Asymptotic Phase for Stochastic Oscillators

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Oscillations and noise are ubiquitous in physical and biological systems. When oscillations arise from a deterministic limit cycle, entrainment and synchronization may be analyzed in terms of the asymptotic phase function. In the presence of noise, the asymptotic phase is no longer well defined. We introduce a new definition of asymptotic phase in terms of the slowest decaying modes of the Kolmogorov backward operator. Our stochastic asymptotic phase is well defined for noisy oscillators, even when the oscillations are noise dependent. It reduces to the classical asymptotic phase in the limit of vanishing noise. The phase can be obtained either by solving an eigenvalue problem, or by empirical observation of an oscillating density’s approach to its steady state.

Introduction. Limit cycles (LC) appear in deterministic models of nonlinear oscillators such as spiking nerve cells [1], central pattern generators [2], and nonlinear circuits [3]. The reduction of LC systems to one-dimensional “phase” variables is an indispensable tool for understanding entrainment and synchronization of weakly coupled oscillators [4, 5]. Within the deterministic framework, all initial points converge to the LC, on which we can define a phase that progresses at a constant rate (θ = ωLC = 2π/TLC). The phase θ(x0) of any point x0 is then defined by the asymptotic convergence of the trajectory to that phase on the LC. However, stochastic oscillations are ubiquitous, for example in biological systems [6], and in this setting the classical definition of the phase breaks down. For a noisy dynamics, all initial densities will converge to the same stationary density. Thus the large-t asymptotic behavior no longer disambiguates initial conditions, and the classical asymptotic phase is not well defined.

Schwabedal and Pikovsky attacked this problem by defining the phase for a stochastic oscillator in terms of the mean first passage times (MFPT) between surfaces analogous to the isochrons (level curves of the phase function θ(x)) of deterministic LC [7, 8]. Here we formulate an alternative definition that is tied directly to the asymptotic behavior of the density, rather than the first passage time, and is grounded in the analysis of the forward and backward operators governing the evolution of system densities. Our operator approach leads to two distinct notions of “phase” for stochastic systems. As we argue below, the phase associated with the backward or adjoint operator is closely related to the classical asymptotic phase.

General framework. Consider the conditional density ρ(y, t|x, s), for times t > s, evolving according to the forward and backward equations

$$\frac{\partial}{\partial t} \rho(y, t|x, s) = \mathcal{L}_y \rho, \quad \frac{\partial}{\partial s} \rho(y, t|x, s) = -\mathcal{L}_x^\dagger \rho,$$

where $\mathcal{L}$ and $\mathcal{L}^\dagger$ are adjoint with respect to the usual inner product on the space of densities. We assume that the conditional density can be written as a sum

$$\rho(y, t|x, s) = P_0(y) + \sum_\lambda e^{\lambda(t-s)} P_\lambda(y) Q_\lambda^*(x),$$

where the eigentriple $(\lambda, P, Q^*)$ satisfy

$$\langle Q\lambda | P\lambda \rangle = \lambda P_\lambda, \quad \mathcal{L}^\dagger Q\lambda = \lambda Q\lambda,$$

$$\int dx Q\lambda(x) P_\lambda(x) = \delta_{\lambda,\lambda'}.$$

Here $P_0$ is the unique stationary distribution corresponding to eigenvalue 0, $Q_0 \equiv 1$, and for all other eigenvalues $\lambda$, we assume $\Re[\lambda] < 0$. Thus, as $(t-s) \to \infty$, $\rho(y, t|x, s) \to P_0(y)$. We refer to the system as robustly oscillatory if (i) the nontrivial eigenvalue with least negative real part $\lambda_1 = \mu + i\omega$ is complex (with $\omega > 0$), (ii) $|\omega/\mu| \gg 1$ and (iii) for all other eigenvalues $\lambda'$, $\Re[\lambda'] \leq 2\mu$. These conditions guarantee that the slowest decaying mode, as the density approaches its steady state, will oscillate with period $2\pi/\omega$, and decay with time constant $1/|\mu|$. Writing the eigenfunctions of $\lambda_1$, the slowest decaying eigenvalue of the forward and backward operators, in polar form, we have $P_{\lambda_1} = ve^{-i\phi}$ and $Q_{\lambda_1} = ve^{i\phi}$, where $u, v \geq 0$ and $\psi, \phi \in [0, 2\pi)$. Asymptotically, we obtain with this notation from eq. [1]

$$\frac{\rho(y, t|x, s) - P_0(y)}{2u(x)v(y)} \simeq e^{\mu(t-s)} \cos(\omega(t-s) + \psi(x) - \phi(y)).$$

