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, in addition to the natural frequencies, also the phase-response curves (PRCs) are heterogeneous. In the first part of the paper we derive an approximate (or averaged) model, in which the oscillators are coupled through their phase differences. Remarkably, this simplified model is the 'Kuramoto model with distributed shear' (or a close variant) studied a few years ago. 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 an exact analysis of the full model for Lorentzian heterogeneities, resorting to the Ott-Antonsen ansatz. The boundary of stable asynchrony is determined, observing 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 most common PRC.

Keywords: Winfree model, Kuramoto model, Synchronization

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1. Introduction

The Winfree model (Winfree 1967, Winfree 1980) is a milestone in the mathematical description of collective synchronization. Motivated by many natural phenomena, see e.g. (Pikovsky et al. 2001, Strogatz 2003), Winfree's insight led him to propose the first model made of a large number $N \gg 1$ of interacting 'oscillators' capable of self-synchronizing macroscopically. As simplifying assumptions, he prescribed that the phases θ_i ($i = 1, \ldots, N$) where the only degrees of freedom, and that the interactions were all-to-all, i.e. mean-field type. In spite of its deep conceptual influence, the theoretical description of the Winfree model is a challenging problem, with few analytical results (Ariaratnam & Strogatz 2001, Quinn et al. 2007, Pazó & Montbrió 2014, Gallego et al. 2017).

In the Winfree model, each oscillator has a different intrinsic frequency ω_i, and reacts to the pulses coming from the rest of the population according to the value of the phase response curve (PRC) Q. With our definition the PRC, also called infinitesimal PRC, phase resetting curve, or sensitivity function (Izhikevich 2007), is a function only of the own phase, and determines the advance or delay of the phase in response to a certain input. The PRC plays a fundamental role, particularly in neuroscience (Smeal et al. 2010, Schultheiss et al. 2012), and it has been determined experimentally in neurons from different cortex areas (Reyes & Fetz 1993*b*, Reyes & Fetz 1993*a*, Netoff et al. 2005, Tateno & Robinson 2007, Tsubo, Takada, Reyes & Fukai 2007, Mancilla et al. 2007), the hippocampus (Lengyel et al. 2005), mitral cells (Galán et al. 2005), or the abdominal ganglia (Preyer & Butera 2005). Other natural systems 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 important also for technological applications such as electric oscillators (Hajimiri & Lee 1998) or wireless sensor nets, see e.g. (Nishimura & Friedman 2011) and references therein.

In mathematical studies of ensembles of phase oscillators it is customary to assume that heterogeneity is given by the natural frequencies and/or the external noise. But, logically, any degree of heterogeneity in a population of oscillators will cause disparity in both natural frequencies and PRCs. Indeed, broad cell-to-cell differences in PRCs have been recently measured in the olfactory bulb mitral cells (Burton et al. 2012). And, on the theoretical side, the collective phase dynamics of a synchronized ensemble of oscillators depends crucially on the PRC heterogeneity (Nakao et al. 2018). It is therefore desirable to improve our knowledge of the effects of PRC heterogeneity. However, due to its mathematical complexity, previous attempts to tackle oscillator ensembles with heterogeneous PRCs are scarce, and have relied on approximate methods (Tsubo, Teramae & Fukai 2007, Ly 2014).

In this paper, we study, and partly solve, 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 θ_i $(i = 1, \ldots, N)$ evolve according to the following set of N coupled ordinary differential equations (ODEs):

$$\dot{\theta}_i = \omega_i + Q_i(\theta_i)\frac{\varepsilon}{N}\sum_{j=1}^{N} P(\theta_j). \tag{1}$$

Here ω_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 ith 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) subscript i appears twice in the right hand-side: at the natural frequencies, and at the PRCs. Specifically, we consider the monoparametric family of PRCs

$$Q_i(\theta) = q_i(1 - \cos\theta) - \sin\theta, \tag{2}$$

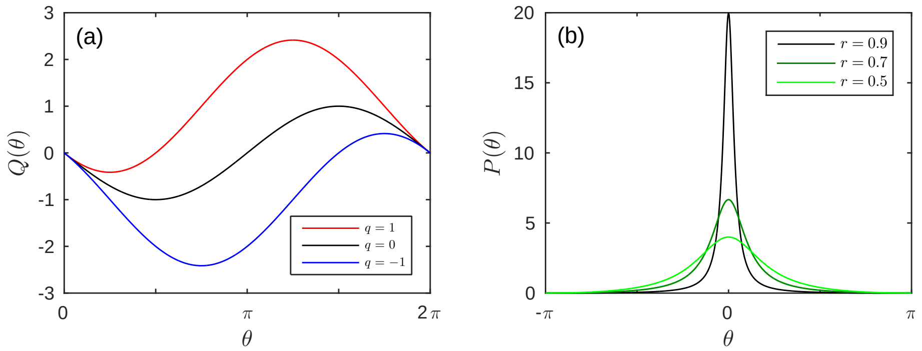

Figure 1. (a) Phase response curve and (b) pulse shape for three representative values of q and r, respectively.

