplicity. The periodic behaviour is destroyed in a saddle-node bifurcation of periodic orbits as g_i is decreased, but there is also a supercritical Hopf bifurcation and a second saddle-node bifurcation of periodic orbits which destroys the periodic orbit created in the Hopf bifurcation. Note that there is a small range of parameters over which there is bistability between the PING rhythm and a steady state (as observed by [5]) to the left of the Hopf bifurcation, and an even smaller window over which there is bistability between two PING rhythms (just to the right of the Hopf bifurcation). This type of fine detail, found using numerical continuation [36], is unlikely to be found using purely numerical simulations of (22)-(25).

- In the third scenario there is too much drive to i cells, i.e. I_i is increased. The corresponding bifurcation diagram is shown in Fig. 7 where we see a supercritical
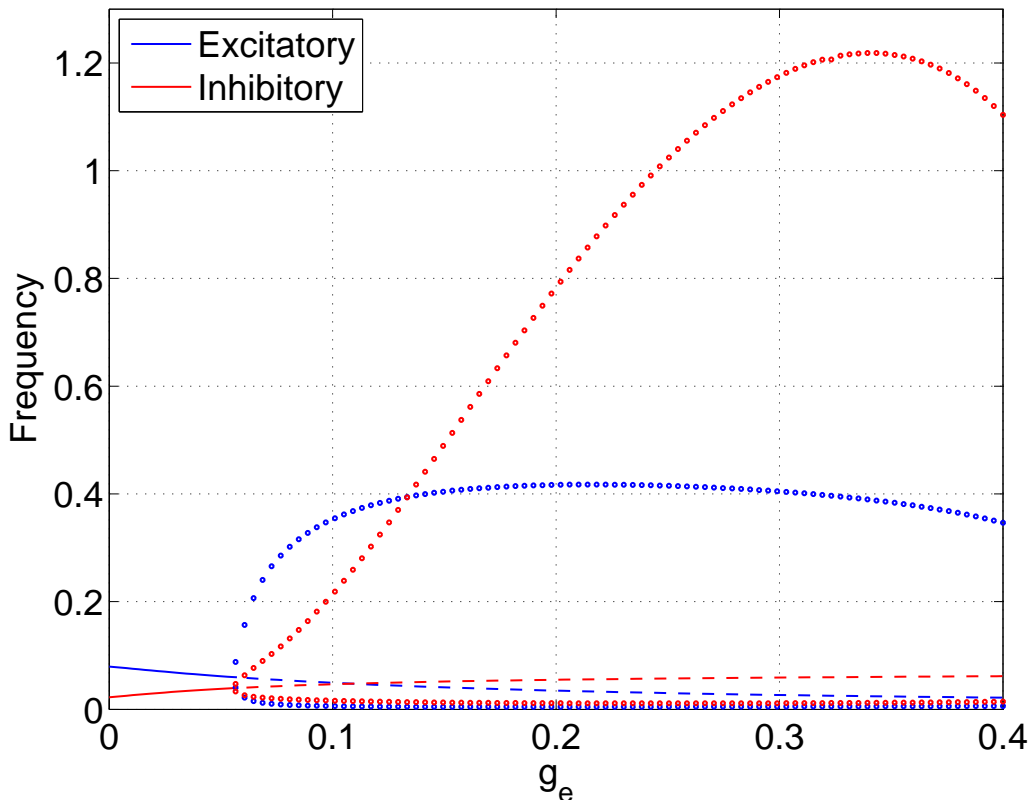
FIGURE 5. Behaviour of (22)-(25) as g_e is varied. Solid lines, stable; dashed lines: unstable. Circles show maximum and minimum values of f over one period of oscillation when no steady states are stable. Parameters: $I_i = 0, I_e = 0.1, g_i = 0.4, \Delta = 0.01, \tau_e = 0.2, \tau_i = 1, n = 2$.

Hopf bifurcation occurring as I_i is increased, leading to the cessation of the PING rhythm.

