Collective synchronization in populations of globally coupled phase oscillators with drifting frequencies

Jacques Rougemont*

Vital-IT, Swiss Institute of Bioinformatics, CIG-UNIL, 1015 Lausanne, Switzerland

Felix Naef

Swiss Institute for Experimental Cancer Research (ISREC), Ecole Polytechnique Fédérale de Lausanne (EPFL), School of Life Sciences,

and Swiss Institute of Bioinformatics, 1015 Lausanne, Switzerland

(Received 27 July 2005; revised manuscript received 27 September 2005; published 18 January 2006)

We generalize the Kuramoto model for coupled phase oscillators by allowing the frequencies to drift in time according to Ornstein-Uhlenbeck dynamics. Such drifting frequencies were recently measured in cellular populations of circadian oscillator and inspired our work. Linear stability analysis of the Fokker-Planck equation for an infinite population is amenable to exact solution and we show that the incoherent state is unstable past a critical coupling strength $K_c(\gamma, \sigma_f)$, where γ is the inverse characteristic drifting time and σ_f the asymptotic frequency dispersion. Expectedly K_c agrees with the noisy Kuramoto model in the large γ (Schmolukowski) limit but increases slower as γ decreases. Asymptotic expansion of the solution for $\gamma \rightarrow 0$ shows that the noiseless Kuramoto model with Gaussian frequency distribution is recovered in that limit. Thus varying a single parameter allows us to interpolate smoothly between two regimes: one dominated by the frequency dispersion and the other by phase diffusion.

DOI: 10.1103/PhysRevE.73.011104

PACS number(s): 05.40.-a, 05.45.Xt, 89.75.-k

I. INTRODUCTION

Synchronization phenomena occur recurrently in physical, chemical, and biological systems. A few examples worth noting include superconducting currents in Josephson junction arrays [1,2], emerging coherence in populations of chemical oscillators [3], or the accuracy of central circadian pacemakers in insects and vertebrates [4–6]. The latter serve as biomolecular time-keeping devices, which most organisms have evolved to coordinate their physiology and metabolic activities with the geophysical light-dark and temperature cycles [7].

The present work was motivated by recent experiments in mammalian cell cultures in which the levels of proteins implicated in the circadian (with ~ 24 hr periods) clockwork were monitored using fluorescent reporters [8-10]. It was demonstrated that individual cellular oscillators generate self-sustained rhythms in protein abundance and that populations can be synchronized by treatment with a short serum shock or light pulse. Importantly frequencies of individual oscillators are not strictly constant but drift in time (see, for example, Fig. S2 in [10] showing the results in the zebrafish). Several chemical kinetics models thought to capture the biochemistry responsible for generating oscillations in living cells were shown to exhibit oscillatory instabilities and limit cycles [11,12]. Experimental and theoretical evidence therefore supports a description of oscillator populations in terms of phase variables.

Our understanding of the onset of collective synchronization in coupled nonlinear oscillator models has greatly benefited from a large body of work on the Kuramoto model [13–17]

$$\dot{\varphi}_i = f_i + \frac{K}{N} \sum_{j=1}^N \sin(\varphi_j - \varphi_i) + \xi_i(t), \qquad (1)$$

describing the phase dynamics in a set of weakly coupled identical nonlinear oscillators. Here, $\varphi_i(t)$ represent the phase of the *i*th oscillator at time *t*, and $\xi_i(t)$ are white noise sources with expectation and covariance

$$E(\xi_i(t)) = 0,$$

$$\operatorname{cov}(\xi_i(s),\xi_j(t)) = 2D\delta_{ij}\delta(s-t).$$

The frequencies f_i are static and taken from a distribution g(f) symmetric around μ_f . Equation (1) is an effective model for the phase degrees of freedom in a population of limitcycle oscillators and assumes a regime where phase and amplitude dynamics decouple. The parameter K measures the strength of the all-to-all coupling. Most exact results are given for the coupling function $U(\varphi_i - \varphi_i) = \sin(\varphi_i - \varphi_i)$. More general interactions lead to a much greater analytical complexity and were investigated in [18,19]. Critical properties of the model are conveniently studied using the complex order parameter $R(t)e^{i\psi(t)} = (1/N)\sum_{j=1}^{N}e^{i\varphi_j(t)}$ so that collective synchronization occurs when $R_{\infty} = \lim_{T \to \infty} (1/T) \int_0^T R(t) dt$ remains positive in the infinite population limit. For the sine coupling model a bifurcation occurs at $K_c = 2/\int [D/(D^2)]$ $(f+\mu_f)$ state $R_{\infty}=0$ becomes unstable and a macroscopic number of oscillators phase lock to the average phase $\psi(t) = \mu_f t [20-22]$. For $D \rightarrow 0$ the classical Kuramoto result $K_c = 2/\pi g(\mu_f)$ [23] is recovered. Below the critical coupling, the incoherent state