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 $Q_i(0) = 0$, since we choose $\theta = 0$ as the point where the pulse peaks, and this is the usual situation in natural systems.

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

$$P(\theta) = \frac{(1-r)(1+\cos\theta)}{1-2r\cos\theta + r^2}. \tag{3}$$

that vanishes at $\theta = \pi$. Parameter r, controlling the narrowness of the pulse, spans between -1 (flat pulse) and 1 (Dirac delta, $P(\theta) = 2\pi\delta(\theta)$), see three examples in figure 1(b). Irrespective of r the integral of the pulse is fixed to 2π: $\int_{-\pi}^{\pi} P(\theta)d\theta = 2\pi$.

In section 3 we study the approximation of (1)-(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 ω and q, and at the same time, the results obtained serve as a guide for section 4, where an exact analysis is presented. 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. For the PRCs in (2) we have:

$$\dot\theta_i = \omega_i + \varepsilon q_i + \Pi\frac{\varepsilon}{N}\sum_{j=1}^{N}[\sin(\theta_j - \theta_i) - q_i\cos(\theta_j - \theta_i)], \tag{4}$$

at the lowest order in ε. The constant $\Pi = \hat{p}_1$ is a shape factor that equals the first Fourier mode of the pulse $P(\theta) = \sum_{n=-\infty}^{\infty} \hat{p}_n e^{in\theta}$. The dependence only on the first Fourier mode stems from the sinusoidal shape of the PRC. Specifically, for the specific pulse type in (3),

$$\Pi = \frac{1+r}{2}, \tag{5}$$

and therefore $0 < \Pi < 1$ for this and other pulses (Gallego et al. 2017). The largest Π 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 (4) coincides with the 'Kuramoto model with distributed shear' (Montbrió & Pazó 2011, Pazó & Montbrió 2011). Originally, it was deduced as a phase approximation for globally coupled Stuart-Landau oscillators with distributed natural frequencies and shears (nonisochronicities). While here, instead, (4) is derived from the extension of the Winfree model with PRC heterogeneity. This coincidence permits to transfer the results from (Montbrió & Pazó 2011, Pazó & Montbrió 2011) for $\Pi = 1$, or simply borrow the analysis used there for $\Pi < 1$.

In terms of the Kuramoto order parameter, $Z \equiv R\, e^{i\psi} = N^{-1} \sum_j e^{i\theta_j}$, model (4) can be alternatively written as,

$$\dot{\theta}_i = \omega_i + \varepsilon\, q_i + \Pi\, \varepsilon\, R[\sin(\psi - \theta_i) - q_i \cos(\psi - \theta_i)], \tag{6}$$

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

3.1. 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 ω and PRC-parameter q at time t. The mean field Z in this continuous formulation becomes

$$Z(t) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} p(\omega, q) \int_{-\pi}^{\pi} f(\theta|\omega, q, t) e^{i\theta}\, d\theta\, d\omega\, dq, \tag{7}$$

where $p(\omega, q)$ is the joint probability distribution of ω 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 & Mirollo 1991, Montbrió & Pazó 2011):

$$\partial_t f = -\partial_\theta \left(\left\{ \omega + \varepsilon q + \frac{\Pi\varepsilon}{2i} \left[Z e^{-i\theta}(1 - iq) - \text{c.c.} \right] \right\} f \right) \tag{8}$$

(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 (7). For the analysis that follows we write the Fourier series of f:

$$f(\theta|\omega, q, t) = \frac{1}{2\pi} \sum_{l=-\infty}^{\infty} \hat{f}_l(\omega, q, t) e^{il\theta}, \tag{9}$$

with $\hat{f}_0 = 1$, and $\hat{f}_l = \hat{f}^*_{-l}$. We can insert (9) into (8) obtaining an infinite set of integro-differential equations governing the evolution of $\hat{f}_l$ in terms of itself, $\hat{f}_{l\pm1}$, and the mean field Z:

$$\partial_t \hat{f}_l = -i(\omega + \varepsilon q)\hat{f}_l - \frac{\Pi\, \varepsilon\, l}{2} \left[Z \hat{f}_{l+1}(1 - iq) - Z^* \hat{f}_{l-1}(1 + iq) \right], \tag{10}$$

where the asterisk denotes the complex conjugation. It is crucial to note that, according to (7), Z depends only on the first Fourier mode of the density:

$$Z^*(t) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} p(\omega,q)\hat{f}_1(\omega,q,t)\,\mathrm{d}\omega\,\mathrm{d}q \equiv \left\langle \hat{f}_1 \right\rangle. \tag{11}$$