2.2.3. *Spatially extended networks.* Of course, realistic networks of neurons are not all-to-all coupled, as above, but rather have some spatial extent. Suppose we have N neurons equally-spaced on a one-dimensional domain of length L. Then we replace (2) by

$$(26) \qquad \frac{d\theta_j}{dt} = 1 - \cos\theta_j + (1 + \cos\theta_j)(I_j + gs_j); \qquad j = 1, 2 \ldots N$$

and each s_j satisfies the equation

$$(27) \qquad \tau \frac{ds_j}{dt} = \frac{a_n L}{N} \sum_{k=1}^{N} w_{jk}(1 - \cos\theta_k)^n - s_j; \qquad n \in \mathbb{N}^+$$

and w_{jk} is the strength of synapse from neuron k to neuron j. (Here we assume that all synapses have the same dynamics.) We will assume that $w_{jk} = w(|j - k|\Delta x)$ for some coupling function w, where $\Delta x = L/N$, i.e. the strength of connection between neurons
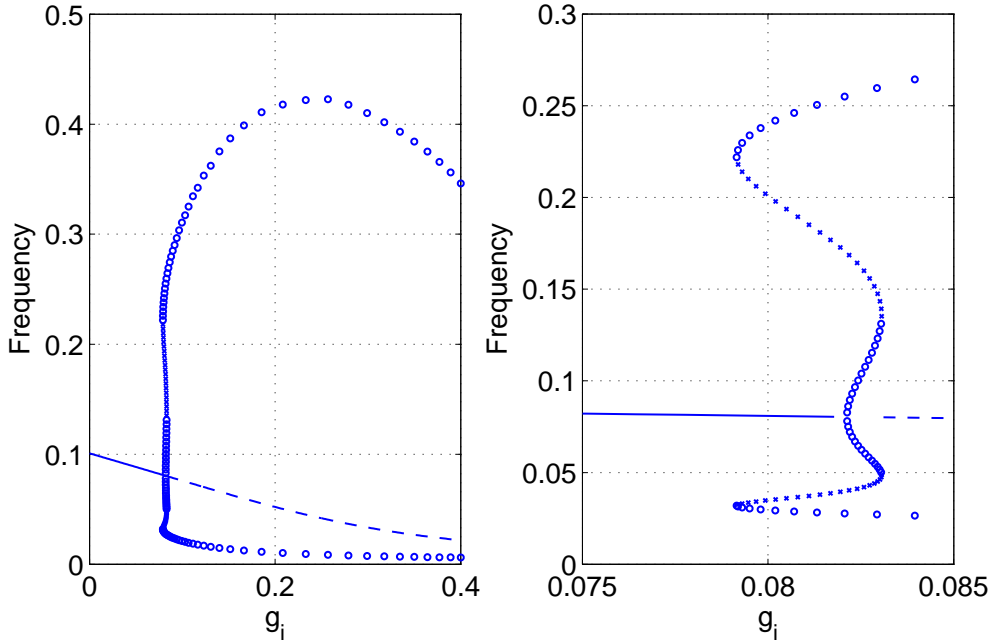
FIGURE 6. Behaviour of (22)-(25) as g_i is varied. Solid lines, stable; dashed lines: unstable. Circles (crosses) show maximum and minimum values of f over one period of stable (unstable) oscillation for the excitatory population. The right panel is a zoom of the left one. Parameters: $I_i = 0, I_e = 0.1, g_e = 0.4, \Delta = 0.01, \tau_e = 0.2, \tau_i = 1, n = 2$.

depends only on the distance between them. Taking the limit $N \to \infty$ as above and performing similar manipulations (or see [37, 35]), one obtains a spatially-dependent order parameter $z(x, t)$ which satisfies

$$(28) \qquad \frac{\partial z}{\partial t} = \frac{(iI_0 - \Delta)(1 + z)^2 - i(1 - z)^2}{2} + \frac{ig(1 + z)^2 S}{2}$$

where

$$(29) \qquad \tau \frac{\partial S(x, t)}{\partial t} = \int_0^L w(x - y)H(z(y, t); n) \, dy - S(x, t)$$

Equations (28), (29) are a "neural field" model — integro-differential equations governing the dynamics of several macroscopic variables. Unlike classical neural field models [6, 22], however, (28), (29) are derived directly from a network of spiking model neurons [35]. If $w(x)$ is of "Mexican-hat" shape, i.e. positive for small x and negative for large x, (28), (29) is known to support "bump" solutions, for which the region of active neurons is spatially localised [35]. Such solutions have been studied in the past due to their presumed role in working memory [38, 22, 6, 13], and an example is shown in Fig. 8, where periodic boundary conditions in space are used.

