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Traveling waves in non-local pulse-coupled networks

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Abstract

Traveling phase waves are commonly observed in recordings of the cerebral cortex and are believed to organize behavior across different areas of the brain. We use this as motivation to analyze a one-dimensional network of phase oscillators that are nonlocally coupled via the phase response curve (PRC) and the Dirac delta function. Existence of waves is proven and the dispersion relation is computed. Using the theory of distributions enables us to write and solve an associated stability problem. First and second order perturbation theory is applied to get analytic insight and we show that long waves are stable while short waves are unstable. We apply the results to PRCs that come from mitral neurons. We extend the results to smooth pulse-like coupling by reducing the nonlocal equation to a local one and solving the associated boundary value problem.

Keywords Phase-resetting curves · Nonlocal coupling · Traveling waves

Mathematics Subject Classification 92C20 · 45M15 · 37G15

1 Introduction

Traveling waves are now known to be a ubiquitous property of rhythmic neural networks (Muller et al. 2018) in the cerebral cortex. Multi-electrode arrays and imaging methods have established that what was once believed to be synchronous activity actually takes the form of propagating phase-waves (Zhang et al. 2018; Halgren et al. 2019; Roberts et al. 2019). Unlike the well-known reaction diffusion (RD) models, neuronal networks are characterized by nonlocal coupling that is generally modeled by convolutional equations. Such spatially distributed networks are modeled in a variety

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of ways that vary in complexity and detail, ranging from biophysically based compartmental models (Bazhenov et al. 2002) to simpler integrate-and-fire models (Bressloff et al. 1997; Bressloff and Coombes 1998) to so-called firing rate or Wilson-Cowan type models (Pinto and Ermentrout 2001; Coombes 2005; Goulet and Ermentrout 2011; Bressloff 2014). Nonlocal equations are mathematically challenging, but there has been progress recently, particularly in the case where the intrinsic dynamics is excitable and solitary pulses are studied (Faye 2013; Faye and Scheel 2015; Chen and Ermentrout 2017).

Because the types of waves observed in the experimental examples mentioned above are associated with rhythmic behavior, the most straightforward approach is to assume that these waves are occurring in an intrinsically oscillatory medium. For simplicity, we suppose that there is a one population network of nearly identical coupled neurons driven so that in absence of coupling they are firing rhythmically. Such networks of conductance-based neurons (Ermentrout and Terman 2010) are generally coupled by chemical synapses and the voltage of neuron j satisfies the differential equation:

$$C_m \frac{dV_j}{dt} = I_j - I_{ionic}(V_j, \ldots) + \sum_{k=1}^{N} g_{jk} s_k (E - V_j), \quad j = 1, \ldots, N,$$

where I_j is the injected current, $I_{ionic}(V, \ldots)$ are the active currents that allow the neurons to fire, and g_{jk} are the synaptic conductances that specify the connectivity between neurons. The variables $s_k(t)$ are the synapses and may satisfy differential equations themselves, but are dependent *only on* $V_k(t)$. In absence of coupling ($g_{jk} = 0$), if the injected currents are the same and are such that the neurons fire repetitively, we can regard each neuron as an asymptotically stable limit cycle oscillator.

Let X_j denote the vector of the voltage, conductances (and other local variables), and synapse variables for each neuron. Then we can write the dynamics of X_j as

$$\frac{dX_j}{dt} = F(X_j) + G_j(t)$$

where G_j are the synaptic inputs. When $G_j = 0$, then we can express the state of X_j by its phase u_j along the limit cycle, $X_j(t) = Y(u_j)$ where $Y(u)$ is the trajectory of the uncoupled limit cycle and $\frac{du_j}{dt} = \omega_j$ where ω_j is the uncoupled frequency. If $G_j(t)$ is not too large, we can use phase-reduction techniques (Kuramoto 2003; Schwemmer and Lewis 2012; Nakao 2016; Monga et al. 2019; Pietras and Daffertshofer 2019; Ermentrout et al. 2019) to write the dynamics of the phase when there is coupling:

$$\frac{du_j}{dt} = \omega_j + Z(u_j) \cdot G_j + A_j \cdot G_j, \quad j = 1, \ldots N \tag{1}$$

where $Z(u)$ is the generalized phase-response curve and the A_j corresponds to terms that involve deviations from the limit cycle (see Pietras and Daffertshofer 2019; Ermentrout et al. 2019). If G_j is small enough, then we can ignore $A_j \cdot G_j$ as it is of order $|G_j|^2$. In the coupled neuronal models, interactions are mediated only through the voltages and thus, only the voltage-component of Z matters; we call the voltage component of $Z(u)$, $\Delta(u)$. The quantity $\Delta(u)$ is called the infinitesimal phase resetting curve and can be experimentally measured from single neuron recordings (Burton et al. 2012).

Many people have studied variations of Eq. (1) in various geometries and limits (such as $N \to \infty$). In particular, with pulse coupling, $G_j = \sum_{i=1}^{N} k_{ji} R(u_i)$ (Winfree 1967), where k_{ji} are the coupling strengths and we have:

$$\frac{du_j}{dt} = \omega_j + \Delta(u_j) \sum_i k_{ji} R(u_i) \quad j = 1, \ldots, N. \tag{2}$$

Dror et al. sought traveling wave solutions to Eq. (2) in a nearest neighbor ring of oscillators with identical frequencies (Dror et al. 1999). Goel and Ermentrout analyzed the stability of waves for Eq. (2) for nearest-neighbor coupling and $R(u) = \delta(u)$ (Goel and Ermentrout 2002). Much more has been done in the case where $k_{ji} = K/N$ and $N \to \infty$, for example, Ariaratnam and Strogatz Ariaratnam and Strogatz (2001) determined the complete phase diagram for $R(u) = 1 + \cos u$ and $\Delta(u) = -\sin u$ whereas Luke et al. (2013) studied the theta model where $\Delta(u) = 1 + \cos u$. These authors all take advantage of the special form of the equations to significantly reduce the dimensionality of the problem (Bick et al. 2020).

We suppose that the oscillators are arranged uniformly on a ring of circumference, L, the frequencies, ω_j are identical (with $\omega_j = 1$, without loss of generality) and that k_{ji} depends only on the distance (modulo N) on the ring. We let $\Delta x = L/N$ and then take the formal limit as $N \to \infty$ and obtain:

$$\frac{\partial u}{\partial t} = 1 + \left[\int_0^L k_L(x - y) R(u(y, t))\, dy \right] \Delta(u(x, t)) \tag{3}$$

where $k_L(x)$ is an $L-$ periodic even kernel that gives the interaction strength with distance. We assume that it has unit integral. Given a symmetric kernel function $k(x)$ with $\int_R k(x)\, dx = 1$, we can construct a periodic kernel by setting

$$k_L(x) = \sum_{m=-\infty}^{\infty} k(x + mL).$$

Note that $k_L(x)$ is $L-$periodic and is also normalized when integrated over $[0, L]$. For example, if $k(x) = \exp(-|x|)/2$, then

$$k_L(x) = \frac{e^x + e^{L-x}}{2(e^L - 1)}. \tag{4}$$

If $k(x)$ is a Gaussian, then the corresponding kernel, $k_L(x)$ is often called a wrapped Gaussian.

