The Winfree model with heterogeneous phase-response curves: analytical results

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Abstract
We study an extension of the Winfree model of coupled phase oscillators in which both natural frequencies and phase-response curves (PRCs) are heterogeneous. In the first part of the paper we resort to averaging and derive an approximate model, in which the oscillators are coupled through their phase differences. Remarkably, this simplified model is the ‘Kuramoto model with distributed shear’ (Montbrió and Pazó 2011 Phys. Rev. Lett. 106 254101). Using this approximation, we find that above a critical level of PRC heterogeneity the incoherent state is always stable. In the second part of the paper we perform the analysis of the full model for Lorentzian heterogeneities, resorting to the Ott–Antonsen ansatz. As expected, the results obtained using the full model are fully consistent with those obtained using the averaging approximation. However, we find that the critical level of PRC heterogeneity obtained within the averaging approximation has a different manifestation in the full model depending on the sign of the center of the distribution of PRCs.

Keywords: Winfree model, Kuramoto model, phase-response curve, synchronization

(Some figures may appear in colour only in the online journal)

1. Introduction

The Winfree model (Winfree 1967, 1980) is a milestone in the mathematical description of collective synchronization. Inspired by the synchronization of biological oscillators, Winfree proposed a model consisting of a large population \( N \gg 1 \) of interacting limit cycle
oscillators with heterogeneous natural frequencies, capable of self-synchronizing macroscopically, see e.g. Strogatz (2003). As simplifying assumptions, he prescribed that the phases $\theta_i (i = 1, \ldots, N)$ were the only degrees of freedom, and that the interactions were equally weighted and global, i.e. mean-field type. Despite its deep conceptual influence, the theoretical description of the Winfree model remains a challenging problem and analytical progress is scarce, even under several simplifying assumptions. Some works have considered the thermodynamic limit of the model, i.e. $N \to \infty$, obtaining exact results (Ariaratnam and Strogatz 2001, Quinn et al 2007, Basnarkov and Urumov 2009, Pazó and Montbrió 2014, Gallego et al 2017). Conversely, other works have addressed the finite-$N$ case obtaining either bounds for the synchronization region (Oukil et al 2017, 2018) or the behavior for the large coupling regime (Ha et al 2015). Approximations of the Winfree model have been studied in Tsubo et al (2007b) and Politi and Rosenblum (2015). Finally, extensions of the Winfree model include analyzing the case of state-dependent coupling strength (Giannuzzi et al 2007), as well as the proposal of including ‘dynamic synapses’ (Laing 2017).

In the Winfree model, each oscillator responds to the incoming pulses according to the value of the phase-response curve (PRC). Specifically, the PRC—also called infinitesimal PRC, phase resetting curve, or sensitivity function (Izhikevich 2007)—is a function of only the oscillator’s own phase, and determines the advance or delay of its phase in response to a certain perturbation. The PRC plays a fundamental role in neuroscience (Smeal et al 2010, Schultheiss et al 2012), and it has been determined experimentally in cortical neurons (Reyes and Fetz 1993a, 1993b, Netoff et al 2005, Mancilla et al 2007, Tateno and Robinson 2007, Tsubo et al 2007a), hippocampal neurons (Lengyel et al 2005), mitral cells (Galán et al 2005), or in neurons of the abdominal ganglia of Aplysia (Preyer and Butera 2005). Additionally, synchronization of biological oscillators such as fireflies (Buck 1988), tropical katydids (Sismondo 1990) and the human heart (Kralemann et al 2013) have been analyzed through PRCs. The concept of PRC is also important for technological applications such as electric oscillators (Hajimiri and Lee 1998) or wireless sensor nets, see e.g. Nishimura and Friedman (2011) and references therein.

In its original form the Winfree model consists of oscillators with heterogeneous natural frequencies. Yet, it is reasonable to assume that heterogeneity may well also be present in other system’s parameters, and that this may influence synchronization. Indeed, broad cell-to-cell differences in PRCs have been measured in the olfactory bulb mitral cells (Burton et al 2012), and pyramidal cells—specially for different cortical layers (Tsubo et al 2007a). Given that the collective phase dynamics of a synchronized ensemble of oscillators depends crucially on the level of PRC heterogeneity (Nakao et al 2018), it is desirable to deepen our understanding on the effects of heterogeneous PRCs on collective synchronization. However, due to its mathematical complexity, previous attempts to tackle oscillator ensembles with heterogeneous PRCs are scarce, and rely on approximate methods (Tsubo et al 2007b, Ly 2014).

In this paper, we study an extension of the classical Winfree model with heterogeneous natural frequencies and PRCs. In section 2 we present the model. An approximate version of it, based on averaging, is analyzed in section 3. Section 4 presents exact results obtained by means of the Ott–Antonsen theory. Finally, in section 5 we summarize the main conclusions of our work, and suggest future lines of research.

2. Model description

The Winfree model consists of an ensemble of $N \gg 1$ all-to-all coupled phase oscillators whose phases $\theta_i (i = 1, \ldots, N)$ evolve according to the following set of $N$ coupled ordinary differential equations (ODEs):
\[ \dot{\theta}_i = \omega_i + Q_i(\theta_i) \frac{\varepsilon}{N} \sum_{j=1}^{N} P(\theta_j). \]  

(1)

Here, \( \omega_i \) are the natural frequencies, and \( \varepsilon > 0 \) is a parameter controlling the coupling strength.