For these parameter values, the all-off state, in which there is no spatial structure and the firing rate is very low, is also stable. The system is thus bistable, with one attractor
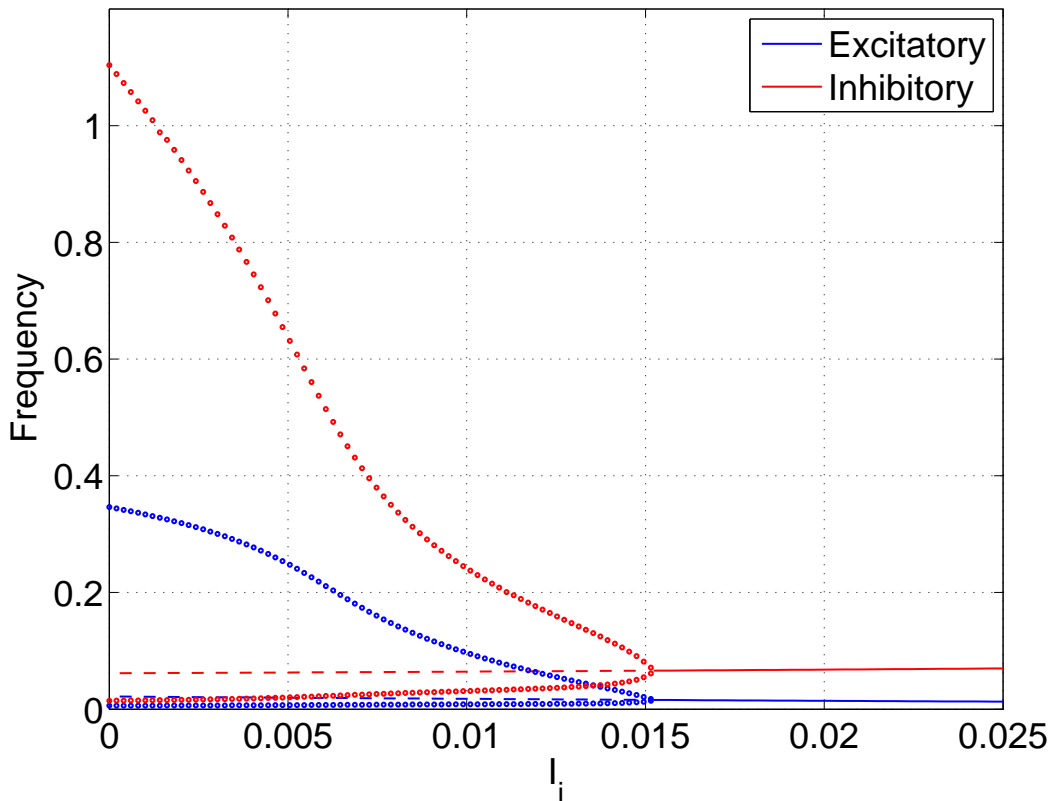
FIGURE 7. Behaviour of (22)-(25) as I_i is varied. Solid lines, stable; dashed lines: unstable. Circles show maximum and minimum values of f over one period of oscillation when no steady states are stable. Parameters: $I_e = 0.1, g_e = 0.4, g_i = 0.4, \Delta = 0.01, \tau_e = 0.2, \tau_i = 1, n = 2$.

being a bump state which, due to the translationally invariant nature of the system, can be centred anywhere in the domain. In a network of spiking neurons Gutkin et al. [24] showed that the network could be switched from a bump state to the all-off state using a transient excitatory pulse which causes most neurons to fire simultaneously. (A transient inhibitory pulse will also be effective, but that is less surprising.) Even though the description (28), (29) no longer contains information about individual action potentials, the instantaneous firing rate can be calculated using (19), (20). The result of applying a transient excitatory stimulus to the bump in Fig. 8 is shown in Fig. 9. The stimulus causes most neurons to fire simultaneously (twice, in this case) as shown by the rapid increase in instantaneous frequency, which disrupts the bump, causing the network to move to the all-off state.