Equation (3) was first studied by Ermentrout (1985) in the weak coupling limit,

$$\frac{\partial u}{\partial t} = 1 + \int_0^L k_L(x-y)H(u(y,t) - u(x,t))\, dy,$$

where $H(v) = (1/2\pi)\int_0^{2\pi} R(v-u)\Delta(u)du$ is the averaged interaction function. Here, we assume that the coupling is sufficiently weak that reduction to a phase-model is justified. However, we do not perform averaging which leads to *phase-difference* models as above and which are easier to analyze as there is an exact expression for the waves (Ermentrout 1985).

The goal of this paper is to characterize the behavior of traveling waves in Eq. (3). We first review simple criteria for the stability of synchrony and then turn to the existence of traveling waves in a ring when the pulse coupling function is the Dirac delta function. We prove existence and numerically compute the dispersion relation (the frequency as a function of the ring length, L). We derive an eigenvalue equation for the stability of the waves and numerically compute the solutions. We then get approximate solutions and stability by assuming the coupling strength is small which we show matches the full simulations. Finally, we derive boundary value problems for the existence and stability of waves for smooth pulse coupled systems in place of the Dirac δ-function.

2 Results

2.1 Synchrony

Let us turn now to the analysis of Eq. (3). We first lay out a few assumptions that make biological sense as well as make the analysis simpler. We assume that $u(x,t)$ lies on $[0, 2\pi)$ (with 0 and 2π identified) and that both Δ and R are $2\pi-$periodic functions. We assume that $R(u)$ is peaked at $u = 0$, the phase at which the neuron produces the coupling pulse, thus fixing the zero phase. We will assume no delays in communication from one neuron to the others. For many real neurons and models, the phase resetting curve, $\Delta(u)$ satisfies $\Delta(0) = 0$; that is, the neuron does not respond to any inputs when it is itself spiking. Thus, we will assume this condition as well. One solution to Eq. (3) is the synchronous one, where $u(x,t) = U(t)$ independent of x. This satisfies:

$$\frac{dU}{dt} = 1 + R(U)\Delta(U) \tag{5}$$

As long as the right-hand side of this equation is positive, there is a periodic solution, $U(t+T) = U(t) + 2\pi$ where the period

$$T = \int_0^{2\pi} \frac{du}{1 + R(u)\Delta(u)}.$$

We can readily determine the stability of the synchronous state. We let

$$k_n = \int_0^L k_L(x) e^{-2\pi i n x/L}\, dx.$$

Plugging in $u(x,t) = U(t) + v(x,t)$, the linearization for Eq. (3) around the synchronous solution is

$$\frac{\partial v}{\partial t} = \int_0^L k_L(x-y)\left[R'(U(t))v(y,t)\Delta(U(t)) + R(U(t))\Delta'(U(t))v(x,t)\right] dy$$

where $\Delta'(U)$, $R'(U)$ are the derivatives of $\Delta(u)$, $R(u)$ with respect to u evaluated at $U(t)$. Let $v(x,t) = w_n(t)\exp(2\pi i n x/L)$. Then we have

$$\frac{dw_n}{dt} = [k_n R'(U(t))\Delta(U(t)) + R(U(t))\Delta'(U(t))]w_n(t).$$

With $w_n(0) = 1$, we see that

$$w_n(T) = \exp\left(\int_0^T [k_n R'(U(t))\Delta(U(t)) + R(U(t))\Delta'(U(t))]\, dt\right).$$

Synchrony is stable as long as $w_n(T) < 1$ for $n > 0$ or, equivalently, the integral is negative. Since $U(t)$ satisfies Eq. (5), if we differentiate with respect to t, we have

$$\frac{dQ}{dt} = [R'(U(t))\Delta(U) + \Delta'(U(t))R(U(t))]Q$$

where $Q = dU/dt$. As $Q(t)$ is T-periodic, it follows that we must have

$$\exp\left(\int_0^T [R'(U(t))\Delta(U) + \Delta'(U(t))R(U(t))]\, dt\right) = 1.$$

Thus, the integral inside the exponential vanishes and

$$\int_0^T [R'(U(t))\Delta(U)\, dt = -\int_0^T \Delta'(U(t))R(U(t))]\, dt.$$

Thus, using this equality, we see that synchrony is stable if and only if

$$\kappa_n \equiv (1-k_n)\int_0^T \Delta'(U(t))R(U(t))\, dt < 0 \tag{6}$$

for $n > 0$. For example, if $R(u)$ is concentrated near $u = 0$ and $\Delta'(0) < 0$, then we obtain stability of synchrony, as long as $k_n < 1$, such as for a Gaussian or exponential kernels (cf Eq. (4)). Throughout the remainder of this paper, we will work in regimes where there is a stable synchronous solution. In most of this paper, we will be considering the limiting case where $R(U)$ is the Dirac delta function. In this case, synchrony is stable if $\Delta'(0) < 0$ and $k_n < 1$.

2.2 Traveling waves

Henceforth, we confine our attention to the case in which $R(u) = \sum_{m=-\infty}^{\infty} \delta(u + 2\pi m)$, the "periodized" Dirac function. We additionally assume, $\Delta(0) = 0$ and $\Delta'(0) < 0$, assuring that synchrony is stable for non-negative kernels. We seek solutions, $u(x, t) = U(\xi)$ with $\xi = ct - x$:

$$c\frac{dU(\xi)}{d\xi} = 1 + \Delta(U(\xi)) \int_0^L k_L(\xi - y)R(U(y))\, dy \tag{7}$$

with the condition that $U(\xi + L) = U(\xi) + 2\pi$. Since the wave is translation invariant, we fix the position by setting $U(0) = 0$. Thus, $U'(0) = 1/c$, so the equation for the traveling wave is just:

$$\frac{dU}{d\xi} = \beta + \Delta(U)k_L(\xi) \tag{8}$$

where $\beta = 1/c$ with $U(0) = 0$ and $U(L^-) = 2\pi$ where by L^- we mean the limit from below. We now prove there is a unique solution.