^{*}Electronic address: jacques.rougemont@isb-sib.ch

[†]Electronic address: felix.naef@isrec.ch

is linearly stable when D > 0 [22] but only neutrally stable when D=0 with R(t) still decaying to zero [16].

II. THE MODEL

To study the effects of the reported drifts on collective synchronization, we generalize the Kuramoto model by introducing a second time scale $1/\gamma$ (besides $1/\sigma_f$) characterizing the frequency drifts. The frequency dynamics is formulated as an Ornstein-Uhlenbeck (OU) process while the phases are coupled following the canonical all-to-all sine interaction. The model for *N* oscillators reads

$$f_{i}(t) = -\gamma(f_{i}(t) - \mu_{f}) + \eta_{i}(t),$$

$$\dot{\varphi}_{i}(t) = f_{i}(t) + \frac{K}{N} \sum_{j=1}^{N} \sin[\varphi_{j}(t) - \varphi_{i}(t)], \qquad (2)$$

where μ_f is the average frequency chosen identical for each oscillator We assume that the η_i are independent and identically distributed white noise sources with

$$E(\eta_i(t))=0,$$

$$\operatorname{cov}(\eta_i(s),\eta_i(t)) = \eta^2 \delta_{ii} \delta(s-t).$$

The solution for f_i is a Gaussian process with mean and covariance

$$E(f_i(t)) = \mu_f + e^{-\gamma t} (f_i(0) - \mu_f),$$

$$\operatorname{cov}(f_i(s), f_j(t)) = \frac{\eta^2}{2\gamma} \delta_{ij} (e^{-\gamma |t-s|} - e^{-\gamma (t+s)})$$

$$\times \xrightarrow{\gamma t \gg 1} \frac{\eta^2}{\gamma^2} \delta_{ij} \delta(t-s).$$
(3)

In the following we use as independent parameters the asymptotic frequency dispersion $\sigma_f^2 = \eta^2/2\gamma$ and the damping γ , which are in principle both accessible experimentally. Then, $\operatorname{cov}(f_i(s), f_i(t)) \rightarrow (2\sigma_f^2/\gamma) \delta(t-s)$ when $\gamma t \ge 1$. To remind the significance of this regime we note for K=0 the phases $\varphi_i(t)$ also follow Gaussian processes with $\operatorname{cov}(\varphi_i(t), \varphi_i(t)) \rightarrow (2\sigma_f^2/\gamma)t$ asymptotically for $\gamma t \ge 1$. Because of the linear time dependence, this regime (Schmolukowski) describes phase diffusion with constant $D = \sigma_f^2/\gamma$.

Although it is *a priori* unclear whether this model exhibits a bifurcation, we expect that the large γ behavior reminiscent of phase diffusion will converge to the Kuramoto model [Eq. (1)] with a frequency distribution given by $g(f) = \delta(f - \mu_f)$ and white noise strength $D = \sigma_f^2 / \gamma$, and thus exhibit a bifurcation at $K_c = 2D$. However the small γ behavior is less obvious since we are simultaneously concerned with long time properties. For fixed σ_f , we anticipate that synchronization should be hardest for strictly static oscillators ($\gamma=0$). This case corresponds to the noiseless D=0 Kuramoto model with Gaussian frequency dispersion $g(f) = \mathcal{N}_{\mu_f,\sigma_f}(f)$ $\equiv (\sqrt{2\pi\sigma_f})^{-1}e^{-(f-\mu_f)^2/2\sigma_f^2}$, so that $K_c = 2\sqrt{2/\pi\sigma_f}$. As the frequency dynamics loses stiffness (when γ increases), we expect the synchronization threshold to be facilitated by the frequency drifts.