One could also study the two-dimensional version of (28), (29) which may support more interesting patterns such as spiral waves [32, 26] or bumps and rings which undergo instabilities in the angular direction [48, 28, 7].
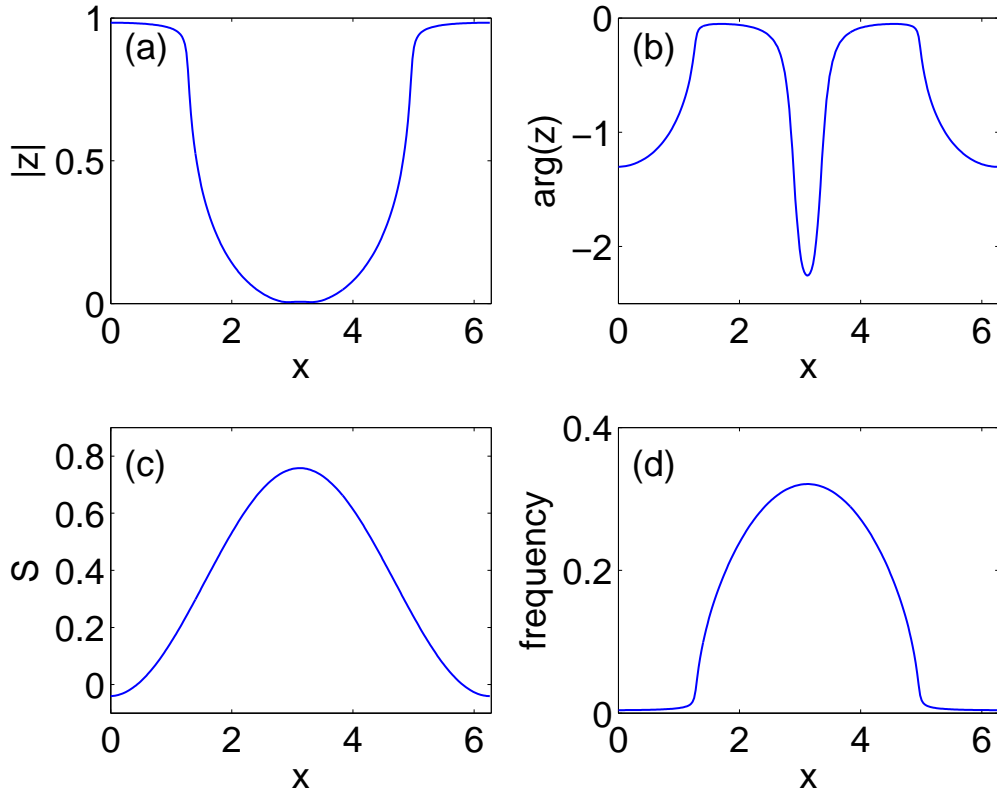
FIGURE 8. Stable stationary bump solution of (28), (29). (a): $|z|$; (b): $\arg(z)$; (c): S; (d): frequency profile of bump, calculated using (19), (20). Coupling function is $w(x) = 0.1 + 0.3\cos x$. Parameters: $L = 2\pi, I_0 = -0.5, g = 2, \Delta = 0.02, \tau = 0.5, n = 2$.

2.2.4. *Gap junctions.* Here we have modelled only synaptic connections between neurons, governed by the variables s_k. However, the other major form of connection between neurons is through gap junctions [11]. These are typically modelled by stating that if two neurons are connected by a gap junction, a current proportional to the difference between their voltages flows between the two neurons, from high voltage to low. Using the fact that a theta neuron is equivalent to a quadratic integrate-and-fire neuron, Laing [37] showed how to generalise the analysis in Sec. 2.1 to include gap junction coupling. The net effect, for an all-to-all coupled network, is to replace (2) by

$$(30) \quad \frac{d\theta_j}{dt} = 1 - \cos\theta_j - \kappa\sin\theta_j + (1 + \cos\theta_j)\left(I_j + \frac{\kappa}{N}\sum_{k=1}^{N} q(\theta_k) + g\bar{s}\right); \qquad j = 1, 2 \ldots N$$