Lemma 1 *Suppose $\Delta(0) = 0$ and $\Delta(u), k_L(\xi)$ are bounded and continuous. Then there is a unique solution to Eq. (7) with $U(0) = 0$, $U(L^-) = 2\pi$.*

Proof Let $w(\xi, \beta)$ be solution to the initial value problem

$$\frac{dw(\xi, \beta)}{d\xi} = \beta + \Delta(w(\xi, \beta))k_L(\xi)$$

with $w(0, \beta) = 0$. By a simple comparison argument, $w(L, \beta_1) > w(L, \beta_2)$ if $\beta_1 > \beta_2$ since $dw(\xi, \beta)/d\xi|_{\xi=0} = \beta$. Clearly, $w(L, 0) = 0$. Furthermore, since $\Delta(u)k_L(\xi)$ is bounded, for β large enough, $w(L, \beta) > 2\pi$. The monotonicity of $w(L, \beta)$ with respect to β guarantees that there is a unique β_L so that $w(L, \beta_L) = 2\pi$. We thus take $U(\xi) = w(\xi, \beta_L)$. □

With existence established, we can numerically compute the period, $P = L/c$ of the wave as a function of L for different types of PRCs. Figure 1 shows the period $P = L/c$ of the traveling wave as a function of L for the exponential kernel, Eq. (4), and $\Delta(u) = a(\sin(b) - \sin(u + b))$ for different pairs, (a, b). We also show one example with the Gaussian kernel (G). In all cases, as L increases all curves converge to 2π, the period of the synchronous oscillation. Note that $c = L/P$, so c increases roughly linearly with L unlike the waves in an excitable medium. On the right panel of the figure, we show the period as b changes for $a = 1$, $L = 20$.

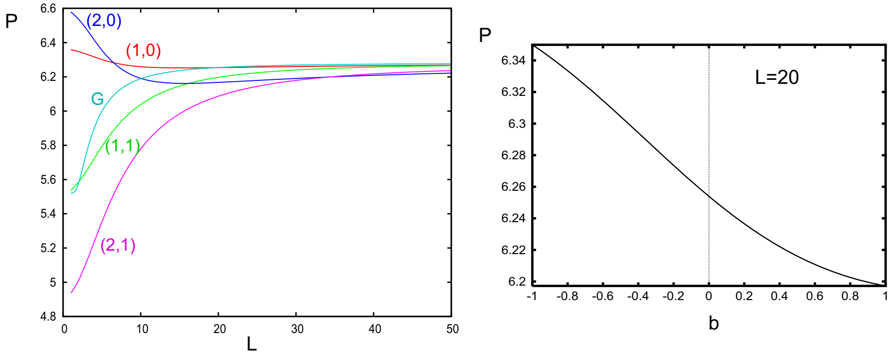

Fig. 1 Period of the wave as a function of the length L of the ring for the exponential kernel and $\Delta(u) = a(\sin(b) - \sin(u + b))$ for pairs (a, b). Curve labeled G is for a Gaussian with $(a, b) = (1, 1)$. Right panel shows $R(b)$ for $a = 1$, $L = 20$

2.3 Stability of traveling waves

We now turn to the formal stability of the traveling waves. We replace x by the moving coordinate, $\xi = ct - x$ so that we have:

$$\frac{\partial u}{\partial t} + c\frac{\partial u}{\partial \xi} = 1 + \Delta(u(\xi, t)) \int_0^L k_L(\xi - y)R(u(y, t))\, dy. \tag{9}$$

The traveling wave solution, $U(\xi)$ is a stationary solution to this evolution equation. We write $u(\xi, t) = U(\xi) + \zeta(\xi, t)$ where ζ is small and take only the terms linear to ζ to get the formal linearization of Eq. (9):

$$\frac{\partial \zeta}{\partial t} + c\frac{\partial \zeta}{\partial \xi} = \Delta(U(\xi)) \int_0^L k_L(\xi - y)R'(U(y))\zeta(y, t)\, dy$$
$$+\Delta'(U(\xi))\zeta(\xi, t) \int_0^L k_L(\xi - y)R(U(y)))\, dy.$$

Letting $\zeta(\xi, t) = e^{\lambda t}v(\xi)$, we obtain the formal linear eigenvalue problem:

$$\lambda v(\xi) + c\frac{dv}{d\xi} = \Delta(U) \int_0^L k_L(\xi - \eta)R'(U(\eta))v(\eta)\, d\eta$$
$$+\Delta'(U)v(\xi) \int_0^L k_L(\xi - \eta)R(U(\eta))\, d\eta. \tag{10}$$

This eigenvalue problem includes the term $R'(U(\eta))$ which is thus the formal derivative of the delta function applied to the solution $U(\eta)$. We will interpret these formal terms in the sense of distributions and, thus, to use them in the stability equation, we must compute their meaning in terms of elementary distributions such as the Dirac

δ function, the dipole function (negative "derivative" of the δ function) and others (Keener 2019).

Lemma 2 *Suppose $u(0) = 0$, $u'(0) > 0$, and $u''(0)$ exists, then for any test function $f(x)$ ($C^\infty(\mathbb{R})$ functions with compact support):*

$$\begin{aligned}\int_R f(\eta)\delta(u(\eta))\, d\eta &= \frac{f(0)}{|u'(0)|},\\ \int_R f(\eta)\delta'(u(\eta))\, d\eta &= -\frac{f'(0)u'(0) - f(0)u''(0)}{u'(0)^3}.\end{aligned} \tag{11}$$

Proof Proof of the first statement:

$$\int_R f(\eta)\delta(u(\eta))\, d\eta = \int_R \frac{f(u^{-1}(v))\delta(v)}{u'(u^{-1}(\eta))}\, dv = \frac{f(u^{-1}(0))}{\left|u'(u^{-1}(0))\right|} = \frac{f(0)}{|u'(0)|}$$

Proof of the second statement:

$$\begin{aligned}\int_R f(\eta)\delta'(u(\eta))d\eta &= \int_R \frac{f(u^{-1}(z))\delta'(z)}{u'(u^{-1}(z))}dz\\ &= -\frac{d}{dz}\left[\frac{f(u^{-1}(z))}{u'(u^{-1}(z))}\right]\Bigg|_{z=0}\\ &= -\left\{f(u^{-1}(z))\cdot\frac{-u''(u^{-1}(z))}{u'(u^{-1}(z))^2}\cdot\frac{d}{dz}u^{-1}(z) + \frac{f'(u^{-1}(z))\cdot\frac{d}{dz}u^{-1}(z)}{u'(u^{-1}(z))}\right\}\Bigg|_{z=0}\\ &= -\left\{f(0)\cdot\left(\frac{-u''(0)}{u'(0)^3}\right) + \frac{f'(0)}{u'(0)^2}\right\}\\ &= -\frac{f'(0)u'(0) - f(0)u''(0)}{u'(0)^3}\end{aligned}$$