(The bracket is used hereafter to denote the average over ω and q.) Now, it is easily verified in (10) that infinitesimal deviations from uniform incoherence ($\hat{f}_{l\neq 0} = 0$) are governed solely by the first Fourier mode:

$$\partial_t \hat{f}_1 = -\mathrm{i}(\omega + \varepsilon q)\hat{f}_1 + \frac{\Pi\,\varepsilon}{2}(1+\mathrm{i}q)\left\langle \hat{f}_1 \right\rangle. \tag{12}$$

A succession of well-known steps permits to determine the linear stability of incoherence (Strogatz & Mirollo 1991, Strogatz 2000): (i) insert in (12) the ansatz corresponding to an exponential growth rate λ, $\hat{f}_1 = b(\omega,q)\mathrm{e}^{\lambda t}$, (ii) isolate b in the left hand-side, (iii) multiply both sides of the equation by $p(\omega,q)$, and (iv) integrate over ω and q. These steps yield a self-consistent condition:

$$\frac{2}{\Pi\,\varepsilon} = \left\langle \frac{1+\mathrm{i}q}{\lambda + \mathrm{i}(\omega+\varepsilon q)} \right\rangle. \tag{13}$$

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

$$\begin{aligned} 0 &= \left\langle \frac{q\lambda_R - (\omega + \lambda_I + q\varepsilon)}{\lambda_R^2 + (\omega+\lambda_I+q\varepsilon)^2} \right\rangle, \\ \frac{2}{\Pi\,\varepsilon} &= \left\langle \frac{\lambda_R + q(\omega + \lambda_I + q\varepsilon)}{\lambda_R^2 + (\omega+\lambda_I+q\varepsilon)^2} \right\rangle, \end{aligned} \tag{14}$$

where $\lambda_R = \mathrm{Re}\,\lambda$ and $\lambda_I = \mathrm{Im}\,\lambda$. For simplicity, we consider hereafter ω and q to be independently distributed, i.e. $p(\omega,q) = g(\omega)h(q)$. A nonindependent situation with $\Pi = 1$ was considered in (Pazó & Montbrió 2011). Moreover, it is convenient to assume that g and h are unimodal symmetric functions (Strogatz & Mirollo 1991). We can freely choose $g(\omega)$ centered at zero, since this can always be achieved by going to a rotating framework if necessary, while $h(q)$ is centered at a specific q_0 value. Note also that changing the sign of ω and q in (13) transforms λ into λ^*, 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 (14), and obtain:

$$\begin{aligned} 0 &= \left\langle \pi q \delta(\lambda_I + q\varepsilon_c + \omega) - \frac{1}{\lambda_I + q\varepsilon_c + \omega} \right\rangle \\ \frac{2}{\Pi\,\varepsilon_c} &= \left\langle \pi \delta(\lambda_I + q\varepsilon_c + \omega) + \frac{q}{\lambda_I + q\varepsilon_c + \omega} \right\rangle \end{aligned} \tag{15}$$

3.2. Lorentzian heterogeneities

For Lorentzian distributions

$$g(\omega) = \frac{\Delta/\pi}{(\omega-\omega_0)^2 + \Delta^2}, \quad h(q) = \frac{\gamma/\pi}{(q-q_0)^2+\gamma^2}, \tag{16}$$