where κ is the gap junction coupling strength and

$$(31) \qquad\qquad\qquad q(\theta) = \frac{\sin\theta}{1 + \cos\theta + \epsilon}$$
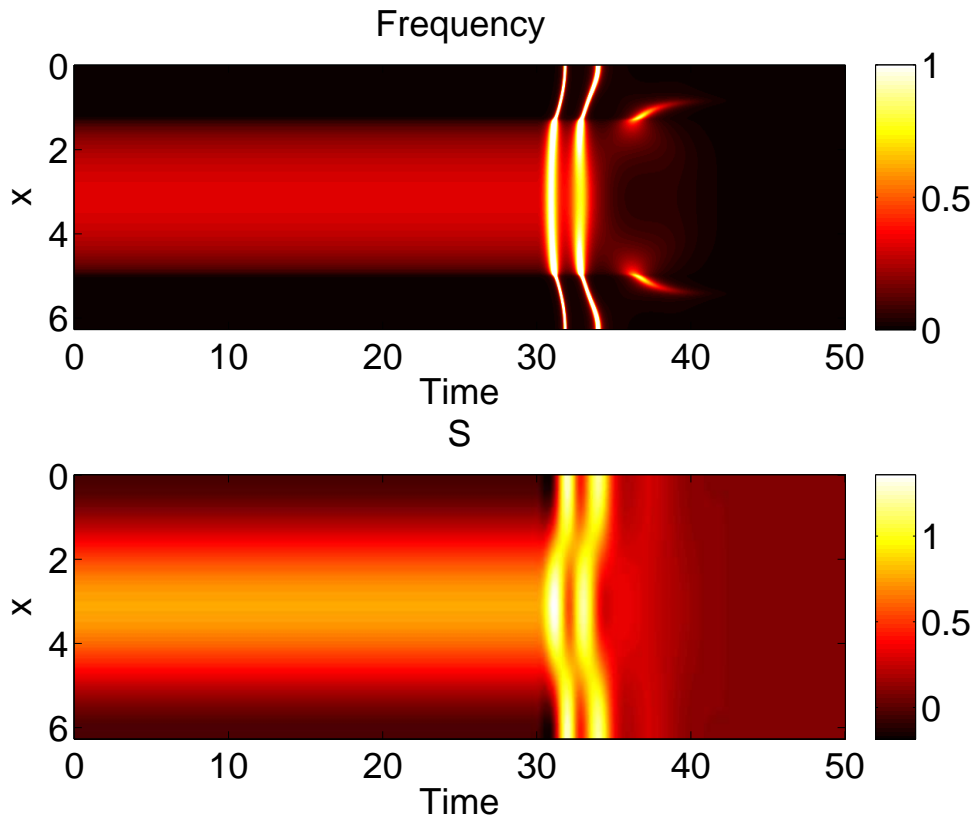
FIGURE 9. $I_0 = -0.5$ except for $30 \leq t \leq 33$, when it is equal to 1.5. Top: instantaneous frequency (the maximum is truncated); bottom: S. Coupling function is $w(x) = 0.1 + 0.3 \cos x$ and periodic boundary conditions are used. Parameters as in Fig. 8.

where $0 \leq \epsilon \ll 1$. Performing similar manipulations as in Sec. 2.1 one obtains, instead of (17),

$$(32) \qquad \frac{dz}{dt} = \frac{(iI_0 - \Delta)(1+z)^2 - i(1-z)^2}{2} + \frac{i(1+z)^2(gS + \kappa Q) + \kappa(1-z^2)}{2}$$

where

$$(33) \qquad Q = \sum_{m=1}^{\infty} b_m z^m + \text{c.c.}$$

and

$$(34) \qquad b_m = \frac{i(\rho^{m+1} - \rho^{m-1})}{2\sqrt{2\epsilon + \epsilon^2}}$$

where $\rho \equiv \sqrt{2\epsilon + \epsilon^2} - 1 - \epsilon$. We still obtain a single differential equation for z, (32), but the addition of the terms describing the gap junction coupling was shown to induce a variety of different behaviours [37]. For example, in both spatially-structured and unstructured networks, including gap junctions was found to induce macroscopic oscillations in z via Hopf bifurcations. Also, in a spatially extended network with purely

excitatory synaptic coupling, the addition of gap junction coupling of sufficient strength allowed travelling waves to exist.