□

In order to use (11) in Eq. (10), we need to evaluate, $v'(0)$ using the fact that $U(0) = 0$ and $\Delta(0) = 0$. Substituting $\xi = 0$ in Eq. (10), we get:

$$\lambda v(0) + cv'(0) = c\Delta'(0)v(0)k_L(0)$$

so that

$$v'(0) = (\Delta'(0)k_L(0) - \frac{\lambda}{c})v(0).$$

Together with Eq. (11), the eigenvalue Eq. (10) becomes:

$$\begin{aligned}\frac{\lambda}{c}v(\xi) + v'(\xi) = \Delta'(U(\xi))v(\xi)k_L(\xi) + c\Delta(U(\xi))k'(\xi)v(0)\\ +\lambda\Delta(U(\xi))k_L(\xi)v(0),\end{aligned} \tag{12}$$

along with the periodic boundary conditions $v(0) = v(L)$. As it is a good "reality check", we show that $\lambda = 0$ is an eigenvalue and $V(\xi) = dU/d\xi$ is an eigenfunction. To see this, note from Eq. (8) that $V(0) = \beta = 1/c$. Differentiate Eq. (8) with respect to ξ to obtain that

$$\frac{dV}{d\xi} = \Delta'(U(\xi))k_L(\xi)V + c\Delta(U(\xi))k_L'(\xi)V(0)$$

as desired where we use the fact that $cV(0) = 1$. We can write down an explicit solution to the equation by solving the linear ODE, but this involves integrals of $\Delta(U(\xi))$ multiplied by exponentials of integrals also involving $U(\xi)$, ultimately leading to:

$$V(\xi) = V(0)M(\xi, \lambda).$$

Setting $\xi = L$ and using periodicity, we get $M(L, \lambda) = 0$. Solving this, generally transcendental, equation for λ yields the eigenvalues and thus the stability. As this approach is not particularly fruitful, we numerically solve Eq. (12) as a linear boundary value problem along with the simultaneous solution to Eq. (8). Before doing so, we provide some intuition about the expected behavior. If we set $\Delta = 0$, we see immediately that $v(\xi) = \exp(2\pi in\xi/L)$ and $\lambda = -2\pi inc/L$ is imaginary for $n \neq 0$. Thus, we expect that there will be complex eigenvalues and we need to determine when the real part is positive. Clearly if $v(0) = 0$, then $v(\xi) = 0$, so we can take $v(0) = 1$. We scale $s = \xi/L$ and write λ, v in terms of real and imaginary parts, $\lambda = \lambda_r + i\lambda_m$, $v = v_r + iv_m$ and solve:

$$\begin{cases} \dfrac{\lambda_r v_r - \lambda_m v_m}{c} + \dfrac{v_r'}{L} = \Delta'(u)v_r k_L(s) + \lambda_r \Delta(u)k_L(s) + c\Delta(u)k_L'(s) \\ \dfrac{\lambda_m v_r + \lambda_r v_m}{c} + \dfrac{v_m'}{L} = \Delta'(u)v_m k_L(s) + \lambda_m \Delta(u)k_L(s) \\ v_r(0) = v_r(1) = 1 \\ v_m(0) = v_m(1) = 0. \end{cases} \tag{13}$$

We numerically solve this boundary value problem for the free parameters λ_r, λ_m starting with $\lambda_m = n$, for $n = 1, 2, \ldots$. Figure 2a shows an example calculation for the exponential kernel, Eq. (4), $\Delta(u) = -\sin(u)$ for $n = 1, 2$. For $n = 1$, if L is smaller than about 9.2, then the wave is unstable to perturbations with $\lambda_m \approx 1$, but is stable to higher modes until L gets very close to 0. For modes $n > 2$, we find that the wave is also stable. Thus, if the domain size is too small, even though the wave exists, it is unstable. We next track the value L^* at which the wave loses stability at the $n = 1$ mode (the most unstable mode) as we vary the amplitude and shape of $\Delta(u) = a(\sin(b) - \sin(b + u))$. This is shown in Fig. 2b. For $b = 0$, the larger amplitude Δ causes a loss of stability for slightly larger values of L. For $b < 0$ the wave is destabilized at larger L while for $b > 0$, it is destabilized at smaller L.

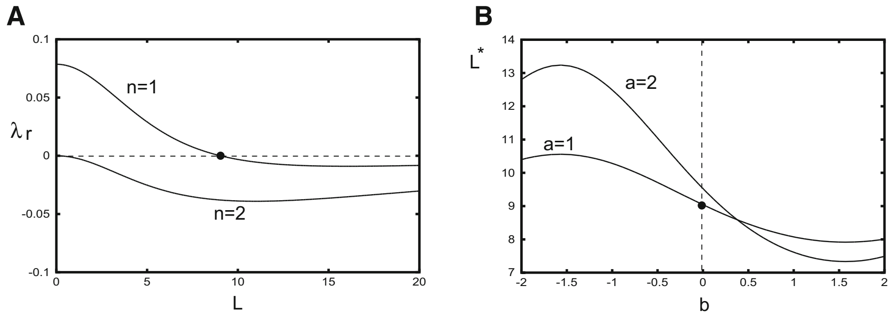

Fig. 2 Numerically determined solutions to the eigenvalue problem (13) for $\Delta(u) = a(\sin(b) - \sin(u+b))$. **a** Real part of the eigenvalue as L varies for $\lambda_m \approx n$. Solid dot shows the value of L at which the λ_r changes sign. **b** The critical value L^* at which $\lambda_r = 0$ when $n = 1$ as b varies for $a = 1, 2$. Solid dot corresponds to the dot in panel A

2.3.1 Other shapes of PRCs

In Burton et al. (2012), the authors measured the PRCs in mitral cells (a type of neuron that responds to different odors) and found that we could parameterize their shape with a function that has the form:

$$\Delta_M(u) = a(\sin(b) - \sin(u+b))\exp(d(u - 2\pi)). \tag{14}$$

This function vanishes at $u = 0, 2\pi$. (Note that $d = 0$ recovers our standard PRC.) Fig. 3a shows example PRCs for different values of the shaping parameter d. This parameter determines how flat the PRC is in the early part of the cycle, with the flatter PRCs occurring when d is larger. Typical values for neurons had values of a, b, d between 0 and 1. Thus, we take $a = 1, b = 0.5$ and let d range over several values. Panels B,C show the dispersion rate and the real part of the most unstable eigenvalue at the same values of d. Qualitatively, d does not have much effect on the dispersion; the shallowing is a consequence of the fact that the average amplitude of the PRC decreases with increasing d. Even with that difference, the dependence on the the length is less sensitive with larger d. In general, flattening of the PRC has the effect of destabilizing waves in the sense that as d increases, the waves are destabilized at longer values of L.