As we now argue, $\psi(x)$, the polar angle associated with the backward eigenfunction, is the natural generalization of the deterministic asymptotic phase.

For a deterministic LC system, a given asymptotic phase is assigned to points off the LC by identifying those points which at an earlier time were positioned so that their subsequent paths would converge. Suppose
we observe a density of points $\rho(y, t)$ concentrated near a position on the LC corresponding to a certain phase $\theta(y) \approx \theta_0$. Fixing a point $x$ away from the LC, the density $\rho(x, s)$ at earlier times $s < t$ will show transient oscillations with period $T_{iLC}$ as the density propagates away from the stable LC in reverse time. The oscillations observed at two distinct points $x$ and $x'$ will be offset by the difference in their asymptotic phase. Looking forward in time, all trajectories will continue converging to the LC, so the density for a point away from the LC will not oscillate – it will remain zero.

Figure 1 illustrates the analogous measurement of the phase at a point $x$ from the conditional density at earlier times, $\rho(x, s|y, t)$, for a stochastic oscillator. For a stationary stochastic time series this density is related to the conditional density $\rho(y, t|x, s)$ appearing in eq. (5) by $\rho_0(x, s|y, t) = \rho(y, t|x, s)P_0(x) = \rho(x, s|y, t)P_0(y)$ (not to be confused with the detailed balance condition), which can be used to rewrite eq. (5) as follows

$$\rho(x, t - \tau|y, t) - P_0(x) \approx \frac{e^{\mu \tau}}{P_0(y)} \cos (\omega \tau + \psi(x) - \phi(y)),$$

where we have switched to $s = t - \tau$ with $\tau > 0$. If we select from a stationary ensemble the trajectories that end up at time $t$ in $y$, we can estimate the conditional density $\rho(x, t - \tau|y, t)$ and the steady state $P_0(x)$. Fitting then the left-hand-side of eq. (6) to a damped cosine in $\tau$ (see Fig. 1), we can by virtue of eq. (4) infer the phase $\psi(x)$ at any point $x$. In contrast to the deterministic oscillator, a stochastic system will converge to a steady state distribution both forward and backward in time. If the system trajectories $Y(t)$ show oscillatory behavior, the steady state density will be approached by a damped oscillation at points with nonvanishing density $P_0$. For the stationary stochastic case, the conditional density at earlier times $s < t$ takes the asymptotic form:

$$\rho(x, s|y, t) - P_0(x) \approx \frac{e^{\mu (t-s)}}{P_0(y)} \cos (\omega (t-s) + \psi(x) - \phi(y)).$$

Therefore we may obtain the backward-looking asymptotic phase $\psi(x)$ through stochastic simulations of an ensemble of trajectories, as illustrated in Fig. 4.

We may also obtain the backward-looking phase by solving the eigenvalue problem eq. (3) for $Q^*$. Comparison with the deterministic case again points to the complex angle of $Q^*$ as the analog of the classical case. For a deterministic system, $dx/dt = A(x)$, the conditional density $\rho(y, t|x, s)$ obeys eq. (4) with $L_1^*[Q] = \sum_i A_i(x) \partial Q(x)/\partial x_i$. The function $Q_1 = \omega \theta(x)$ with $\omega = 1$ and $\psi(x) = \theta(x)$ is an eigenfunction of $L_1$ with eigenvalue $\lambda = i\omega \xi LC$. The analogous eigenfunction of the forward operator, $L_y[P] = -\sum_i \partial (A_i(y) P(y))/\partial y_i$, is identically zero except on the LC, at which it has a delta-mass radial distribution. Thus $P_1$ is unsuitable for defining a “phase” anywhere except on the limit cycle itself.