The function \( P \) specifies the form of the pulses, and the response of the \( i \)th oscillator to the mean field \( N^{-1} \sum_j P(\theta_j) \) is determined by the PRC function \( Q_i(\theta) \).

Note that in (1), the subscript \( i \) appears twice in the right hand-side: in the natural frequencies, and in the PRCs. Specifically, we consider the monoparametric family of PRCs

\[ Q_i(\theta) = q_i (1 - \cos \theta) - \sin \theta, \] 

(2)

where parameter \( q_i \) controls if the PRC is more positive than negative (\( q_i > 0 \)), or the other way around (\( q_i < 0 \)), see figure 1(a). With the parametrization adopted here we have \( Q_i(0) = 0 \), since we choose \( \theta = 0 \) as the point where the pulse peaks.

The pulse \( P(\theta) \) is assumed to be a symmetric unimodal function in the interval \([-\pi, \pi]\], with the normalization \( \int_{-\pi}^{\pi} P(\theta) d\theta = 2\pi \). In section 4, we adopt the pulse function (Gallego et al. 2017):

\[ P(\theta) = \frac{(1-r)(1+\cos \theta)}{1-2r\cos \theta + r^2}, \] 

(3)

which vanishes at \( \theta = \pi \). Parameter \( r \), controlling the width of the pulse, spans between \(-1\) (flat pulse) and 1 (Dirac-delta pulse, \( P(\theta) = 2\pi \delta(\theta) \)), see examples in figure 1(b).

In section 3 we study the approximation of (1) and (2) based on averaging. The results in that section depend exclusively on the first Fourier mode of \( P(\theta) \), and not on the other features of the pulse. The specific pulse type is, nonetheless, relevant for the exact results in section 4. Our study is focused on determining the parameter values where the completely asynchronous state is unstable, making certain level of synchrony unavoidable. By synchrony, we refer to a state in which a macroscopic fraction of the ensemble is entrained to the same frequency and remains phase locked.

### 3. Averaging approximation

In this section we analyze an approximation of the Winfree model with heterogeneous PRCs, which is particularly amenable to theoretical analysis. This permits to study general distributions of \( \omega \) and \( q \), and at the same time, the results obtained serve as a guide for section 4, where an exact analysis is presented.

#### 3.1. Derivation of the averaged model

Using the method of averaging (Kuramoto 1984), valid for weak coupling and small frequency dispersion, the system of \( N \) ODEs (1) may be simplified to a model where interactions are described exclusively by phase differences. First of all, we write the original phases \( \theta_i \) in terms of ‘slow phases’ \( \phi_i \); \( \theta_i(t) = \omega_i t + \phi_i(t) \). The slow dynamics follows

\[ \dot{\phi}_i = \frac{\varepsilon}{N} \sum_{j=1}^{N} \{ q_i [1 - \cos(\omega_j t + \phi_j)] - \sin(\omega_j t + \phi_j) \} P(\omega_j t + \phi_j). \] 

(4)

The exact solution satisfies \( T^{-1}[\phi_i(T) - \phi_i(0)] = T^{-1} \int_0^T \dot{\phi}_i dt \). Assuming \( \omega_j \approx \omega_i \) only a few terms do not average out if the integral is taken over a large period \( T \) (of the order of the
oscillation period). As an example of this reasoning, let us particularize for the cosine term. After writing the Fourier expansion of 

\[ P(\theta) = \sum_{n=\infty}^{-\infty} \hat{p}_n e^{in\theta}, \]

we find that for the cosine term only two terms survive:

\[
\int_0^T \cos(\omega_i t + \phi_i) \left[ \sum_n \hat{p}_n e^{in(\omega_j t + \phi_j)} \right] dt \\
\approx \frac{1}{2} \int_0^T \hat{p}_1 e^{i(\omega_j - \omega_i) t + \phi_j - \phi_i} dt + \hat{p}_{-1} e^{i(\omega_j - \omega_i) t + \phi_j - \phi_i} dt \\
= \hat{p}_1 \int_0^T \cos[(\omega_j - \omega_i) t + \phi_j - \phi_i] dt
\]

where in the last equality we have assumed an even pulse: \( \hat{p}_1 = \hat{p}_{-1} \in \mathbb{R} \). In sum, the dynamics of \( \phi_i \) splits into an averaged part \( \phi_i^{(av)} \) and irrelevant (at order \( \epsilon \)) fast fluctuations. The time derivative of \( \phi_i^{(av)} \) depends on the other phases only through \( \phi_j^{(av)} - \phi_i^{(av)} + (\omega_j - \omega_i)t \). It is more intuitive to return to the original frame defining \( \theta_i^{(av)}(t) = \omega_i t + \phi_i^{(av)}(t) \). We get

\[
\dot{\theta}_i = \omega_i + \epsilon q_i + \Pi \frac{\epsilon}{N} \sum_{j=1}^N [\sin(\theta_j - \theta_i) - q_i \cos(\theta_j - \theta_i)],
\]

at the lowest order in \( \epsilon \) (the superscript \( \text{av} \)) is omitted for simplicity). The sinusoidal shape of the PRCs is responsible of (i) the absence of higher harmonics in the coupling functions, and (ii) the presence of the constant \( \Pi = \hat{p}_1 \), a ‘shape factor’ that equals the first Fourier mode of the pulse. Specifically, for the pulse type in (3),

\[
\Pi = \frac{1 + r}{2},
\]

and therefore \( 0 \leq \Pi \leq 1 \) for this and other pulses (Gallego et al 2017). The largest \( \Pi \) value is 1 and it is attained in the limit case of a Dirac delta Pulse, \( P(\theta) = 2\pi \delta(\theta) \). Remarkably, in this limit the model in (5) coincides with the ‘Kuramoto model with distributed shear’, which was originally deduced as a phase approximation for globally coupled Stuart–Landau oscillators with distributed natural frequencies and shears (or nonisochronities) (Montbrió and Pazó 2011). Instead, here the Kuramoto model (5) is obtained from the Winfree model with
heterogeneous PRCs. This coincidence permits to use the results in Montbrió and Pazó (2011) for \( \Pi = 1 \), and apply the same analysis for the case \( \Pi < 1 \).