2.4 Perturbation approximations

Our results in the preceding section are all numerical, so it is natural to ask whether there any analytic approaches where we can obtain approximations to the dispersion and stability of the traveling waves. Looking at Eq. (3), when $R(u) \equiv 0$ (zero effect of other oscillators) we see that $u(x,t) = t + 2\pi x/L$ is a traveling wave solution with winding number 1. This suggests that we might be able to compute traveling wave solutions if the interaction coupling function $R(u)$ is small in magnitude, say,

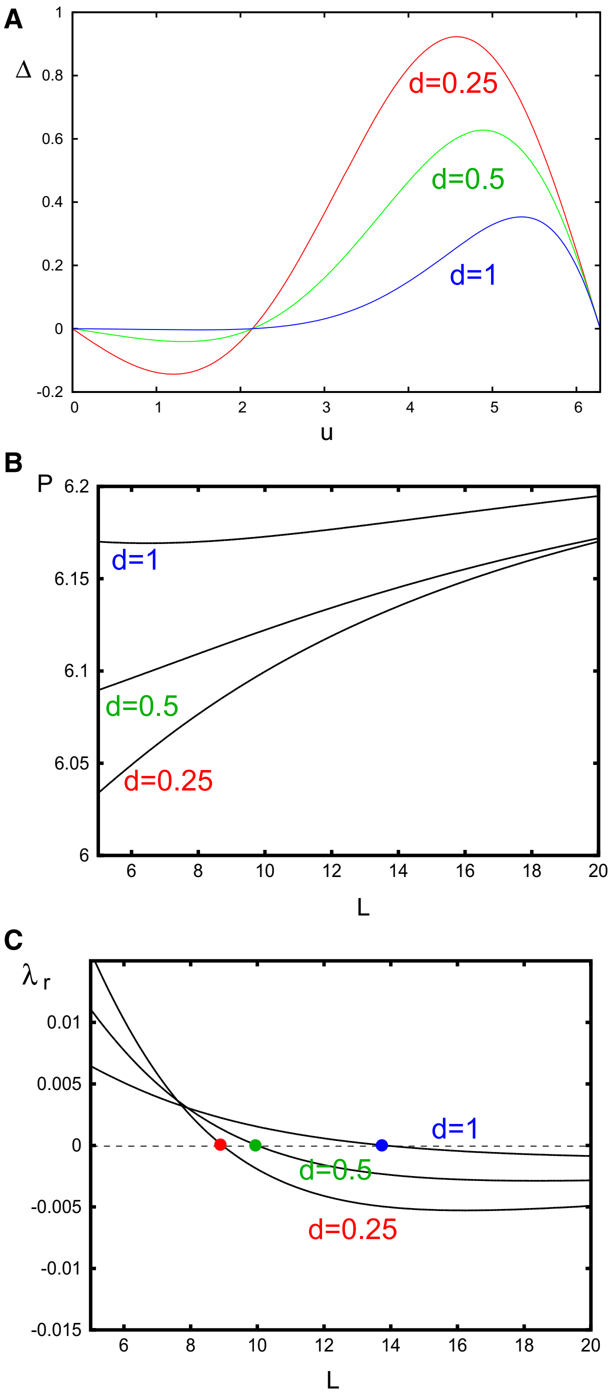

Fig. 3 Dispersion relation (period, P) and stability of waves as the ring length, L varies for approximations (14) of the PRC for a mitral cell. **a** PRC with $a = 1, b = 0.5$ and $d = 0.25, 0.5, 1.0$. **b** Dispersion relation corresponding to the PRCs in A. **c** Stability of waves (dots indicate the critical ring length where stability is lost)

$R(u) = O(\epsilon)$, where $0 < \epsilon \ll 1$. With this assumption, we should be able to develop a perturbation approximation in powers of ϵ for the dispersion relation and stability.

2.4.1 Perturbation and dispersion

We first compute the dispersion relation, $P(L)$ by assuming the amplitude that $R(u) = \epsilon\delta(u)$ where $0 < \epsilon \ll 1$. We rewrite Eq. (8) as

$$\frac{dU}{ds} = P + \epsilon L k_L(Ls)\Delta(U) \tag{15}$$

where $s = \xi/L$, $P = L/c$. We write the solution to Eq. (15) as a function $U(s,\epsilon)$ where we explicitly include the ϵ and assume that we can expand $U(s,\epsilon)$ in a power series in ϵ. Solutions to Eq. (15) must be periodic in s in the sense of phase, so that $U(s+1,\epsilon) = U(s,\epsilon) + 2\pi$. We can fix the 0 phase, by requiring $U(0,\epsilon) = 0$. Thus, we seek solutions to Eq. (15) such that $U(0,\epsilon) = 0$ and $U(1,\epsilon) = 2\pi$. We expand U and P in ϵ, $U(s,\epsilon) = u_0(s) + \epsilon u_1(s) + \ldots$ and $P(\epsilon) = P_0 + \epsilon P_1 + \ldots$ obtaining the series of equations:

$$u_0' = P_0 \quad u_0(0) = 0,\ u_0(1) = 2\pi \tag{16}$$

$$u_1' = P_1 + Lk_L(Ls)\Delta(u_0) \quad u_1(0) = 0,\ u_1(1) = 0 \tag{17}$$

$$u_2' = P_2 + Lk_L(Ls)\Delta'(u_0)u_1 \quad u_2(0) = 0,\ u_2(1) = 0 \tag{18}$$

Clearly, the solution to Eq. (16) is $P_0 = 2\pi$ and $u_0 = 2\pi s$. Integrating the second equation from 0 to 1 and using the boundary conditions, we get

$$P_1 = -L\int_0^1 k_L(Ls)\Delta(2\pi s)\, ds$$

and

$$u_1(s) = P_1 s + L\int_0^s k_L(Ls')\Delta(2\pi s')\, ds'.$$

Similarly, we obtain:

$$P_2 = -L\int_0^1 k_L(Ls)\Delta'(2\pi s)u_1(s)\, ds.$$

As an example, if we take $\Delta(u) = \sin(b) - \sin(b+u)$ and $k_L(Ls)$ the exponential and find:

$$P_1 = -\sin(b)\frac{4\pi^2}{L^2 + 4\pi^2}. \tag{19}$$

We see that if $b = 0$, that is $\Delta(u)$ is an odd periodic function, then, $P_1 = 0$ and the period is independent of L to order ϵ. As Fig. 1 shows, there is dependence of