3. Winfree oscillators

3.1. **Model Network.** We consider a modification of the Winfree model [58] of N all-to-all coupled oscillators with dynamic synapses. The model is written

$$(35) \qquad \frac{d\theta_i}{dt} = \omega_i + \epsilon \frac{Q(\theta_i)}{N} \sum_{j=1}^{N} R_j$$

$$(36) \qquad \tau \frac{dR_i}{dt} = P(\theta_i) - R_i$$

for $i = 1, 2 \ldots N$ where ω_i is the intrinsic frequency of oscillator i, chosen from the distribution $h(\omega)$, ϵ is the coupling strength, Q is the phase response curve of an oscillator, which can be measured experimentally or determined from a model neuron [51] and $P(\theta)$ is the pulsatile signal sent by a neuron whose state is θ. When $\tau = 0$ we recover the usual Winfree model [2, 49]. We will analyse the continuum limit of (35)-(36) in similar way to that of [49].

We choose

$$(37) \qquad Q(\theta) = \frac{\sin \beta - \sin (\theta + \beta)}{\sqrt{\pi(2 - \cos (2\beta))}}$$

which satisfies $Q(0) = 0$ and which has an L^2 norm of 1 [17]. Varying β from 0 to $\pi/2$ changes Q from that corresponding to a Hopf bifurcation to that corresponding to a saddle-node-on-a-circle bifurcation, respectively [15, 8]. For this model a neuron is said to fire when θ increases through zero, and thus we choose

$$(38) \qquad P(\theta) = a_n(1 + \cos \theta)^n$$

where, as in Sec. 2.1, $a_n = 2^n(n!)^2/(2n)!$ so that the integral of P is independent of n. We move to the continuum limit and analyse the network (35)-(36) in a similar way to that done in Sec. 2.1. The system is described by a probability density function $F(\omega, \theta, t)$ which satisfies the continuity equation (6) where now

$$(39) \qquad v(\omega, \theta, t) \equiv \omega + \epsilon Q(\theta) R(t),$$

where $R(t)$ satisfies

$$(40) \qquad \tau \frac{dR}{dt} = \int_{-\infty}^{\infty} \int_{0}^{2\pi} F(\omega, \theta, t) a_n(1 + \cos \theta)^n \ d\theta \ d\omega - R.$$

As above, we write

$$(41) \qquad F(\omega, \theta, t) = \frac{h(\omega)}{2\pi} \left\{ 1 + \sum_{j=1}^{\infty} [\alpha(\omega, t)]^j e^{ji\theta} + \text{c.c.} \right\}$$

and have

$$(42) \qquad z(t) \equiv \int_{-\infty}^{\infty} \int_{0}^{2\pi} F(\omega, \theta, t) e^{i\theta} \, d\theta \, d\omega.$$

Substituting (41) into (42) we have

$$(43) \qquad z(t) = \int_{-\infty}^{\infty} h(\omega) \bar{\alpha}(\omega, t) \, d\omega$$

If $h(\omega)$ is the Lorentzian centered at $\omega = \omega_0$ with width Δ, then we obtain $z(t) = \bar{\alpha}(\omega_0 + i\Delta, t)$ [46]. Substituting (41) into (40) we find that R satisfies

$$(44) \qquad \tau \frac{dR}{dt} = \widehat{H}(z(t); n) - R$$

where

$$(45) \qquad \widehat{H}(z; n) = a_n \left[\widehat{C}_0 + \sum_{j=1}^{n} \widehat{C}_j (z^j + \bar{z}^j) \right]$$

and

$$(46) \qquad \widehat{C}_j = \sum_{k=0}^{n} \sum_{m=0}^{k} \frac{n! \delta_{k-2m,j}}{2^k (n-k)! m! (k-m)!}$$