In terms of the Kuramoto order parameter, \( Z \equiv \Re e^{i\psi} = N^{-1} \sum e^{i\theta} \), model (5) can be alternatively written as,

\[
\dot{\theta}_i = \omega_i + \epsilon q_i + \Pi \epsilon R [\sin(\psi - \theta_i) - q_i \cos(\psi - \theta_i)],
\]

emphasizing in this way the mean-field character of the model.

3.2. Linear stability analysis of incoherence

Hereafter we only consider the thermodynamic limit \( (N \to \infty) \) of the model. Hence, we define a phase density \( f(\theta|\omega, q, t) \) of oscillators with frequency \( \omega \) and PRC-parameter \( q \) at time \( t \). The mean field \( Z \) in this continuous formulation becomes

\[
Z(t) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} p(\omega, q) \int_{-\pi}^{\pi} f(\theta|\omega, q, t) e^{i\theta} \, d\omega \, dq,
\]

where \( p(\omega, q) \) is the joint probability distribution of \( \omega \) and \( q \). In the uniform incoherent state the oscillators are uniformly scattered in the unit circle, or otherwise said, \( f \) equals \((2\pi)^{-1}\), and therefore the mean field vanishes, \( Z = 0 \). In an arbitrary state, \( f \) is constrained to obey the continuity equation (Strogatz and Mirollo 1991, Montbrió and Pazó 2011):

\[
\partial_t f = -\partial_{\theta} \left( \left\{ \omega + \epsilon q + \frac{\Pi \epsilon}{2i} [Ze^{-i\theta} (1 - iq) - \text{c.c.}] \right\} f \right)
\]

(c.c. denotes complex conjugate), because of the conservation of the number of oscillators. Note that this is a nonlinear equation since \( Z \) depends on \( f \) through (8). For the analysis that follows we write the Fourier series of \( f \):

\[
f(\theta|\omega, q, t) = \frac{1}{2\pi} \sum_{l=-\infty}^{\infty} \hat{f}_l(\omega, q, t) e^{i\theta},
\]

with \( \hat{f}_0 = 1 \), and \( \hat{f}_l = \hat{f}_{-l} \). We can insert (10) into (9) obtaining an infinite set of integro-differential equations that govern the evolution of \( \hat{f}_l \) in terms of itself, \( \hat{f}_{l\pm 1} \), and the mean field \( Z \):

\[
\partial_{\theta} \hat{f}_l = -i(\omega + \epsilon q) \hat{f}_l - \frac{\Pi \epsilon}{2} \left\{ Z \hat{f}_{l+1}(1 - iq) - Z^* \hat{f}_{l-1}(1 + iq) \right\},
\]

(the asterisk denotes the complex conjugation). It is crucial to note that, according to (8), \( Z \) depends only on the first Fourier mode of the density:

\[
Z^*(t) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} p(\omega, q) \hat{f}_1(\omega, q, t) \, d\omega \, dq \equiv \langle \hat{f}_1 \rangle.
\]

(12)

(The bracket is used hereafter to denote the average over \( \omega \) and \( q \) ) Then, it can be easily verified in (11) that infinitesimal deviations from uniform incoherence \( (f_{i \neq 0} = 0) \) are governed solely by the first Fourier mode:

\[
\partial_{\theta} \hat{f}_1 = -i(\omega + \epsilon q) \hat{f}_1 + \frac{\Pi \epsilon}{2} (1 + iq) \langle \hat{f}_1 \rangle.
\]

(13)

A succession of well-known steps permits to determine the linear stability of incoherence (Strogatz and Mirollo 1991, Strogatz 2000): (i) insert the ansatz corresponding to an
exponential growth rate \( \lambda \), in (13); (ii) isolate \( b \) in the left hand-side; (iii) multiply both sides of the equation by \( p(\omega, q) \); and (iv) integrate over \( \omega \) and \( q \). These steps yield a self-consistent condition:

\[
\frac{2}{\Pi \varepsilon} \left< \frac{1 + i q}{\lambda + i (\omega + \varepsilon q)} \right> = 0.
\]  

(14)

We can split this equation into a system of two equations for the imaginary and real parts:

\[
0 = \left< \frac{q \lambda_R - (\omega + \lambda_I + q \varepsilon)}{\lambda_R^2 + (\omega + \lambda_I + q \varepsilon)^2} \right>,
\]

\[
\frac{2}{\Pi \varepsilon} = \left< \frac{\lambda_R + q (\omega + \lambda_I + q \varepsilon)}{\lambda_R^2 + (\omega + \lambda_I + q \varepsilon)^2} \right>,
\]