We study the infinite population model $N \rightarrow \infty$ by formulating a Fokker-Planck equation for the time dependent joint density $p(\varphi, f, t)$. The all-to-all interaction term

$$\frac{K}{N}\sum_{j=1}^{N} \sin[\varphi_j(t) - \varphi_i(t)] = KR(t)\sin[\psi(t) - \varphi_i(t)]$$
(4)

has well known mean-field character and can be replaced for $N \rightarrow \infty$ by

$$K \int_{0}^{2\pi} d\theta \int dg p(\theta, g, t) \sin[\theta - \varphi_i(t)].$$
 (5)

We obtain

$$\frac{\partial p}{\partial t} = \gamma \sigma_f^2 \frac{\partial^2 p}{\partial f^2} - f \frac{\partial p}{\partial \varphi} + \gamma (f - \mu_f) \frac{\partial p}{\partial f} + \gamma p - K \frac{\partial (c(p,\varphi)p)}{\partial \varphi}.$$
(6)

This is the known expression for an OU process augmented by a phase coupling involving $c(p,\varphi) = \int_0^{2\pi} d\theta \int dg p(\theta, g, t) \sin(\theta - \varphi)$, which makes Eq. (6) nonlinear as a consequence of Eq. (5).

III. STABILITY ANALYSIS

We next discuss the linear stability of the incoherent stationary solution $p_0(\varphi, f) = \mathcal{N}_{\mu_f, \sigma_f}(f)/(2\pi)$ in first order. For reasons that will become clear, we factorize a term $\mathcal{N}_{\mu_f, \sigma_f}^{1/2}(f)$ off the perturbation and write

$$p(\varphi, f, t) = p_0(f) + \mathcal{N}_{\mu_f, \sigma_f}^{1/2}(f) \varepsilon(\varphi - \mu_f t, \sigma_f^{-1}(f - \mu_f), \gamma t),$$

where $\varepsilon(\tilde{\varphi}, \tilde{f}, \tilde{t})$ is a small perturbation expressed in a rotating frame using rescaled frequency and time variables. By plugging this ansatz into Eq. (6) we obtain the linearized problem $\partial \varepsilon / \partial t = \mathcal{L}\varepsilon + O(\varepsilon^2)$ where \mathcal{L} is the linear operator

$$\begin{split} \mathcal{L}\varepsilon &= \frac{\partial^2 \varepsilon}{\partial f^2} - \frac{\sigma_f}{\gamma} f \frac{\partial \varepsilon}{\partial \varphi} + \left(\frac{1}{2} - \frac{1}{4} f^2\right) \varepsilon \\ &+ \frac{K}{2\pi\gamma} \mathcal{N}_{0,1}^{1/2}(f) \int_0^{2\pi} d\theta \int dg \mathcal{N}_{0,1}^{1/2}(g) \varepsilon(\theta,g,t) \mathrm{cos}(\theta - \varphi). \end{split}$$

Decomposing ε as a Fourier series in φ , $\varepsilon(\varphi, f, t) = \sum_{n=-\infty}^{\infty} \varepsilon_n(f, t) e^{-in\varphi}$, we obtain for the coefficients ε_n

$$\frac{\partial \varepsilon_n}{\partial t} = \frac{\partial^2 \varepsilon_n}{\partial f^2} + \left(\frac{1}{2} - \frac{1}{4}f^2 + \frac{in\sigma_f}{\gamma}f\right)\varepsilon_n \\
+ \delta_{1|n|}\frac{K}{2\gamma}\mathcal{N}_{0,1}^{1/2}(f)\int dg\mathcal{N}_{0,1}^{1/2}(g)\varepsilon_n(g,t) \\
\equiv \mathcal{L}_n\varepsilon_n + \delta_{1|n|}\frac{K}{2\gamma}\langle\varepsilon_n, \mathcal{N}_{0,1}^{1/2}\rangle\mathcal{N}_{0,1}^{1/2}.$$
(7)