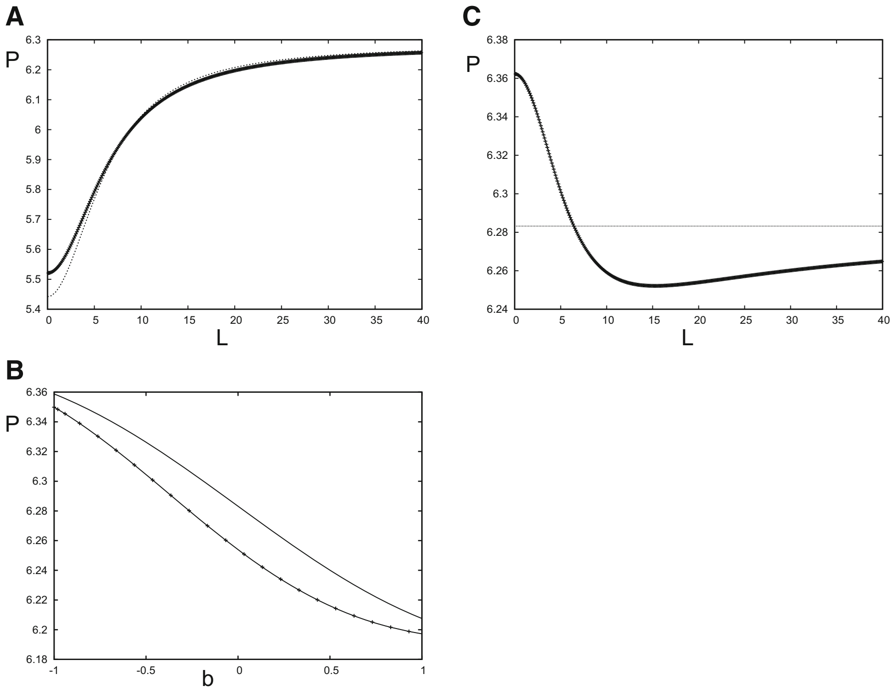

Fig. 4 Comparison of the perturbation expansion with the numerically determined dispersion relations. **a** $2\pi + \epsilon P_1$ (Eq. (19)) for $\epsilon = 1, b = 1$ (thin dotted line) compared to the numerical calculation (crosses); **b** For $L = 20, \epsilon = 1$ perturbation (solid line, Eq. (19)) compared to numerical results (line points); **c** For $\epsilon = 1, b = 0$, second order $2\pi + \epsilon^2 P_2$ (Eq. (20)) compared to numerical results (curves indistinguishable)

the period on L when $b = 0$, so to explain this dependence, we go to higher order. Evaluating the integrals when $b = 0$, we obtain:

$$P_2(b = 0) = \frac{\pi L}{4}\left(\frac{[L^2 - 4\pi^2][1 - \exp(2L)] + 2L\exp(L)[L^2 + 4\pi^2]}{[L^2 + 4\pi^2]^2[\exp(L) - 1]^2}\right). \quad (20)$$

Figure 4 shows some comparisons of the perturbation expansions with the numerically determined dispersion relation for $\epsilon = 1$. In panel A, we show the comparison for $b = 1$ over a range of L. Even though $\epsilon = 1$, the approximation is pretty good with a small deviation for L near 0. Panel B fixes $L = 20$ and varies b between -1 and 1. There is a small error. In panel C, we set $b = 0$ which to order ϵ yields $P = 2\pi$ (shown as the dotted line). But, including the higher order terms, we obtain results indistinguishable from the numerical calculations. In sum, the perturbation theory works quite well even for reasonably large ϵ.

2.4.2 Perturbation and stability

We begin with Eq. (12) which we rewrite to include ϵ:

$$\frac{\lambda}{c}v(\xi)+v'(\xi)=\epsilon\left(\varDelta'(U(\xi))v(\xi)k_L(\xi)+c\varDelta(U(\xi))k_L'(\xi)v(0)+\lambda\varDelta(U(\xi))k_L(\xi)v(0)\right)$$

subject to the boundary conditions, $v(0) = v(L) = 1$. (Note that we could enforce some other type of normalization on the eigenfunction; this is just convenient and will not change λ. Indeed, if we choose $v(0) = 0$, then by uniqueness, $v(\xi) = 0$ for all ξ, so any eigenfunction must have $v(0) \neq 0$.) We recall from the previous section that $c \equiv L/P = L/(2\pi) + O(\epsilon)$ and $U(\xi) = 2\pi\xi/L + O(\epsilon)$. We write $v = v_0 + \epsilon v_1 + \ldots$ and $\lambda = \lambda_0 + \epsilon\lambda_1 + \ldots$. Plugging in this perturbation series, we obtain to zero order:

$$\frac{\lambda_0}{c}v_0+v_0'=0$$

with $v_0(0) = v_0(L) = 1$. We immediately find, $\lambda_0 = 2\pi inc/L$ and $v_0(\xi) = \exp(-2\pi ni\xi/L)$ where n is an integer. The next order equation is

$$\begin{aligned}\frac{2\pi in}{L}v_1+v_1' &= -\frac{\lambda_1}{c}v_0(\xi)+\varDelta'(u_0)v_0(\xi)k_L(\xi)\\ &\quad+\lambda_0\varDelta(u_0)k_L(\xi)+c\varDelta(u_0)k_L'(\xi)v_0(0):=S(\xi,\lambda_1)\end{aligned}\tag{21}$$

With the inner product,

$$\langle u(\xi),v(\xi)\rangle=\int_0^L\bar{u}(\xi)v(\xi)\,d\xi$$

The linear operator on the left-hand side is self-adjoint in the space of $L-$periodic functions and has a one-dimensional nullspace, $v_0(\xi)$ Thus, to obtain a periodic solution, we must have that, $\langle v_0(\xi), S(\xi, \lambda_1)\rangle = 0$. With this, we obtain:

$$\begin{aligned}\Re\lambda_1=\frac{L}{2\pi}\int_0^1&\Big(\varDelta'(2\pi s)k_L(Ls)-n\sin(2\pi ns)\varDelta(2\pi s)k_L(Ls)\\ &+\frac{L}{2\pi}\,k_L'(Ls)\varDelta(2\pi s)\cos(2\pi ns)\Big)\,ds.\end{aligned}$$

where we have substituted $c_0 = L/(2\pi)$ where it appears. This expression is a bit unwieldy, but we note that $dk_L(Ls)/ds = Lk_L'(Ls)$ so that we can write

$$-n\sin(2\pi ns)\varDelta(2\pi s)k_L(Ls)+\frac{L}{2\pi}k_L'(Ls)\varDelta(2\pi s)\cos(2\pi ns)$$

as

$$\frac{1}{2\pi}\frac{d}{ds}(\cos(2\pi ns)k_L(Ls))\varDelta(2\pi s)$$

and then integrate by parts to get a much more compact expression:

$$\Re\lambda_1=\frac{L}{2\pi}\int_0^1k_L(Ls)\varDelta'(2\pi s)[1-\cos(2\pi ns)]\,ds.\tag{22}$$