(15)

where \( \lambda_R = \text{Re} \lambda \) and \( \lambda_I = \text{Im} \lambda \). For simplicity, we consider hereafter \( \omega \) and \( q \) to be independently distributed, i.e. \( p(\omega, q) = g(\omega)h(q) \)—for correlated distributions with \( \Pi = 1 \), see Pazó and Montbró (2011). Moreover, it is convenient to assume that \( g \) and \( h \) are unimodal symmetric functions (Strogatz and Mirollo 1991). We can freely choose \( g(\omega) \) centered at zero, since this can always be achieved by going to a rotating frame if necessary, while \( h(q) \) is centered at a specific \( q_0 \) value. Note also that changing the sign of \( \omega \) and \( q \) in (14) transforms \( \lambda \) into \( \lambda^* \), meaning that within the averaging approximation the sign of \( q_0 \) is irrelevant concerning the stability properties. To compute the stability boundary we take the limit \( \lambda_R \to 0^+ \) in (15), and obtain:

\[
0 = \left< \pi q \delta (\lambda_I + q \varepsilon + \omega) - \frac{1}{\lambda_I + q \varepsilon + \omega} \right>,
\]

\[
\frac{2}{\Pi \varepsilon} = \left< \pi \delta (\lambda_I + q \varepsilon + \omega) + \frac{q}{\lambda_I + q \varepsilon + \omega} \right>.
\]  

(16)

3.3. Lorentzian heterogeneities

For Lorentzian distributions

\[
g(\omega) = \frac{\Delta / \pi}{(\omega - \omega_0)^2 + \Delta^2}, \quad h(q) = \frac{\gamma / \pi}{(q - q_0)^2 + \gamma^2},
\]

(17)

solving (16) yields the critical coupling strength\(^4\) where incoherence becomes unstable

\[
\varepsilon_c = \frac{2 \Delta}{\Pi - \gamma (2 - \Pi)},
\]

(18)

which holds only for positive \( \varepsilon \). Notably, (18) is independent of \( q_0 \), a peculiarity of the Lorentzian distribution (in contrast to the independence on \( \omega_0 \) discussed above). For a given \( \Pi \) value, see figure 2(a), the function \( \varepsilon_c(\gamma) / \Delta \) in (18) defines a curve in the \( (\gamma, \varepsilon / \Delta) \) plane that emanates from the \( \varepsilon / \Delta \)-axis at \( 2 / \Pi \) and grows monotonically up to a critical value

\[
\gamma_c = \frac{\Pi}{2 - \Pi}.
\]

(19)

\(^4\)In this case is perhaps easier to resort to the Ott–Antonsen ansatz, rather than (16). The result is obviously independent of the method chosen.
where the curve diverges. In turn, incoherence is always stable for $\gamma > \gamma_\infty$. As can be seen in figure 2(c), the formula (18) can be condensed into a single curve with rescaled variables:

$$\frac{\varepsilon_c \Pi}{\Delta} = \frac{2}{1 - \gamma/\gamma_\infty}. \quad (20)$$

### 3.4. Gaussian heterogeneities

The analysis of distributions different from (17) is more cumbersome. We consider here only Gaussian heterogeneities:

$$g(\omega) = \frac{1}{\sqrt{2\pi\sigma}} e^{-\omega^2/(2\sigma^2)}, \quad h(q) = \frac{1}{\sqrt{2\pi\nu}} e^{-(q-q_0)^2/(2\nu^2)}. \quad (21)$$

The calculations are greatly simplified if $h(q)$ is centered at zero, i.e. $q_0 = 0$. In this case, after some manipulations of (16), we get a closed formula for the critical coupling

$$\varepsilon_c^{(q_0=0)} = \frac{4\sigma}{\sqrt{\pi\Pi^3(16\nu^2 + \pi\Pi) + \pi\Pi^2 + 8\nu^2(\Pi - 2)}}^{1/2}. \quad (22)$$

For $\Pi = 1$ we recover the result in Montbrió and Pazó (2011). Equation (22) defines a region in the $(\nu, \varepsilon/\sigma)$ plane that is maximal for $\Pi = 1$ and progressively shrinks as $\Pi$ is decreased, see figure 2(b) for several $\Pi$ values. The line (22) is born at $\nu = 0$ with $\varepsilon_c/\sigma = \sqrt{8/\pi}/\Pi$, and diverges at a critical value of $\nu$:

$$\nu^{(q_0=0)} = \frac{\Pi}{2 - \Pi} \sqrt{\frac{\pi}{2}}. \quad (23)$$

Equation (22) cannot be recast into a single formula valid for all $\Pi$ values, rescaling $\varepsilon_c$ and $\nu$. We see in figure 2(d) that a rescaling analogous to (20) yields an imperfect collapse of the boundaries.

Finally, we stress that our stability analysis is local, and hence stable incoherence does not preclude its coexistence with a partially synchronized state, as it may occur for $\Pi = 1$ see Montbrió and Pazó (2011).

### 3.5. Critical PRC heterogeneity

The Lorentzian (17) and Gaussian (21) joint distributions exhibit a critical value of heterogeneity in $q$ such that, if $q$ is too heterogeneous, incoherence becomes stable for all $\varepsilon$. Next, we investigate if a general rule—for unimodal symmetric $h(q)$—exists. First of all we neglect the diversity of $\omega$ in (16), since we are interested in the limit $\varepsilon_c \to \infty$. Intuitively, the term $\varepsilon q_1$ in (5) can be as large in magnitude with respect to $\omega_i$ as desired. Mathematically, we can hence neglect the heterogeneity of $\omega$ taking $g(\omega) = \delta(\omega)$. In addition, we rescale $\lambda_I$ by $\varepsilon_c$ and define $\lambda_I = \Lambda \varepsilon_c$. In this way the dependence on $\varepsilon_c$ in (16) cancels out, and we obtain the conditions:

$$0 = -\pi \Lambda h_\infty(-\Lambda) - \int_{-\infty}^{\infty} \frac{1}{\Lambda + q} h_\infty(q) \, dq. \quad (24a)$$

$$2 \Pi^{-1} = \pi h_\infty(-\Lambda) + \int_{-\infty}^{\infty} \frac{q}{\Lambda + q} h_\infty(q) \, dq. \quad (24b)$$
Here, $h_\infty$ means the critical distribution of $h(q)$ such that the stability boundary is at $\varepsilon_c = \infty$. In other words, if $h(q)$ becomes infinitesimally broader, incoherence becomes stable for all $\varepsilon$. To get rid of the integral, we can multiply (24a) by $\Lambda$ and subtract (24b) obtaining:

$$2 \Pi^{-1} - 1 = h_\infty (-\Lambda).$$

(25)

Additionally, multiplying (24b) by $\Lambda$ and adding (24a) yields after trivial manipulations:

$$\left(2 \Pi^{-1} - 1\right) \Lambda = -(1 + \Lambda^2) \int_{-\infty}^{\infty} h_\infty (q - \Lambda) \frac{dq}{q}.$$

(26)

### 3.5.1. Centered $h(q) (q_0 = 0)$

If $h(q)$ is centered at zero, symmetry imposes the trivial solution $\Lambda = 0$ in (26) (we are interpreting the integral in the Cauchy principal value sense). If $\Lambda > 0$ the integral in (26) is positive and the condition cannot be fulfilled, likewise for $\Lambda < 0$. In consequence we get from (25) the remarkable result that the divergence of $\varepsilon_c$ is linked to a simple condition for the distribution maximum:

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**Figure 2.** (a) and (b) Stability boundary of incoherence in the different values of $\Pi$, with (a) Lorentzian, and (b) Gaussian PRC heterogeneities. In panel (a) the value of $q_0$ is irrelevant, while in panel (b) $q_0 = 0$. The shaded regions correspond to unstable incoherence for $\Pi = 1$. Panels (c) and (d) show the same boundaries after rescaling the axes. In the case of Gaussian heterogeneity, panel (d), the curves fail to collapse.

3.5.1. Centered $h(q) (q_0 = 0)$. If $h(q)$ is centered at zero, symmetry imposes the trivial solution $\Lambda = 0$ in (26) (we are interpreting the integral in the Cauchy principal value sense). If $\Lambda > 0$ the integral in (26) is positive and the condition cannot be fulfilled, likewise for $\Lambda < 0$. In consequence we get from (25) the remarkable result that the divergence of $\varepsilon_c$ is linked to a simple condition for the distribution maximum:
Indeed, imposing this condition to the Lorentzian and Gaussian distributions, we recover (19) and (23), respectively. As expected, the region of stable incoherence widens as $\Pi$ decreases, since in the limit $\Pi \to 0$ the contribution of the first harmonic vanishes. Equation (27) is a generalization for arbitrary $\Pi$ of $h_\infty(0) = \pi^{-1}$ for $\Pi = 1$ (Montbrió and Pazó 2011).

3.5.2. Off-centered $h(q)$ ($q_0 \neq 0$). If the distribution of $q$ is not centered at zero, criterion (27) is not valid. Apart of solving equations (25) and (26) numerically, one may resort to perturbation theory for small values of $|q_0|$. To avoid further complications we adopt $\Pi = 1$ in the calculation that follows—we can rescale (25) and (26) by $2 \Pi^{-1} - 1$ and recover this factor at the end of the calculation. Thus, let us define first an even function $\tilde{h}$ setting the origin at $q_0$,

$$\tilde{h}(q) = h(q + q_0).$$

Equations (25) and (26) become then:

$$\frac{1}{\pi(1 + \Lambda^2)} = \tilde{h}_\infty(-q_0 - \Lambda),$$

$$\Lambda = -(1 + \Lambda^2) \int_{-\infty}^{\infty} \tilde{h}_\infty(q - q_0 - \Lambda) \frac{dq}{q}. \tag{29b}$$

At criticality we expect a generalization of (27) of the form

$$\tilde{h}_\infty(q_0)(0) = \tilde{h}_\infty^{(q_0=0)}(0) + \eta(q_0), \tag{30}$$

where $\tilde{h}_\infty^{(q_0=0)}(0) = \pi^{-1}$, and $\eta$ is an even function with $\eta(0) = 0$.

Assuming small $|q_0|$ and $|\Lambda|$ and twice differentiability of $\tilde{h}(q)$ we approximate (29a) and (29b) at leading order

$$0 = \Lambda^2 + \eta(q_0) + \frac{\pi}{2} (\Lambda + q_0) \frac{d^2}{dq^2} \tilde{h}_\infty^{(q_0=0)}(0), \tag{31a}$$

$$\Lambda = (\Lambda + q_0) I, \tag{31b}$$

where $I = \int_{-\infty}^{\infty} q^{-1} \frac{d^2}{dq^2} \tilde{h}_\infty^{(q_0=0)}(q) \, dq$. Then, after some algebra we get $\eta(q_0) = bq_0^2$, with the constant $b$:

$$b = -\frac{I^2 + \frac{\pi}{2} \frac{d^2}{dq^2} \tilde{h}_\infty^{(q_0=0)}(0)}{(1 - I)^2}. \tag{32}$$