We notice that the first term representing the frequency dynamics resembles the harmonic oscillator plus a complex part, which can be removed by applying the translation operator U_{θ} defined by $(U_{\theta}f)(x) = f(x-\theta)$. We note that $\mathcal{L}_n = U_{2in\sqrt{a}}\hat{\mathcal{L}}_n U_{-2in\sqrt{a}}$, where we have set $a = (\sigma_f/\gamma)^2$ and the operator $\hat{\mathcal{L}}_n = \partial_f^2 + \frac{1}{2} - n^2 a - \frac{1}{4}f^2$ is self-adjoint on $L^2(\mathbb{R})$ and has pure point spectrum $\Sigma(\hat{\mathcal{L}}_n) = \{\lambda_{n\ell} = -\ell - n^2 a : \ell = 0, 1, 2, ...\}$. Its eigenfunctions are given in terms of the Hermite functions [24]

$$H_0(x) = \pi^{-1/4} e^{-x^2/2},$$

$$H_\ell(x) = (2^\ell \ell! \sqrt{\pi})^{-1/2} (-1)^\ell e^{x^2/2} \partial_x^\ell e^{-x^2}, \quad \ell = 1, 2, \dots$$

as follows:

$$\hat{\mathcal{L}}_n \Phi_\ell = \lambda_{n\ell} \Phi_\ell, \quad \Phi_\ell(f) = 2^{-1/4} H_\ell(2^{-1/2} f).$$

Therefore $\{U_{2in\sqrt{a}}\Phi_{\ell}: \ell=0,1,2,...\}$ forms an orthonormal family which diagonalizes \mathcal{L}_n . Notice that the largest eigenvalue for each *n* is $\lambda_{n0} = -n^2 a$.

Linear stability follows directly except for $|n| \neq 1$ and K > 0. Indeed, for n=0, we find $\lambda_{00}=0$ with corresponding eigenfunction is $\Phi_0 = \mathcal{N}_{0,1}^{1/2}$. However, this function lies outside the space of relevant perturbations because the normalization of p, $\int_0^{2\pi} d\varphi \int df p(\varphi, f, t) = 1$, requires orthogonality of $\mathcal{N}_{0,1}^{1/2}$ and $\varepsilon_0(f, t)$ through $\int \mathcal{N}_{0,1}^{1/2} \varepsilon_0(f, t) df = 0$. Subsequent eigenvectors have negative eigenvalues. For all other $|n| \neq 1$ the coupling term in Eq. (7) vanishes and the incoherent state $p(\varphi, f, t) = p_0(f)$ is linearly stable as a consequence of the strictly negative spectrum of \mathcal{L}_n . The same holds for all n in the absence of coupling K=0.

For the remaining case $n=\pm 1$ and K>0, we notice that the coupling term in Eq. (7) also vanishes for all directions orthogonal to $\mathcal{N}_{0,1}^{1/2}$, leaving a one-dimensional space that could develop an instability. We write the eigenvalue problem for Eq. (7) implicitly as

$$\mathcal{L}_{n}\varepsilon_{n}+\delta_{1|n|}\frac{K}{2\gamma}\langle\varepsilon_{n},\mathcal{N}_{0,1}^{1/2}\rangle\mathcal{N}_{0,1}^{1/2}=\lambda\varepsilon_{n}.$$

Using the resolvent equation

$$(\lambda - \mathcal{L}_n)^{-1} = (\lambda - U_{2in\sqrt{a}}\hat{\mathcal{L}}_n U_{-2in\sqrt{a}})^{-1}$$
$$= U_{2in\sqrt{a}}(\lambda - \hat{\mathcal{L}}_n)^{-1} U_{-2in\sqrt{a}}$$

we obtain

$$\begin{split} \varepsilon_n &= \frac{K}{2\gamma} \langle \varepsilon_n, \mathcal{N}_{0,1}^{1/2} \rangle U_{2in\sqrt{a}} (\lambda - \hat{\mathcal{L}}_n)^{-1} U_{-2in\sqrt{a}} \mathcal{N}_{0,1}^{1/2} \\ &= \frac{K}{2\gamma} \langle \varepsilon_n, \mathcal{N}_{0,1}^{1/2} \rangle \sum_{j=0}^{\infty} \frac{\langle \Phi_j, U_{-2in\sqrt{a}} \mathcal{N}_{0,1}^{1/2} \rangle}{\lambda - \lambda_{nj}} U_{2in\sqrt{a}} \Phi_j, \end{split}$$

where we have used the spectral decomposition $\hat{\mathcal{L}}_n f = \sum_j \lambda_j \langle \Phi_j, f \rangle \Phi_j$.