**Noisy Heteroclinic Oscillator.** Consider the system

$$\dot{Y}_1 = \cos(Y_1) \sin(Y_2) + \alpha \sin(2Y_1) + \sqrt{2} \delta \xi_1(t)$$

$$\dot{Y}_2 = -\sin(Y_1) \cos(Y_2) + \alpha \sin(2Y_2) + \sqrt{2} \delta \xi_2(t),$$

with $\alpha = 0.1$, reflecting boundary conditions on the domain $-\pi/2 \leq \{Y_1, Y_2\} \leq \pi/2$, and independent white noise sources $\langle \xi_i(t)\xi_j(t') \rangle = \delta(t-t')\delta_{ij}$. Without noise ($D = 0$) the system has an attracting heterocycle, but does not possess a finite-period limit cycle. Therefore, in the noiseless case, there is no classical asymptotic phase [10].

For weak noise, the system displays pronounced oscillations (Fig. 4 B), manifest as irregular clockwise rotations in the $(y_1, y_2)$ plane (Fig. 4 A). We can use large trajectories and condition them on their end point (red box in Fig. 4 A). As argued above, looking back into the past of such an ensemble of trajectories, we see for large times a damped oscillation (Fig. 4 C and D), the damping constant and frequency of which should be related to the real and imaginary parts of the first non-vanishing eigenvalue. Indeed, we have checked by fitting a damped cosine according to eq. (7) to the counting histograms of the backward probability at different positions, that the estimate of $\mu$ and $\omega$ is largely independent of location (not shown). More importantly, fitting a damped
the remaining eigenvalues. As we would expect, for a
plex conjugate pair (framed) that is well separated from
conditions, the first nonvanishing eigenvalues form a com-
Fig. 2C for two different noise values. Under both noise
values and eigenvectors of the corresponding matrix equa-
We solve the eigenvalue problem eq. (3) for the sys-
backward operator reads explicitly
eigenvalue of the system. For the process eq. (8), the
by the complex phase of the eigenfunction for the slowest
point (\(y_1, y_2\)).
As outlined above, the asymptotic phase is also given
by the complex phase of the eigenfunction for the slowest
value of the system. For the process eq. (8), the
backward operator reads explicitly
\[
L^f = \left[ \cos(x_1) \sin(x_2) + \alpha \sin(2x_1) \right] \partial_{x_1} + D \partial_{x_1}^2 \\
+ \left[ -\sin(x_1) \cos(x_2) + \alpha \sin(2x_2) \right] \partial_{x_2} + D \partial_{x_2}^2 .
\]
We solve the eigenvalue problem eq. (3) for the sys-
tem by expanding the eigenfunctions in a Fourier basis
\(Q_n = \sum c_{m,n} e^{\i (m x_1 + n x_2)}\) and computing the eigenval-
and eigenvectors of the corresponding matrix equation
numerically. The leading eigenvalues are shown in
Fig. 2C for two different noise values. Under both noise
conditions, the first nonvanishing eigenvalues form a com-
plex conjugate pair (framed) that is well separated from
the remaining eigenvalues. As we would expect, for a
lower noise level \((D = 0.01125, \text{black filled circles})\) this
separation is more pronounced than for a higher level
\((D = 0.1, \text{red empty circles})\).

The complex phase of the eigenfunction for the two dis-
tinct noise levels is shown in Fig. 2A and B. The phase
increases in the same direction as the local mean velocity
(clockwise) in both cases. For weaker noise, the phase
winds inward more steeply, i.e. the inward radial compo-
ment of \(\nabla \psi\) is larger.

In Fig. 2A and B we also superimpose data (blue
points) generated by the histogram method, subject to a
uniform constant vertical offset. The agreement of these
two surfaces demonstrates that the asymptotic phase can
be obtained by the solution of the partial differential
eq. (3) for model systems, for which this equation is
known, but also from trajectories of the system obtained
either by stochastic simulations (for a model) or mea-
surements (experimental data).