For the Lorentzian distribution $b = 0$, in consistency with the independence of $\gamma_\infty$ on $q_0$. For the Gaussian distribution $b = -(4 - \pi)(2 + \pi)^{-2} = -0.0325 \ldots$ In terms of $\nu_\infty$, and recovering the $(2 \Pi^{-1} - 1)$ factor, this means:

$$\nu_\infty^{(q_0)} \simeq \frac{\Pi}{2 - \Pi} \sqrt{\frac{\pi}{2}} \left(1 - \sqrt{\pi bq_0^2}\right). \tag{33}$$

This is the perturbative extension at order $q_0^2$ of (23), which implies that unstable incoherence may achieve larger values of $\nu$, i.e. broader distributions.
4. Exact analysis: Ott–Antonsen ansatz

Our aim is now the study of the full Winfree model defined by (1)–(3), with no other approximation than the thermodynamic limit. However, to ensure mathematically tractability we restrict our analysis to Lorentzian heterogeneities (17). The stability boundary of asynchrony in the \((\Delta, \varepsilon)\) plane is obtained below for different values of \(q_0, \gamma,\) and \(r.\) An interesting question is to elucidate how the critical value of PRC heterogeneity \(\gamma_\infty\) found in the averaged model translates into the full model. Recalling that \(\Pi(r) = (1 + r)/2\) for the pulse shape (3) and (19) yields:

\[
\gamma_\infty = \frac{1 + r}{3 - r}.
\] (34)

The averaged model in the preceding section predicts that for \(\gamma > \gamma_\infty,\) asynchrony is always stable, and the full model must agree with this in the weak coupling limit. We anticipate that the results that follow are perfectly consistent with (34), but the model will achieve this consistency in a different way depending on the sign of \(q_0.\)

4.1. Derivation of low-dimensional equations

As in section 3, we adopt the thermodynamic limit \(N \to \infty\) and define the density function \(F(\theta|\omega, q, t).\) This function obeys the continuity equation:

\[
\partial_t F = -\partial_\theta \left\{ [\omega + \varepsilon Q(\theta)H(t)] F \right\},
\] (35)

where \(H(t)\) is the mean field

\[
H(t) = \left\langle \int_0^{2\pi} F(\theta|\omega, q, t) P(\theta) d\theta \right\rangle.
\] (36)

For the theoretical analysis that follows we assume that \(F\) satisfies the Ott–Antonsen ansatz (Ott and Antonsen 2008):

\[
F(\theta|\omega, q, t) = \frac{1}{2\pi} \left\{ 1 + \sum_{m=1}^{\infty} \alpha(\omega, q, t)^m e^{im\theta} + \text{c.c.} \right\}.
\] (37)

Here, \(\alpha^*\) is the first Fourier mode of the density, and therefore:

\[
Z^*(t) = \langle \alpha(\omega, q, t) \rangle.
\] (38)

The Ott–Antonsen ansatz can be applied to the Winfree model (1), with the PRC distributed according to (2), since the model belongs to the family of phase models that can be written in the form:

\[
\dot{\theta}(x, t) = B(x, t) + \text{Im} \left[ G(x, t)e^{-it}\right],
\] (39)

where \(x\) is a vector containing different parameters that are distributed (Pikovsky and Rosenblum 2011, Pazó and Móntalván 2014, Pietras and Daffertshofer 2016). In our case \(x = (\omega, q),\) with \(B(x, t) = \omega + \varepsilon qH(t)\) and \(G(x, t) = \varepsilon(1 - iq)H(t).\) It has been shown that, if \(F\) does not initially satisfy (37), it subsequently converges to it—in the sense of Ott and Antonsen (2009) and Ott et al (2011). Theoretical studies (Vlasov et al 2016) suggest that finiteness of the population cannot be expected to drive the system away from the OA manifold, and hence the formulation in terms of densities is reliable. Since the original article of Ott
and Antonsen this has been confirmed numerically in a large number of works, see e.g. Pietras and Daffertshofer (2016) and references therein.

Inserting (37) into the continuity equation (35) we get an equation for $\alpha(\omega, q, t)$:

$$\partial_t \alpha = -i\omega\alpha + \frac{\varepsilon H}{2} \left[ 1 - \alpha^2 + iq(1 - \alpha)^2 \right].$$

(40)

Note that each $\alpha(\omega, q, t)$ is coupled to all the other $\alpha(\omega', q', t)$ through the mean field $H$, see (36). It was found in Gallego et al. (2017)—see also the supplemental material of Montbrió and Pazó (2018)—that for the pulse type (3) $H$ is related with $Z$ via

$$H(Z) = \text{Re} \left[ \frac{1 + Z}{1 - rZ} \right].$$

(41)

To proceed further with the analysis, we note that the equation governing $|\alpha|$ is

$$\partial_t |\alpha| = \frac{\varepsilon H}{2} (\cos \phi + q \sin \phi) \left( 1 - |\alpha|^2 \right),$$

(42)

where $\phi = \arg(\alpha)$. As the velocity vanishes at $|\alpha| = 1$, $\alpha$ cannot leave the unit disk—otherwise (37) is not convergent. In close analogy to previous work (Ott and Antonsen 2008, Montbrió and Pazó 2011) the next key observation is that $\alpha$ admits an analytic continuation into the lower half complex $\omega$-plane, and the lower half complex $q$-plane (for positive $\varepsilon$). If the field $\alpha(\omega, q, t)$ admits an analytic continuation at $t = 0$, this will be the case for $t > 0$ since $\alpha$ obeys the differential equation (40) (Coddington and Levinson 1955). The complexification of $\omega = |\omega|e^{i\xi}$ and $q = |q|e^{i\vartheta}$, transforms (42) into:

$$\partial_t |\alpha| = \omega |\alpha| \sin \xi + \frac{\varepsilon H}{2} \left\{ \cos \phi (1 - |\alpha|^2) \right. \left. + |q| \left[ \sin(\phi - \vartheta) + 2|\alpha| \sin \vartheta - |\alpha|^2 \sin(\phi + \vartheta) \right] \right\}. $$