To find the critical coupling K_c above which the incoherent state becomes linearly unstable, we need to monitor when the largest eigenvalue crosses the imaginary axis. After



FIG. 1. The behavior of K_c as a function of γ as given by Eq. (8) with $a = (\sigma_f / \gamma)^2$ (continuous line). The dashed line represents the Kuramoto model with identical frequencies and $K_c = 2D = 2\sigma_f^2 / \gamma$. The $\gamma \rightarrow 0$ limit reproduces the $\gamma = 0$ model with Gaussian frequency dispersion and gives $K_c / \sigma_f = 2\sqrt{2/\pi} = 1.5957$ (dotted line).

projecting onto $\mathcal{N}_{0,1}^{1/2}$, simplifying the factors $\langle \varepsilon_n, \mathcal{N}_{0,1}^{1/2} \rangle$ on both sides of the equation, and setting $\lambda = 0$ we find an equation for K_c

$$\frac{2\gamma}{K_c} = \sum_{j=0}^{\infty} \frac{\langle \Phi_j, U_{-2i\sqrt{a}} \mathcal{N}_{0,1}^{1/2} \rangle^2}{-\lambda_{1j}}$$
$$= e^a \sum_{j=0}^{\infty} \frac{(-a)^j}{j!(j+a)} = e^a a^{-a} \int_0^a t^{a-1} e^{-t} dt = e^a a^{-a} \gamma(a,a),$$
(8)

where $\gamma(a,x)$ is the lower incomplete Γ function.

The behavior of K_c together with the Kuramoto model asymptotes for $\gamma \rightarrow \infty$ and $\gamma \rightarrow 0^+$ limit are shown in Fig. 1. It is noticeable that we find a bifurcation for all values of γ . K_c strictly decreases from a finite $\gamma=0$ as γ increases, asymptotically behaving as $K_c = 2\sigma_f^2 / \gamma$. The analytical result thus supports the following picture: for small γ , the dominant source of fluctuations against which the coupling must work to achieve synchronization is the (Gaussian) frequency dispersion. As γ increases while σ_f is kept fixed, faster frequency drifts help synchrony by preventing individual oscillators with detuned frequency to stay out of tune for too long. Indeed with drifting frequencies every individual oscillator fluctuates around the mean frequency μ_f with a time scale γ^{-1} . In the large γ regime, the effective frequency dispersion vanishes and the coupling force needs to synchronize noisy but otherwise identical frequency oscillators. As predicted by the phase diffusion limit, the effective white noise strength D and hence K_c decrease as γ^{-1} .

We now discuss the asymptotic regimes in detail: the small γ limit follows from reverting to the original variables and using the asymptotic expansion of $\gamma(a,a)$ (using Stirling's formula and [25]: 6.5.3, 6.5.22, and 6.5.35). We obtain in the limit $\gamma \rightarrow 0^+$

$$2\left(\frac{K_c}{\sigma_f}\right)^{-1} = \sqrt{\frac{\pi}{2}} + \frac{1}{3}\frac{\gamma}{\sigma_f} + \frac{\sqrt{2\pi}}{24}\frac{\gamma^2}{\sigma_f^2} + O(\gamma^3).$$

This proves that the model continuously interpolates to the noiseless (D=0) model and that the $\gamma \rightarrow 0$ recovers the $\gamma = 0$ transition predicted in the original Kuramoto model at $K_c/\sigma_f = 2\sqrt{2/\pi}$. In the opposite regime $\gamma \rightarrow \infty$ (thus $a \rightarrow 0$) we find ([25] 6.5.12, 13.1.2)

$$a^{-a}e^{a}\gamma(a,a) = a^{-1}M(1,1+a,a) \sim a^{-1}(1+O(a)),$$

where $M(\cdot, \cdot, \cdot)$ is the confluent hypergeometric function. This leads $K_c \sim 2\sigma_f^2 / \gamma + O(\gamma^{-2})$ and hence proves the convergence to the white noise model [Eq. (1)] with $D = \sigma_f^2 / \gamma$.

Finally, we mention a generalization that includes a white noise source in the phase equation [as in Eq. (1)] in addition to the correlated frequency fluctuations. This leads an additional diffusion term $-D(\partial^2 p / \partial \varphi^2)$ in Eq. (6). Following the steps above readily extends Eq. (8) to

$$\frac{2\gamma}{K_c} = e^a a^{-(a+b)} \gamma(a+b,a),$$

where $b=D/\gamma$, with similar qualitative behavior. In particular, K_c asymptotes to $2(\sigma_f^2/\gamma+D)$ for large γ and has finite $\gamma \rightarrow 0$ limit.