Note that for $n = 0$, $\Re\lambda_1 = 0$ as expected. We write $\Delta(u) = \sum_{m=0}^{\infty} a_m \sin(mu) + b_m \cos(mu)$. Since $k_L(Ls)$ and $\cos(2\pi ns)$ are even functions, we see that $\Re\lambda_1$ is independent of b_m to this order. Recall that $k_L(Ls)$ is the periodized version of some connectivity kernel, $K(x)$. Let $\hat{K}(\nu)$ be the Fourier transform of $K(x)$. Then, using trigonometric identities and the Fourier expansion of $\Delta(u)$, we obtain:

$$\Re\lambda_1 = L \sum_{m>0} m a_m \Big[\hat{K}(2\pi m/L) - (1/2)(\hat{K}(2\pi(m-n)/L) + \hat{K}(2\pi(m+n)/L)) \Big]. \tag{23}$$

Setting $n = \pm m$ and letting $L \to 0$, we see that

$$\frac{\Re\lambda_1}{L} \to -n a_n \hat{K}(0)/2.$$

Recall in the remarks after Eq. (6), that we showed that synchrony was stable if $\Delta'(0) < 0$. This implies $\sum_m m a_m < 0$. Thus, there must be some n such that $n a_n < 0$. Thus, for short waves (L small), we find that $\Re\lambda_1 > 0$ for some n and these waves are unstable. For long waves, $L \to \infty$, we see that

$$L\Re\lambda_1 \to -(1/2)\hat{K}''(0) n^2 \sum_{m>0} m a_m.$$

For kernels like the exponential and the Gaussian, 0 is a local maximum for $\hat{K}$, so $\hat{K}''(0) < 0$ and so with the hypothesis that $\Delta'(0) < 0$ (synchrony is stable), we see that waves that are sufficiently long are stable.

If we suppose $a_1 < 0$ and $m = 1$ is the dominant mode in $\Delta(u)$, then we can solve Eq (23) for the critical value of L, L_c by solving

$$\hat{K}(\nu) - (1 + \hat{K}(2\nu))/2 = 0 \tag{24}$$

for $\nu > 0$ and then $L_c = 2\pi/\nu$ is the minimal stable wave-length.

Example For our present model (sinusoidal PRC and exponential kernel), we find that

$$\Re\lambda_1 = -2n^2 L^2 \pi \cos(b) \frac{L^2 + \pi^2(4n^2 - 12)}{(L^2 + 4\pi^2)(4(n+1)^2\pi^2 + L^2)(4(n-1)^2\pi^2 + L^2)}.$$

For $n > 1$ and $b \in (-\pi/2, \pi/2)$, $\Re\lambda_1 < 0$, so that all lengths are stable to these modes independent of L. However, for $n = 1$, we see that $\Re\lambda_1$ is positive for $L < 2\pi\sqrt{2} \approx 8.88$, so that waves on short rings are unstable. We note that the Fourier transform of the exponential is $1/(1 + \nu^2)$ so that solving Eq. (24) we find $\nu = \sqrt{2}/2$ and get the same value for the critical L. This value of L is pretty close to the value of 9.2 that we saw in Fig. 2a where $\epsilon = 1$. For a Gaussian kernel, the Fourier transform is $\exp(-n^2/4)$, the solution to Eq. (24) is $\nu \approx 1.559$ and the critical value is approximately 4.03. So Gaussian kernels tolerate much smaller values of L than exponentials.

Finally, turning to the "mitral cell" PRC, Eq. (14), we can obtain an expression for the real part of the eigenvalue (although it is very cumbersome). We find, just as in Fig. 3c, that for $b = 0.5$, the critical length for stability increases with d; specifically, $L_c = 8.96, 9.79, 13.26$ for $d = 0, 25, 0.5, 1.0$ respectively. These are very close matches with the filled circles in Fig. 3c, even though $\epsilon = 1$.

2.5 Smooth coupling

In the previous sections, we have focused on coupling that is via a Dirac δ-function. Thus, it would be interesting to check if the qualitative behavior such as the dispersion relation and stability persists for smooth functions. For this reason, we return to Eq. (3) and numerically analyze the behavior for the case in $R(u) = N(\gamma)\exp(-\gamma(1-\cos u))$ where $N(\gamma)$ is chosen so that the integral of $R(u)$ is 1. A qualitatively similar form of pulse coupling, $R(u) = A(\gamma)(1 + \cos u)^\gamma$, was used in Luke et al. (2013); both approach a periodic Dirac δ-function as the parameter $\gamma \to \infty$. In the context of coupled neurons, the effects of one neuron on the other are typically quite short-lived and centered near the peak of the sending neuron's action potential. For purposes of illustration, we take $\gamma = 20, 50$ so that the pulse is fairly sharp (Fig. 5a) and choose $\Delta(u) = a(\sin(b) - \sin(u+b))$ with $a = 2$, $b = 0.5$. We use the periodized exponential kernel so that we can convert the the existence of a pulse into a simple boundary value problem. If we write

$$W(x,t) = \int_0^L k_L(x-y)R(u(y,t))\,dy$$

with $k_L(x)$, exponential, then

$$\frac{\partial^2 W(x,t)}{\partial x^2} = W(x,t) - R(u(x,t)). \tag{25}$$

Traveling waves satisfy:

$$\begin{aligned} c\frac{du}{d\xi} &= 1 + \Delta(u)W \\ \frac{d^2 W}{d\xi^2} &= W - R(u) \end{aligned}$$

with $W(0) = W(l)$, $W_\xi(0) = W_\xi(L)$. Fig. 5b shows the period, $P = L/c$ as a function of L for the smooth model for the two values of γ along with the same for the delta function. The shapes are qualitatively the same and the $\gamma = 50$ case sits between the $\gamma = 20$ case and the δ-function as is expected. Finally, we can also numerically determine the stability of the pulse by linearizing about the traveling wave. We solve the eigenvalue problem:

$$\lambda v + c\frac{dv}{d\xi} = \Delta(u)w + \Delta'(u)Wv$$

$$\frac{d^2w}{d\xi^2} = w - R'(u)v$$

for (v, w, λ). By starting with $\Im\lambda = n$ we can examine the stability to different modes. We find that $n > 1$ always leads to $\Re\lambda < 0$, but $n = 1$ induces an instability, just as in the δ-function case. Figure 5c shows $\Re\lambda$ as a function of L for $\gamma = 20, 50$ and the δ-function case. The curves are nearly indistinguishable and cross zero at nearly the same value of L. Thus, just as in previous sections, we see that waves on short rings are unstable.