We will set $n = 2$ in all following calculations and thus $a_2 = 2/3, \widehat{C}_0 = 3/2, \widehat{C}_1 = 1, \widehat{C}_2 = 1/4$. Substituting (41) into (6) and using (39) we find [41] that α satisfies

$$\frac{\partial \alpha}{\partial t} = -i \left[\frac{-\epsilon R e^{i\beta}}{2i\sqrt{\pi(2 - \cos(2\beta))}} + \left(\omega + \frac{\epsilon R \sin \beta}{\sqrt{\pi(2 - \cos(2\beta))}} \right) \alpha \right.$$

$$(47) \qquad \left. + \left(\frac{\epsilon R e^{-i\beta}}{2i\sqrt{\pi(2 - \cos(2\beta))}} \right) \alpha^2 \right]$$

and evaluating this at $\omega = \omega_0 + i\Delta$ we obtain

$$(48) \qquad \frac{dz}{dt} = \frac{\epsilon R e^{-i\beta}}{2\gamma} + \frac{(i\omega_0 - \Delta)\gamma + i\epsilon R \sin \beta}{\gamma} z - \frac{\epsilon R e^{i\beta}}{2\gamma} z^2$$

where $\gamma \equiv \sqrt{\pi(2 - \cos(2\beta))}$. Equations (48) and (44) (a pair of ODEs, one real and one complex) form a complete description of the infinite network. Setting $\tau = 0$ we recover essentially the same equation as studied by [49]. The case of $\tau \neq 0$ remains unstudied.

3.2. **Results for a spatially-extended network.** As in Sec. 2.2.3, we will consider here a spatially extended network of Winfree oscillators on a domain of length L with periodic boundary conditions, coupled with connectivity function w. The governing

equations are then

$$(49) \quad \frac{\partial z(x,t)}{\partial t} = \frac{\epsilon R(x,t)e^{-i\beta}}{2\gamma} + \frac{(i\omega_0 - \Delta)\gamma + i\epsilon R(x,t)\sin\beta}{\gamma} z(x,t) - \frac{\epsilon R(x,t)e^{i\beta}}{2\gamma} z^2(x,t)$$

(50)
$$\tau\frac{\partial R(x,t)}{\partial t} = \int_0^L w(x-y)\widehat{H}(z(y,t);n) \ dy - R(x,t)$$

As an example of the sorts of solutions supported by this model, the results of simulations for a variety of different values of ϵ are shown in Fig. 10. For $\epsilon = 1.8$ there is a uniformly propagating travelling wave, which seems to undergo a Hopf bifurcation as ϵ is increased, leading to a periodically-modulated travelling wave ($\epsilon = 1.89$). For $\epsilon = 2.03$ the pattern appears chaotic, while for $\epsilon = 2.07$ the systems supports a stable "bump".

4. Conclusion and Discussion

In this chapter we have discussed two types of model neurons described by phase oscillators: the theta neuron and the Winfree oscillator. When coupled in a plausible fashion, infinite heterogeneous networks of both types of oscillators are amenable to analysis using the Ott/Antonsen ansatz, which allows one to derive evolution equations for a macroscopic order parameter. All-to-all coupled networks are thus described by several ordinary differential equations, while spatially-extended networks are described by partial differential equations with as many spatial variables as the network. Differential equations of these forms can be thought of as "building blocks" with which to form more realistic "networks of networks" models of the brain [40].

We have only considered modelling individual neurons as oscillators, but networks of neurons can synchronise and thus a synchronous network can be regarded as a single oscillator. Recent work using this idea includes [25, 29]. As shown in Sec. 2.2.2, and has been known for many years [57, 27], several interacting populations of neurons can produce macroscopic oscillations. The theory of coupled oscillators can then be applied if several of these interacting populations themselves interact.