(43)

At $|\alpha| = 1$ the velocity is

$$\partial_t |\alpha| = \omega |\alpha| \sin \xi + \varepsilon H |q| \sin \vartheta (1 - \cos \phi).$$

(44)

Provided $\sin \xi \leq 0$, and $\sin \vartheta \leq 0$ (for positive $\varepsilon$), $\partial_t |\alpha| \leq 0$. Therefore if $\alpha$ takes values initially inside the unit disk, this will hold for all $t > 0$.

The analytic continuation of $\alpha$ allows to apply twice the residue’s theorem to the integrals in (38) by closing the respective integration contours by large semicircles in the lower half $\omega$- and $q$-planes. As the Lorentzian distribution has only one pole inside the integration contour, a simple relation between $Z$ and $\alpha$ is found:

$$Z^*(t) = \alpha(\omega_p, q_p, t),$$

(45)

where $\omega_p = \omega_0 - i\Delta$ and $q_p = q_0 - i\gamma$ are the poles of $g(\omega)$ and $h(q)$, respectively. Hence we only have to evaluate (40) at $(\omega_p, q_p)$, in order to obtain one complex-valued ODE for $Z$:

$$\dot{Z} = i\omega_p^* Z + \frac{\varepsilon H(Z)}{2} \left[ 1 - Z^2 - iq_p^* (1 - Z)^2 \right].$$

(46)

where $H(Z)$ is given by (41). Equation (46) completely describes the asymptotic dynamics of the model (in the thermodynamic limit). Hereafter, we set $\omega_0 = 1$, since this can be achieved through trivial rescalings of time, $\Delta$ and $\varepsilon$ by $\omega_0 > 0$ in (46).
4.2. Analysis of the low-dimensional system (46)

Equation (46) is a planar system, generically with two possible attractor types: fixed point and limit cycle. Our previous work with homogeneous PRCs (Pazó and Montbrió 2014, Gallego et al 2017) revealed that the model may exhibit two simultaneously stable fixed points, and that limit cycles correspond to partially synchronized states. For small coupling, in particular, only one fixed point with $|Z| \ll 1$ (asynchrony) exists, which corresponds to the incoherent solution $Z = 0$ of the averaging approximation (7). We focus next on the stability boundary of the asynchronous state, which is determined applying the matcont toolbox of MATLAB to (46).

4.2.1. Dirac delta pulses. As reference case, let us determine first the stability boundary of asynchrony for the Dirac delta pulse, $r = \Pi = 1$, and in the absence of PRC diversity, $\gamma = 0$. As depicted in figure 3 for $q_0 = 1.0, -1$, the stability boundary of asynchrony is a line in the $(\Delta, \varepsilon)$ plane that emanates from $(0, 0)$ with a slope equal to 2, as correctly predicted by the averaging approximation, see (18). This line is the locus of a (supercritical) Hopf bifurcation of asynchrony. Contrary to what could be naively inferred from (18), the boundary is not a straight line: it folds back at a certain value and approaches the $\varepsilon$-axis asymptotically as $\varepsilon \to \infty$. This behavior is common to all $q_0$ values, see figure 9 in Gallego et al (2017).

Introducing heterogeneity in the PRCs must have an important effect, because—according to the averaging approximation—incoherence is always stable for $\gamma > \gamma_{\infty} = 1$. Strictly speaking, this only applies to small $\varepsilon$ and $\Delta$, where the averaging approximation is valid. As can be see in figure 3(a), for $q_1 = 1$, the instability boundary detaches from the origin when $\gamma$ exceeds $\gamma_{\infty} = 1$. However, as shown in figure 3(c), for $q_0 = -1$ the disappearance of the boundary from the neighborhood of the origin occurs in a completely different way: the domain of unstable asynchrony progressively shrinks as $\gamma$ grows, collapsing with the origin exactly when $\gamma = \gamma_{\infty} = 1$. We notice also that, in the $q_0 = -1$ case, as $\gamma$ grows from zero a generalized Hopf (GH) point appear, in such a way that the Hopf boundary is of subcritical type above that point. For $\gamma = 0.5$ we depict with dashed line the locus of the saddle-node bifurcation of limit cycles emanating from GH—as for other $\gamma$ values, we skip this information. Finally, for the singular case $q_0 = 0$, see figure 3(b), the domain of unstable asynchrony shrinks as $\gamma$ approaches $\gamma_{\infty} = 1$, collapsing with the entire $\varepsilon$-axis. Indeed for $q_0 = 0$ the exact boundary can be obtained in parametric form, but the formulas are convoluted and we skip them here.