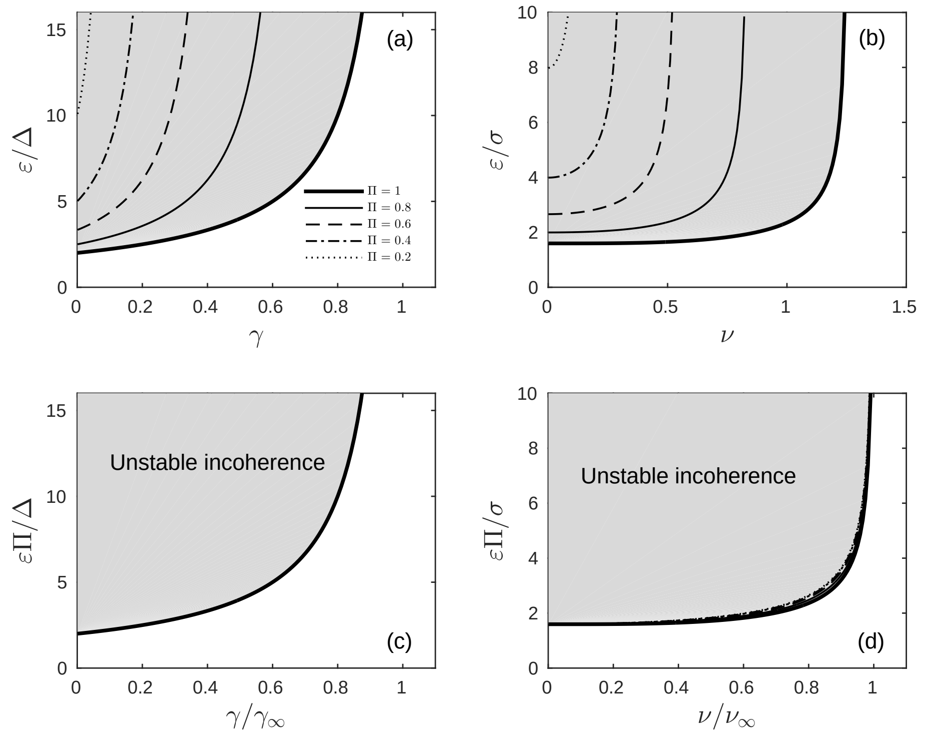

Figure 2. (a,b) Stability boundary of incoherence in the different values of Π, with (a) Lorentzian, and (b) Gaussian PRC heterogeneities. In (b) $q_0 = 0$. The shaded are corresponds to unstable incoherence for $\Pi = 1$. (c,d) The same data boundaries after rescaling the axes. In the case of Gaussian heterogeneity, panel (d), the curves fail to collapse.

solving (15) yields the critical coupling strength‡ where incoherence becomes unstable

$$\varepsilon_c = \frac{2\,\Delta}{\Pi - \gamma(2-\Pi)}, \tag{17}$$

which holds only for positive ε. Notably, (17) is independent of q_0, a peculiarity of the Lorentzian distribution (in contrast to the independence on ω_0 discussed above). For a given Π value, see figure 2(a), the function $\varepsilon_c(\gamma)/\Delta$ in (17) defines a curve in the $(\gamma, \varepsilon/\Delta)$ plane that emanates from the ε/Δ-axis at $2/\Pi$ and grows monotonically up to a critical value

$$\gamma_\infty = \frac{\Pi}{2-\Pi}, \tag{18}$$

where the curve diverges. In turn, incoherence is always stable for $\gamma > \gamma_\infty$. As can be seen in figure 2(c), the formula (17) can be condensed into a single curve with rescaled variables:

$$\frac{\varepsilon_c \Pi}{\Delta} = \frac{2}{1-\gamma/\gamma_\infty}. \tag{19}$$

‡ In this case is perhaps easier to resort to the Ott-Antonsen ansatz, rather than (15). The result is obviously independent of the method chosen.

3.3. Gaussian heterogeneities

The analysis of distributions different from (16) is more cumbersome. We consider here only Gaussian heterogeneities:

$$g(\omega) = \frac{1}{\sqrt{2\pi}\sigma} \mathrm{e}^{-\omega^2/(2\sigma^2)}, \quad h(q) = \frac{1}{\sqrt{2\pi}\nu} \mathrm{e}^{-(q-q_0)^2/(2\nu^2)}. \tag{20}$$

Calculations greatly simplify if $h(q)$ is centered at zero, i.e. $q_0 = 0$. In this case, after some manipulations of (15), we get a closed formula for the critical coupling

$$\varepsilon_c^{(q_0=0)} = \frac{4\,\sigma}{\left[\sqrt{\pi\Pi^3(16\nu^2+\pi\Pi)} + \pi\Pi^2 + 8\nu^2(\Pi-2)\right]^{1/2}}. \tag{21}$$

For $\Pi = 1$ we recover the result in in (Montbrió & Pazó 2011). Equation (21) defines a region in the $(\nu, \varepsilon/\sigma)$ plane that is maximal for $\Pi = 1$ and progressively shrinks as Π is decreased, see figure 2(b) for several Π values. The line (21) is born at $\nu = 0$ with $\varepsilon_c/\sigma = \sqrt{8/\pi}/\Pi$, and diverges at a critical value of ν:

$$\nu_\infty^{(q_0=0)} = \frac{\Pi}{2-\Pi}\sqrt{\frac{\pi}{2}}. \tag{22}$$

Equation (21) cannot be recast into a single formula valid for all Π values, rescaling ε_c and ν. We see in figure 2(d) that a rescaling analogous to (19) yields an imperfect collapse of the boundaries.

Finally, we stress that our stability analysis is local, and stable incoherence does not preclude its coexistence with a partially synchronized state, as is indeed the case with $\Pi = 1$, for $\nu > \nu_\infty$ at large enough ε (Montbrió & Pazó 2011).