We have only considered simple oscillators whose state can be described by a single angular variable. However, many neurons undergo "bursting," firing a number of action potentials and then moving to a quiescent state before repeating the process [50, 12, 9, 19]. The mathematical analysis of coupled bursters remains a challenge. Another area of interest involves the effects of noise on the dynamics of networks of neurons, as noise is ubiquitous in such systems [33]. For the types of models studied here the Ott/Antonsen ansatz no longer applies once noise is added to the dynamics, and instead one typically has a Fokker-Planck equation to analyse [16, 19] (although see [31, 43] for applications of the Ott/Antonsen ansatz to networks of phase oscillators with *common* noise).
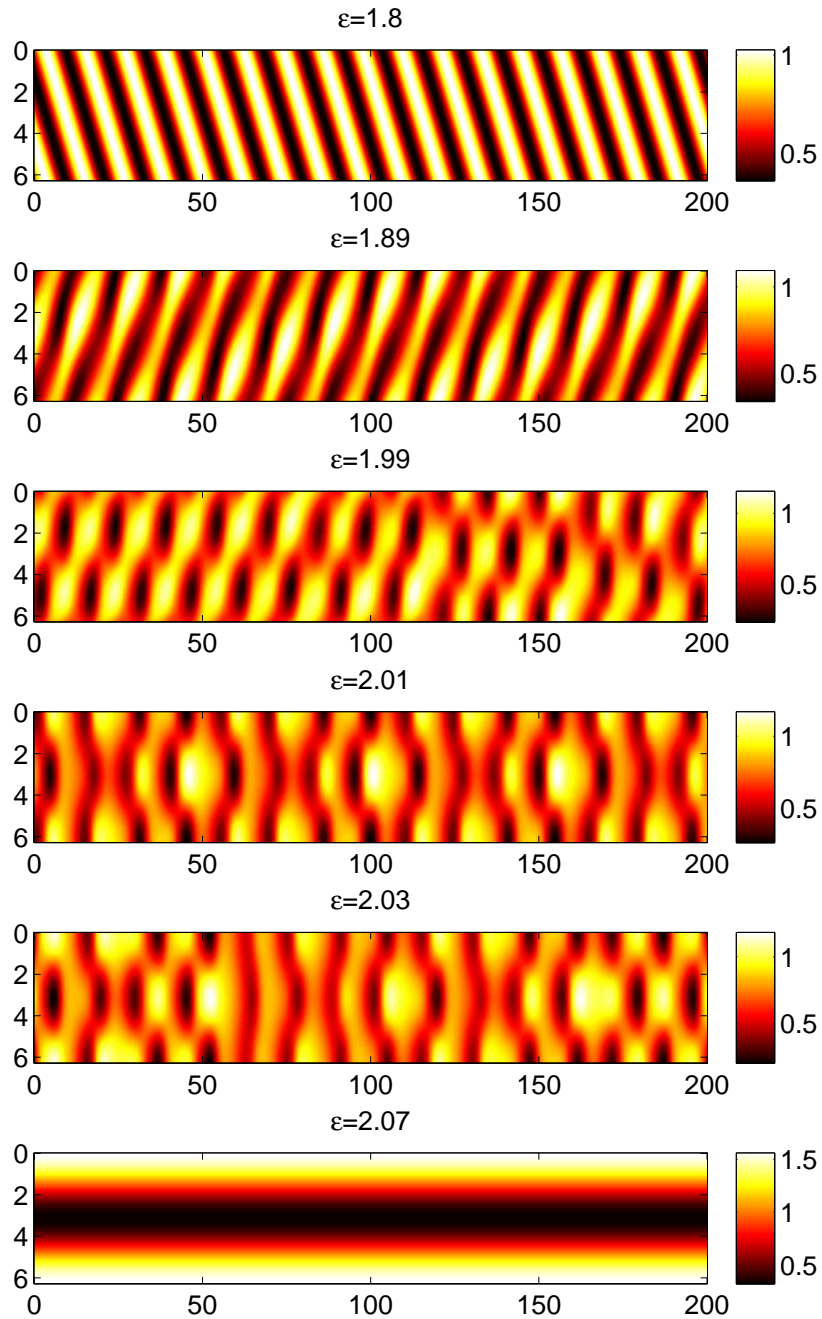
FIGURE 10. Typical solutions of (49)-(50) for different values of ϵ. R is shown colour-coded, and in each panel the vertical axis is x while t increases from left to right. Coupling function is $w(x) = 0.1 + 0.3\cos x$ and periodic boundary conditions are used. Parameters: $\beta = 0, L = 2\pi, g = 2, \Delta = 0.1, \omega_0 = 1, \tau = 1.5, n = 2$.

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