IV. NUMERICAL SIMULATIONS

We have performed numerical simulations of Eq. (2) to explore the behavior of R(t) [see Eq. (4)] and in particular R_{∞} in function of the reduced coupling $K_r = (K - K_c)/K_c$. To verify the analytical results and study the scaling $R_{\infty} = \kappa K_r^{\beta}$ above the bifurcation, we simulated a finite number of oscillators using the exact solution for the frequency part, leading $f_i(t+dt) = f_i(t)e^{-\gamma dt} + \mu_f(1-e^{-\gamma dt})$ to the updates $+ \eta \sigma_f \sqrt{1 - e^{-2\gamma dt}}$ and $\varphi_i(t + dt) = \varphi_i(t) + (f_i(t) + K/N \Sigma_i \sin(\varphi_i))$ $(-\varphi_i)$) dt where η is a Gaussian random number. We used Eq. (4) to compute R(t) and transients were removed by waiting until the solutions from two different initial conditions $\varphi_i(t)$ =0)=0 and $\varphi_i(t=0)$ taken randomly converged to the same trajectory. The steady state value R_{∞} was subsequently estimated by averaging R(t) over time.

Figure 2 fully supports the analytical solution and also indicates that the behavior of K_c above the bifurcation depends only weakly on γ over the simulated range. To inspect more closely whether $R_{\infty} \sim \sqrt{K_r}$ as in the Kuramoto model, we used refined spacing and larger sizes in the vicinity of $K_r=0^+$. As shown in Fig. 3, the simulations are compatible with an exponent $\beta=0.5$, the slightly higher exponents probably reflect a finite size effect. On the other hand κ correlates negatively with γ which is visible in both Figs. 2 and 3.

V. DISCUSSION

We have extended the Kuramoto model to frequencies which can drift in time following Ornstein-Uhlenbeck dynamics. The net effect is that the white noise source in Eq. (1) is replaced by colored noise (with a Cauchy distributed power spectrum), hereby adding a new time scale describing



FIG. 2. Numerical simulation of Eq. (2). The estimation of R_{∞} was obtained using finite size scaling for systems of sizes N = 5000, 10 000, and 20 000. Equation (8) was used for K_c to set the reduced coupling $K_r = (K - K_c)/K_c$. Values for γ were 4 (\bigcirc), 3 (\triangle), 2.5 (+), 2 (×), 1.8 (\diamond), and 1.6 (\bigtriangledown) and $\sigma_f = 1$. In each simulation, 10⁵ time steps of size dt = 0.01 were performed. We verified that the dependence in the step size was weak. Inset: 1/N finite size scaling for $\gamma = 1.8$. $K_r = 0$ is the solid line, smaller (larger) K_r are below (above) $K_r = 0$. The extrapolated value for 1/N = 0 is used in the main panel.

memory or frequency stiffness to the problem. Apart from mean field coupling among the phases which introduces a nonlinearity, the stochastic phase and frequency dynamics lead to a linear Fokker-Planck operator which can be solved. Consequently the linear stability of the incoherent state can be addressed analytically using spectral calculus. The expression for the critical coupling above which macroscopic phase



FIG. 3. Critical behavior above the bifurcation using step dK_r =0.01. Here, γ is 4 (\bigcirc), 3 (\triangle), 2 (+), 1.6 (\times), 1.2 (\diamond), and 0.8 (\bigtriangledown). Notice the log-log scale to emphasize the power law. Lines are fits to $R_{\infty} = \kappa K_r^{\beta}$. Systems of sizes $N=10\ 000$, 20 000, and 50 000 were simulated with the same parameters and same scaling procedure as in Fig. 2. The right panels show parameter estimates from the left panel.

coherence emerges can be resummed and expressed in terms of incomplete Γ functions. Asymptotic expansion for small and large γ shows that the full model continuously interpolates between two limits of the original Kuramoto model: one dominated by noise (large γ) and the other by the frequency dispersion (small γ). Therefore, the coupling force must counteract different sources of fluctuations to induce collective synchrony in drifting frequency oscillators, depending on the regime set by γ . Specifically, for slowly drifting (small γ) frequencies the model approaches the noiseless model [Eq. (1) with D=0 and $g(f)=\mathcal{N}_{\mu_{f},\sigma_{f}}(f)$] where the coupling splits the population into distinct locked and incoherent subpopulations, depending on the proximity of individual frequencies to the population mode. As γ increases (while σ_f is held fixed), the frequencies lose their stiffness which results in a reduction in the critical coupling K_c needed for synchrony. Finally for very rapidly drifting oscillators (large γ) cancel out the frequency distribution and generate an effective white noise source acting on the phases of otherwise equal frequency oscillators. At the same time the locked and incoherent subgroups become indistinguishable.