3 Discussion

In this paper, we have analyzed the existence and stability of traveling waves for a continuum network on a one-dimensional ring of non-locally coupled oscillators where the phase-resetting curve allows for stable synchrony. We have shown that if synchrony is stable then, traveling waves on sufficiently long rings are also stable. We also showed that if the ring length is too short, then the waves are unstable. We have focused on homogeneous networks in this study since we are able to reduce the existence and stability to the study of two-point boundary value problems (BVP). One obvious extension of this work would be to explore the susceptibility to noise or heterogeneity. For sinusoidal PRCs and δ-function coupling, it is possible to extend the Ott-Antonsen approach (Laing 2014, 2016; Wolfrum et al. 2016) to incorporate spatially distributed networks. The advantage of this formulation is that one can still find the wave via a BVP. The approach we have taken here is reminiscent of that used in Chen and Ermentrout (2017) for the existence of pulses in a non-locally coupled excitable medium. In that paper, the authors analyzed a solitary pulse on the infinite line and did not compute the dispersion relation or the stability of the waves. In general, stability is difficult to compute except in cases where the dynamics is governed by non-smooth systems such as the present δ-function approach and the work of Coombes and collaborators (Coombes 2005) where the step function figures prominently.

We found a close connection between the present work and that of Ermentrout (1985) which studied the case nonlocal coupling in phase-difference oscillators. Indeed, the first order perturbation agrees with that paper and the stability calculation. Interestingly, the dispersion relation is flat to lowest order when the PRC is a pure sinusoid, as also predicted by weak coupling analysis. However, here we are able to compute higher order terms in the pure sine case that show dispersive behavior seen in the finite amplitude simulations.

We have focused exclusively on waves with *winding number 1*, that is $u(x, t)$ advances by 2π as x goes from 0 to L. Waves with winding number $m > 1$ are equivalent to waves of winding number 1 on a ring of length L/m. In our case, a wave with winding number 0 is just synchrony. However, an interesting question is whether there are other types of waves besides these simple plane waves. In Heitmann and Ermentrout (2015), the authors found so-called “ripple waves”, modulated periodic solutions could bifurcate from the simple plane waves when the coupling kernel, $k_L(x)$

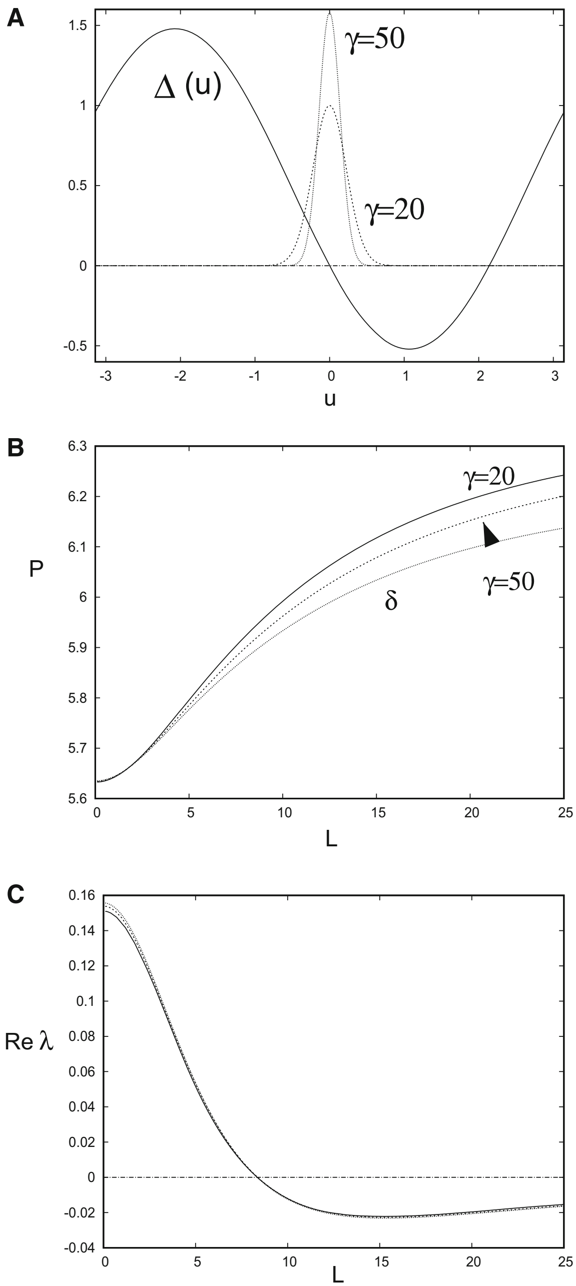

Fig. 5 Behavior of Eq. (7) when the kernel $R(u) = N(\gamma)\exp(-\gamma(1-\cos(u)))$ for $\Delta(u) = 2(0.5 - \sin(u+0.5))$. **a** The PRC, $\Delta(u)$ along with $R(u)$ for $\gamma = 20, 50$ (all scaled to fit in the figure); **b** Period (P) as a function of ring-length, L for the smooth kernel and the Dirac δ-function for comparison; **c** Stability ($\Re\lambda$) to $n = 1$ mode perturbations as a function of ring-length for the smooth functions and the Dirac δ-function

is positive for x near 0 and sufficiently negative for x near $\pm L/2$. We conjecture that if $k_L(x) \geq 0$, then the plane waves are the only stable solutions.

Another interesting question is whether there are rotating waves in two-dimensions with non-local pulse coupling. In Ermentrout and van der Ventel (2016) the authors looked an excitable phase models on an annulus with diffusive coupling. Extending this work to non-local coupling and oscillatory dynamics may be relevant to behavior in the brain where there is strong evidence of rotating waves both *in vitro* Huang et al. (2004), Huang et al. (2010) and *in vivo* Muller et al. (2016). Unlike the case in the brain slice, the *in vivo* waves appear to be phase waves generated by oscillators. Thus, the approach here may be of use. As we have shown in this paper, waves that occur in a ring lose stability as the length of the ring decreases. This suggests that there may be a limit to the size of the hole in the annulus such that the rotating waves are stable.

Finally, it remains to be seen how much of this work could be extended beyond phase models. One intriguing approach is the use of so-called isostable reductions (Wilson and Ermentrout 2019; Ermentrout et al. 2019) or higher order phase models (León and Pazó 2019). Thus, in addition to Eq. (7), there would be an amplitude equation (or multiple amplitude equations) that are coupled to the spatial phase. It is unclear whether the behavior in this extended case would be qualitatively different or richer than the simple phase models. Typically, the amplitude terms have little effect unless near bifurcations.

In conclusion, we have shown that a continuum network of nonlocally coupled oscillators that show stable synchrony is able to additionally support stable traveling waves on rings that are sufficiently long. Traveling phase waves have been shown to occur in cortex and our work shows that such behavior is expected whenever are intrinsically oscillatory dynamics and synchronizing coupling.

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