3.4. Critical PRC heterogeneity

The Lorentzian (16) and the Gaussian (20) joint distributions, exhibit a critical value of heterogeneity in q, such that if q is too heterogeneous incoherence becomes stable for all ε. We investigate next if a general rule —for unimodal symmetric $h(q)$— exists. First of all we neglect the diversity of ω in (15), since we are interested in the limit $\varepsilon_c \to \infty$. Intuitively, the term εq_i in (4) can be as large in magnitude with respect to ω_i as desired. Mathematically, we can hence neglect the heterogeneity of ω taking $g(\omega) = \delta(\omega)$. In addition, we rescale λ_I by ε_c and define $\lambda_I = \Lambda\varepsilon_c$. In this way, the dependence on ε_c in (15) cancels out, obtaining thus the conditions:

$$0 = -\pi\Lambda h_\infty(-\Lambda) - \int_{-\infty}^{\infty} \frac{1}{\Lambda+q} h_\infty(q)\,\mathrm{d}q \tag{23a}$$

$$2\,\Pi^{-1} = \pi h_\infty(-\Lambda) + \int_{-\infty}^{\infty} \frac{q}{\Lambda+q} h_\infty(q)\,\mathrm{d}q \tag{23b}$$

Here, h_∞ means the critical distribution of $h(q)$ such that the stability boundary is at $\varepsilon_c = \infty$, or in other words if $h(q)$ is infinitesimally broader incoherence becomes stable for all ε. To get rid of the integral, we can multiply (23a) by Λ and subtract (23b) obtaining:

$$\frac{2\,\Pi^{-1} - 1}{\pi(1+\Lambda^2)} = h_\infty(-\Lambda). \tag{24}$$

Additionally, multiplying (23*b*) by Λ and adding (23*a*) yields after trivial manipulations:

$$\left(2\,\Pi^{-1}-1\right)\Lambda = -(1+\Lambda^2)\int_{-\infty}^{\infty}\frac{h_\infty(q-\Lambda)}{q}\,\mathrm{d}q. \qquad (25)$$

3.4.1. Centered $h(q)$ ($q_0 = 0$) If $h(q)$ is centered at zero, symmetry imposes the trivial solution $\Lambda = 0$ in (25) (we are interpreting the integral in the Cauchy principal value sense). If $\Lambda > 0$ the integral in (25) is positive and the condition cannot be fulfilled, likewise for $\Lambda < 0$. In consequence we get from (24) the remarkable result that the divergence of ε_c is linked to a simple condition for the distribution maximum:

$$h_\infty^{(q_0=0)}(0) = \frac{2\,\Pi^{-1}-1}{\pi}. \qquad (26)$$

Indeed, imposing this condition to the Lorentzian and Gaussian distributions, we recover (18) and (22), respectively. As expected, the region of stable incoherence widens as Π decreases, since in the limit $\Pi \to 0$ the contribution of the first harmonic vanishes. Equation (26) is a generalization for arbitrary Π of $h_\infty(0) = \pi^{-1}$ for $\Pi = 1$ (Montbrió & Pazó 2011).

3.4.2. Off-centered $h(q)$ ($q_0 \neq 0$) If the distribution of q is not centered at zero, criterion (26) is not valid. Apart of solving equations (24) and (25) 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 (24) and (25) 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,

$$\tilde{h}(q) = h(q+q_0). \qquad (27)$$

Equations (24) and (25) become then:

$$\frac{1}{\pi(1+\Lambda^2)} = \tilde{h}_\infty(-q_0-\Lambda), \qquad (28a)$$

$$\Lambda = -(1+\Lambda^2)\int_{-\infty}^{\infty}\frac{\tilde{h}_\infty(q-q_0-\Lambda)}{q}\,\mathrm{d}q. \qquad (28b)$$

At criticality we expect a generalization of (26) of the form

$$\tilde{h}_\infty^{(q_0)}(0) = \tilde{h}_\infty^{(q_0=0)}(0) + \eta(q_0), \qquad (29)$$

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

Assuming small $|q_0|$ and $|\Lambda|$ and twice differentiability of $\tilde{h}(q)$ we approximate (28*a*) and (28*b*) at leading order

$$0 = \Lambda^2 + \eta(q_0) + \frac{\pi}{2}(\Lambda+q_0)^2\frac{\mathrm{d}^2}{\mathrm{d}q^2}\tilde{h}_\infty^{(q_0=0)}(0), \qquad (30a)$$

$$\Lambda = (\Lambda+q_0)\,I, \qquad (30b)$$

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

$$b = -\frac{I^2 + \frac{\pi}{2}\frac{\mathrm{d}^2}{\mathrm{d}q^2}\tilde{h}_\infty^{(q_0=0)}(0)}{(1-I)^2}. \qquad (31)$$

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

$$\nu_\infty^{(q_0)} \simeq \frac{\Pi}{2-\Pi}\sqrt{\frac{\pi}{2}}\left(1-\sqrt{\pi}bq_0^2\right). \tag{32}$$

This is the perturbative extension at order q_0^2 of (22), implying that unstable incoherence may achieve larger values of ν, i.e. broader distributions.