- K. Wiesenfeld, P. Colet, and S. H. Strogatz, Phys. Rev. Lett. 76, 404 (1996).
- [2] K. Wiesenfeld, P. Colet, and S. H. Strogatz, Phys. Rev. E 57, 1563 (1998).
- [3] I. Z. Kiss, Y. Zhai, and J. L. Hudson, Science 296, 1676 (2002).
- [4] C. Liu, D. R. Weaver, S. H. Strogatz, and S. M. Reppert, Cell 91, 855 (1997).
- [5] A. T. Winfree, J. Theor. Biol. 16, 15 (1967).
- [6] S. H. Strogatz, Sync: The Emerging Science of Spontaneous Order (Hyperion, New York, 2003).
- [7] U. Schibler and F. Naef, Curr. Opin. Cell Biol. 17, 223 (2005).
- [8] E. Nagoshi, C. Saini, C. Bauer, F. Naef, and U. Schibler, Cell 119, 693 (2004).
- [9] D. K. Welsh, S. H. Yoo, A. C. Liu, J. S. Takahashi, and S. A. Kay, Curr. Biol. 14, 2289 (2004).
- [10] A. J. Carr and D. Whitmore, Nat. Cell Biol. 7, 319 (2005).
- [11] J. Leloup and A. Goldbeter, Proc. Natl. Acad. Sci. U.S.A. 100, 7051 (2003).
- [12] J. M. Vilar, H. Y. Kueh, N. Barkai, and S. Leibler, Proc. Natl.

For intermediate γ , our numerical simulations indicate that the model belongs to the same $\beta = 0.5$ universality class as the Kuramoto model.

Because of analytical tractability and few parameters we expect this solution to be relevant for oscillatory systems in the presence of complex noise sources. Such cases include populations of neural oscillators or biochemical oscillators where bioluminescence recordings have shown how intracellular noise sources generate frequency dispersion through drifts.

ACKNOWLEDGMENTS

We thank Benoit Kornmann and Ueli Schibler for initiating our interest in the drifting frequency model and Olivier Hernandez for pointing out useful references. The simulations were performed on an Itanium2 cluster from HP/Intel at the Vital-IT facilities. F.N. acknowledges funding from the Swiss National Science Foundation NCCR Molecular Oncology program and NIH administrative supplement to parent Grant No. GM54339.

Acad. Sci. U.S.A. 99, 5988 (2002).

- [13] Y. Kuramoto, Prog. Theor. Phys. Suppl. 79, 223 (1984).
- [14] H. Sakaguchi and Y. Kuramoto, Prog. Theor. Phys. 76, 576 (1986).
- [15] Y. Kuramoto and I. Nishikawa, J. Stat. Phys. 49, 569 (1987).
- [16] S. H. Strogatz, R. E. Mirollo, and P. C. Matthews, Phys. Rev. Lett. 68, 2730 (1992).
- [17] S. H. Strogatz, Physica D 143, 1 (2000).
- [18] J. D. Crawford, Phys. Rev. Lett. 74, 4341 (1995).
- [19] J. D. Crawford and K. T. R. Davies, Physica D 125, 1 (1999).
- [20] J. D. Crawford, J. Stat. Phys. 74, 1047 (1994).
- [21] H. Sakaguchi, Prog. Theor. Phys. 79, 29 (1988).
- [22] S. H. Strogatz and R. E. Mirollo, J. Stat. Phys. 63, 613 (1991).
- [23] Y. Kuramoto, *Chemical Oscillations, Waves, and Turbulence* (Springer, Berlin, 1984).
- [24] M. Reed and B. Simon, Methods of Modern Mathematical Physics, I: Functional Analysis (Academic Press, San Diego, 1980).
- [25] *Handbook of Mathematical Functions*, edited by M. Abramowitz and I. A. Stegun (Dover, New York, 1972).