Besides the results shown in figure 3 for particular $q_0$ values, the analysis of equation (46) permits to corroborate that the scenarios for $q_1 = 1$ and $q_0 = -1$ apply, respectively, to all positive and negative values of $q_0$. To analyze equation (46), it is convenient to define a new complex variable $w \equiv x + iy = (1 + Z)/(1 - Z)$. This is a conformal mapping from the unit disk $|Z| \leq 1$ onto the right half plane $x \geq 0$. The ODEs for the real and imaginary parts of $w$ are:

$$\begin{align*}
    \dot{x} &= \frac{\Delta}{2}(1 - x^2 + y^2) - xy + \varepsilon (x + \gamma)H(x, y), \\
    \dot{y} &= -\frac{1 - x^2 + y^2}{2} - \Delta xy + \varepsilon (y - q_0)H(x, y).
\end{align*}$$

For the Dirac delta pulse $H$ turns out to be very simple: $H(x, y) = x$. Still the system (47) is too convoluted to find a closed expression of the Hopf boundary. Useful information can be obtained nonetheless setting $\Delta = 0$, in order to find out at which point the Hopf line intersects the $\varepsilon$-axis. After getting the fixed point $(x_*, y_*)$, with coordinates
\[ x^* = \frac{\varepsilon q_0 + \sqrt{1 + \varepsilon^2(1 + q_0^2 + \gamma^2) + \varepsilon^4 \gamma^2}}{1 + \varepsilon^2} \]  \hspace{1cm} (48)

and \( y^* = \varepsilon(x^* + \gamma) \), trivial calculations yield the nontrivial \( \varepsilon \)-intercept of the Hopf line:

\[ \varepsilon_H^{(\Delta=0)} = \frac{\gamma^2 - 1}{2\gamma q_0} \]  \hspace{1cm} (49)

which is only valid for \( \varepsilon_H^{(\Delta=0)} > 0 \), i.e. \( \gamma > 1 \) if \( q_0 > 0 \) or \( \gamma < 1 \) if \( q_0 < 0 \). This formula is in fully agreement with the results in figure 3, and gives support to the general distinction between positive, negative, and vanishing \( q_0 \) cases.

4.2.2. Pulse with finite width. When the pulse has finite width, in the absence of PRC diversity (\( \gamma = 0 \)), the asynchronous state is bounded by two bifurcation lines: The supercritical Hopf-bifurcation line that emanates from the origin (with the slope predicted by the averaging approximation) terminates at a double-zero eigenvalue, Bogdanov–Takens (BT), point, see e.g. the lines for \( r = 0.9 \) in panels (a) and (b) of figure 4. Additionally, from the BT point up

Figure 3. Stability boundary of asynchrony when the distribution of PRCs is centered at (a) \( q_0 = 1 \), (b) \( q_0 = 0 \), and (c) \( q_0 = -1 \). Asynchrony is unstable at the left of the solid lines. The pulse is \( P(\theta) = 2\pi\delta(\theta) \).

Figure 4. Stability boundary of the asynchronous state when the distribution of PRCs is centered at (a) \( q_0 = 1 \) and (b) \( q_0 = -1 \). The pulse form is given by (3) with \( r = 0.9 \).
to the $\varepsilon$ axis, a line corresponding to a saddle-node bifurcation bounds the region of unstable asynchrony in its upper part. We decided to limit our presentation to $r = 0.9$, a value corresponding to a quite narrow pulse, see figure 1(b), since sharp pulses are often observed in reality. As can be seen in the two panels of figure 4, the displacement of the lines as $\gamma$ grows from zero is clearly reminiscent of what is observed for Dirac delta pulses, but now the detachment ($q_0 = 1$) or collapse ($q_0 = -1$) of the synchronization region occurs for a smaller $\gamma$ value, which, according to (34), is $\gamma_\infty = 1.9/2.1 = 0.90476\ldots$

5. Conclusions

In the first part of our paper, we showed that the averaging approximation of the Winfree model with heterogeneous PRCs and Dirac delta pulses ($\Pi = 1$) turns out to be the Kuramoto model with distributed shear (Montbrió and Pazó 2011). We found that, under the averaging approximation, the incoherent state becomes always stable beyond a critical level of PRC heterogeneity. These results hold for general distributions of heterogeneity, and different pulse widths ($\Pi$ values). We have focused our attention on the stability of the asynchronous state, but one should keep in mind that regions of bistability between partial synchrony and incoherence are expected, see figure 1(b) in Montbrió and Pazó (2011). Our work yields somewhat different results from those in Tsubo et al (2007b) where a different averaging approximation is obtained for the Winfree model with asymmetric (exponential) pulses. The main difference is that the nonhysteretic discontinuous transition between incoherence and partial synchronization observed there is not found here. We do not know if the reason lays on the discrepancies between both averaged models or on the different parametrization of the PRCs chosen$^5$.

In the second part of this work we analyzed the full model. To achieve the maximal dimensionality reduction with the Ott–Antonsen ansatz we restricted our analysis to Lorentzian distributions. The resulting system of ODEs describes the system exactly in the thermodynamic limit. An important result is the verification that above a certain PRC heterogeneity threshold $\gamma_\infty$, the averaged model becomes mostly useless. Only the study of the full model permitted us to elucidate that the sign of parameter $q_0$, controlling the offset of the PRC distribution, plays a fundamental role in the response of the system against PRC heterogeneity.

In future work, nonindependent joint distributions of $\omega$ and $q$ could be explored following Pazó and Montbrió (2011). Adaptation-mediated changes in the PRCs appears to be another plausible line of research. In contrast, changing the mean-field interactions by short-range, long-range or networked interactions is quite a challenge.

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$^5$The PRCs in Tsubo et al (2007b) are $Q_i(\theta) = \sin a_i \pi \left[ \frac{1}{\tan \pi (1 - \cos \theta)} - \sin \theta \right]$, where $a_i$ is the heterogeneous parameter. Note that in our parametrization (2) type-1 PRCs cannot be set.
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