4. Exact analysis: Ott-Antonsen ansatz

Our aim in what remains is to study the full model defined by (1)-(3), with no other approximation than the thermodynamic limit. However, due to mathematically tractability we restrict our analysis to Lorentzian heterogeneities (16). The stability boundary of asynchrony in the (Δ, ε) plane is obtained below for different values of q_0, γ, and r. One interesting question is to elucidate how the finding of a critical PRC heterogeneity γ_∞ in the averaged model translates into the full model. Recalling that $\Pi(r) = (1+r)/2$ for the pulse shape (3), (18) yields:

$$\gamma_\infty = \frac{1+r}{3-r}. \tag{33}$$

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 (33), but the model will achieve the consistency in a different way depending on the sign of q_0.

4.1. Derivation of low-dimensional equations

As in section 3, working in the thermodynamic limit $N \to \infty$, permits to define the density $F(\theta|\omega, q, t)$. It obeys the continuity equation:

$$\partial_t F = -\partial_\theta \left\{ \left[\omega + \varepsilon Q(\theta) H(t)\right] F \right\}, \tag{34}$$

where $H(t)$ is the mean field

$$H(t) = \left\langle \int_0^{2\pi} F(\theta|\omega, q, t)\, P(\theta)\, d\theta \right\rangle. \tag{35}$$

For the theoretical analysis to follow we assume that F belongs to the Ott-Antonsen manifold (Ott & Antonsen 2008):

$$F(\theta|\omega, q, t) = \frac{1}{2\pi}\left\{1 + \left[\sum_{m=1}^{\infty} \alpha(\omega, q, t)^m \mathrm{e}^{im\theta} + \text{c.c.}\right]\right\}. \tag{36}$$

Here, α^* is the first Fourier mode of the density, and therefore:

$$Z^*(t) = \langle \alpha(\omega, q, t) \rangle. \tag{37}$$

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

$$\dot{\theta}(\mathbf{x}, t) = B(\mathbf{x}, t) + \mathrm{Im}\left[G(\mathbf{x}, t)\mathrm{e}^{-\mathrm{i}\theta(t)}\right], \tag{38}$$

where $\mathbf{x}$ is a vector containing different parameters that are distributed (Pikovsky & Rosenblum 2011, Pietras & Daffertshofer 2016). In our case $\mathbf{x} = (\omega, q)$, with

$B(\mathbf{x},t)=\omega+\varepsilon q H(t)$ and $G(\mathbf{x},t)=\varepsilon(1-\mathrm{i}q)H(t)$. It is proven that if F does not initially satisfy (36), it subsequently converges to it (in the sense of (Ott & Antonsen 2009, Ott et al. 2011)). Apart from the empirical observation, 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 therefore the formulation in terms of densities is reliable.

Inserting (36) into the continuity equation (34) we get an equation for $\alpha(\omega,q,t)$:

$$\partial_t\alpha = -\mathrm{i}\omega\alpha + \frac{\varepsilon H}{2}\left[1-\alpha^2+\mathrm{i}q(1-\alpha)^2\right]. \tag{39}$$

Note that every $\alpha(\omega,q,t)$ is coupled with all others $\alpha(\omega',q',t)$ through the mean field H, see (35). It was found in (Gallego et al. 2017), see also the Supplemental Material of (Montbrió & Pazó 2018), that for the pulse type (3) H is related with Z via

$$H(Z)=\mathrm{Re}\left[\frac{1+Z}{1-rZ}\right]. \tag{40}$$

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

$$\partial_t|\alpha| = \frac{\varepsilon H}{2}(\cos\phi+q\sin\phi)\left(1-|\alpha|^2\right), \tag{41}$$

where $\phi=\arg(\alpha)$. As the velocity vanishes at $|\alpha|=1$, α cannot leave the unit disk —otherwise (36) is not convergent. The next key observation, analogously to previous works (Ott & Antonsen 2008, Montbrió & Pazó 2011), is that α admits an analytic continuation into the lower half complex ω-plane, and the lower half complex q-plane (for positive ε). If the field $\alpha(\omega,q,t)$ admits an analytic continuation at $t=0$, this will be the case for $t>0$ since α obeys the differential equation (39) (Coddington & Levinson 1955). The complexification of $\omega=|\omega|\mathrm{e}^{\mathrm{i}\xi}$ and $q=|q|\mathrm{e}^{\mathrm{i}\vartheta}$, transforms (41) into:

$$\begin{aligned}\partial_t|\alpha| = |\omega||\alpha|\sin\xi + \frac{\varepsilon H}{2}&\left\{\cos\phi\left(1-|\alpha|^2\right)\right.\\ &\left.+|q|\left[\sin(\phi-\vartheta)+2|\alpha|\sin\vartheta-|\alpha|^2\sin(\phi+\vartheta)\right]\right\}.\end{aligned} \tag{42}$$

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

$$\partial_t|\alpha| = |\omega|\sin\xi+\varepsilon H|q|\sin\vartheta(1-\cos\phi). \tag{43}$$

Provided $\sin\xi\le 0$, and $\sin\vartheta\le 0$ (for positive ε), $\partial_t|\alpha|\le 0$, and therefore α cannot leave the unit disk, if initially inside.

The analytic continuation of α allows to apply twice the residue's theorem to the integrals in (37) by closing the respective integration contours by large semicircles in the lower half ω- and q-planes. As the Lorentzian distribution has only one pole inside the integration contour, a simple relation between Z and α is found:

$$Z^*(t)=\alpha(\omega_p,q_p,t), \tag{44}$$

where $\omega_p=\omega_0-\mathrm{i}\Delta$ and $q_p=q_0-\mathrm{i}\gamma$ are the poles of $g(\omega)$ and $h(q)$, respectively. Hence we only have to evaluate (39) at (ω_p,q_p), in order to obtain one complex-valued ODE for Z:

$$\dot Z=\mathrm{i}\omega_p^*\,Z+\frac{\varepsilon H}{2}\left[1-Z^2-\mathrm{i}q_p^*\,(1-Z)^2\right]. \tag{45}$$

This equation 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, Δ and ε by $\omega_0>0$ in (45).

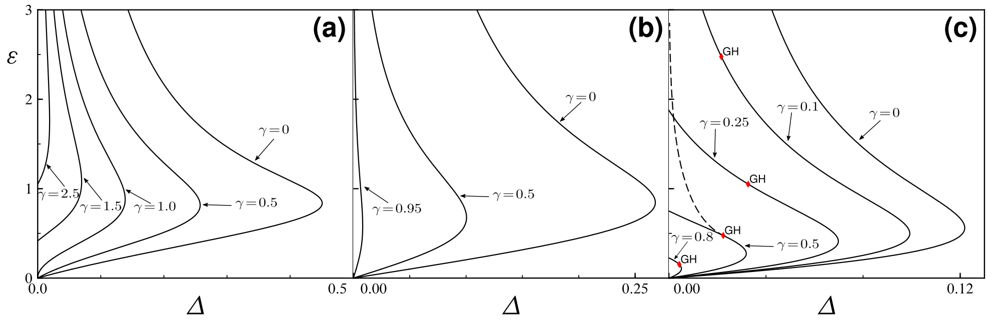

Figure 3. Stability boundary of asynchrony when the distribution of PRCs is centered at (a) $q_0 = 1$, (b) $q_0 = 0$, and (c) $q_0 = -1$. Asynchrony is unstable at the left of the solid lines. The pulse is $P(\theta) = 2\pi\delta(\theta)$.

4.2. Analysis of the low-dimensional system (45)

Equation (45) is a planar system, generically with two possible attractor types: fixed point and limit cycle. Our previous work with homogeneous PRCs (Pazó & 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 (6). We focus next on the stability boundary of the asynchronous state, which is determined applying the MATCONT toolbox of MATLAB to (45).

4.2.1. Dirac delta pulses As reference case, let us determine first the stability boundary of asynchrony for the Dirac delta pulse, corresponding to $r = \Pi = 1$. In the absence of PRC diversity ($\gamma = 0$). As can be seen, in figure 3 for $q_0 = 1, 0, -1$, the stability boundary of asynchrony is a line in the (Δ, ε) plane that emanates from $(\Delta, \varepsilon) = (0, 0)$ with a slope equal to 2, as correctly predicted by the averaging approximation, see (17). This line is the locus of a (supercritical) Hopf bifurcation of asynchrony. Contrary to what could be naively inferred from (17), the boundary is not a straight line: it folds back at a certain Δ value and approaches the ε-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 $\gamma > \gamma_\infty = 1$. Of course, this only applies to small ε and Δ, where the averaging approximation is valid. As can be see in figure 3(a), for $q_0 = 1$, the instability boundary detaches from the origin when γ 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 γ grows, collapsing with the origin exactly when $\gamma = \gamma_\infty = 1$. We notice also that, in the $q_0 = -1$ case, as γ 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. (For other γ values, we skip this information.) Finally, for the singular case $q_0 = 0$, see figure 3(b), the domain of unstable asynchrony shrinks as γ approaches $\gamma_\infty = 1$, collapsing with the entire ε-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).

Apart from the results in figure 3 for particular q_0 values, the analytical study of (45) permits to corroborate that the scenarios for $q_0 = 1$ and $q_0 = -1$ apply, respectively, to all positive and negative values of q_0. For the analysis of (45), we found it 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:

$$\begin{aligned} \dot{x} &= \frac{\Delta}{2}(1 - x^2 + y^2) - x\,y + \varepsilon\,(x + \gamma)H(x, y), \\ \dot{y} &= -\frac{1 - x^2 + y^2}{2} - \Delta\,x\,y + \varepsilon\,(y - q_0)H(x, y). \end{aligned} \tag{46}$$

For the Dirac delta pulse H turns out to be very simple: $H(x, y) = x$. Still the system (46) 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 ε-axis. After getting the fixed point (x_*, y_*), with coordinates

$$x_* = \frac{\varepsilon q_0 + \sqrt{1 + \varepsilon^2(1 + q_0^2 + \gamma^2) + \varepsilon^4\gamma^2}}{1 + \varepsilon^2} \tag{47}$$

and $y_* = \varepsilon(x_* + \gamma)$, trivial calculations yield the nontrivial ε-intercept of the Hopf line:

$$\varepsilon_H^{(\Delta=0)} = \frac{\gamma^2 - 1}{2\gamma q_0}, \tag{48}$$

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 to the ε 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 γ 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 γ value, which, according to (33), is $\gamma_\infty = 1.9/2.1 = 0.90476\ldots$

5. Conclusions

In this work we have carried out the first exact analysis of the Winfree model with heterogeneous PRCs. These results are limited to Lorentzian heterogeneities, since

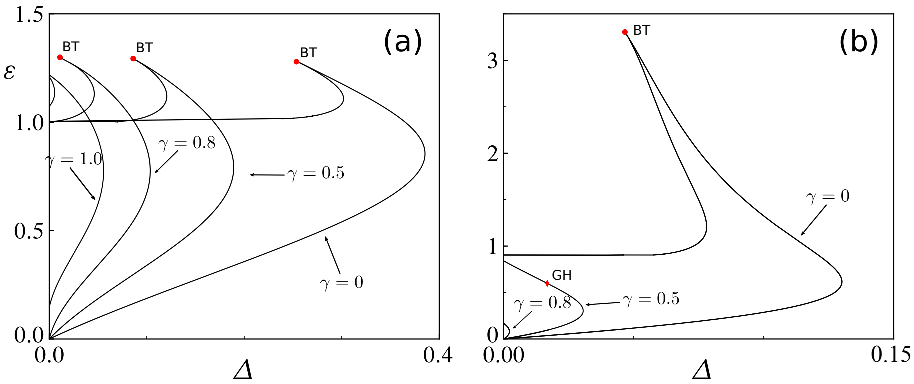

Figure 4. Stability boundary of the asynchronous state when the distribution of PRCs is centered at (a) $q_0 = 1$ and (b) $q_0 = -1$. The pulse form is given by (3) with $r = 0.9$.

only in this case does the Ott-Antonsen theory achieve the maximal dimensionality reduction. 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.

The averaging approximation of the model turns out to be like the Kuramoto model with distributed shear already studied a few years ago. It is mathematically tractable, and the effect of the first harmonic of the pulse function on the critical PRC heterogeneity has been studied systematically. Analytical works on distributed PRCs are scarce, the most similar system to ours in (Tsubo, Teramae & Fukai 2007) is hardly comparable because of the different parametrizations of the PRCs§ and the discontinuous coupling function used there.

For the application of the Ott-Antonsen ansatz, sinusoidally shaped PRCs are crucial. In contrast, the shape of the pulse can be modified without major difficulties in the theoretical analysis (Gallego et al. 2017). As a matter of future work, nonindependent joint distributions of ω and q, $p(\omega, q)$, can be explored following (Pazó & 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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§ In (Tsubo, Teramae & Fukai 2007) $Q_i(\theta) = \cos(a_i\pi) - \cos(\theta - a_i\pi)$, where a_i is the distributed parameter. When this $Q_i(\theta)$ written in a form closer to (2), $Q_i(\theta) = \cos(a_i\pi)(1-\cos\theta) - \sin(a_i\pi)\sin\theta$, it becomes evident that no direct mapping between q and a distributions exists.

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