Neural Oscillator with Ion Channel Noise. Izhikevich
introduced a planar conductance-based model for ex-
citable membrane dynamics that is similar to the well
known two-dimensional Morris-Lecar model. We
consider a jump Markov process version of Izhikevich’s
model, in which noise arises from the random gating of
a small, discrete population of \(N_{\text{tot}}\) potassium (\(K\)) chan-
nels, which switch between an open and a closed state.
Conditional on \(N(t)\), the number of open channels at
time \(t\), the voltage \(V\) evolves deterministically:
\[
C \frac{dV}{dt} = I_0 - I_L(V) - I_{\text{NaP}}(V) - I_K(V, N)
= C f(V, N)
\]
where \(I_0\) is an applied current, \(I_L\) is a passive leak cur-
cent, \(I_{\text{NaP}}\) is a deterministic “persistent sodium” current
and \(I_K\) is a potassium current gated by the number of
open potassium channels, \(0 \leq N \leq N_{\text{tot}}\). We used stan-
dard parameters.

The number of open channels \(N(t)\) comprises a con-
tinuous time Markov jump process with voltage dependent
per capita transition rates \(\alpha(v)\) for channel opening and
\(\beta(v)\) for channel closing. We generated trajectories
of the joint \((V, N)\) process using an exact stochastic simu-
lation algorithm that takes into account the time-varying
transition rates \(\alpha\) and \(\beta\). Fig. 3A shows a tra-
jectory in the \((v, n)\) plane for \(N_{\text{tot}} = 100\) channels and
applied current \(I_0 = 60\). The light and dark blue dashed
lines show the \(v\)-nullcline and \(n\)-nullcline, respectively.
In contrast to the noisy heteroclinic oscillator, this system
has a stable limit cycle in the limit of vanishing noise
\((N_{\text{tot}} \to \infty)\) with finite period \(T_{1,CL} \approx 5.9825\).

The forward and backward equations for this system
are given in terms of \(f(v, n)\) (eq. 10), \(\alpha(v)\) and \(\beta(v)\)
We approximate the operator $\mathcal{L}^0$ with a finite difference scheme by discretizing the voltage axis $-80 \leq v \leq 20$ into 200 bins of equal width. We obtain the eigenvalues and eigenvectors of the matrices approximating $\mathcal{L}$ and $\mathcal{L}^0$ using standard methods (MATLAB, The Mathworks). Fig. 3B shows the dominant (slowest decaying) part of the eigenvalue spectrum. Note the occurrence of a family of eigenvalues of the form $\lambda_k = \pm i\omega_k - \mu k^2$, $k = 0, 1, 2, \ldots$. The quadratic relationship between the real and imaginary parts of the eigenvalues of this form is consistent with the existence of a change of coordinates under which the evolution takes the approximate form of diffusion on a ring with constant drift, $\dot{\varphi} = \omega + \sqrt{2} \mu \xi(t)$. Here the eigensystem is exactly solvable, and the spectrum lies on the same parabola.

In Figure 3B, the first nonzero pair (framed) for $N_{\text{tot}} = 100$ is $\lambda_1 \approx -0.031 \pm 1.0475i$, corresponding to a period for the decaying oscillation of $T = 5.9985$ (cf. $T_{\text{LC}}$ above) and $\omega/|\mu| \approx 33.7 > 1$. All other eigenvalues have real part less than or equal to $4\mu$, so the system is “robustly oscillatory” according to our criteria (i-iii).

![Diagram](A) ![Diagram](B) ![Diagram](C)

**FIG. 3**: (color online) Trajectory, nullclines, eigenvalues of the backward operator, and asymptotic phase lines for the persistent-sodium–potassium model. (A) Sample trajectory (thin black line) for the $(V, N)$ process for $N_{\text{tot}} = 100$ channels, and nullclines for the deterministic $v$ (thick grey line) and $n$ (thick black line) dynamics. (B) Low-lying spectrum for $\mathcal{L}^0$ for two different channel numbers, $N_{\text{tot}} = 100$ (black dots) and $N_{\text{tot}} = 25$ (red crosses). Dashed boxes indicate the leading complex conjugate eigenvalue pairs. (C) Level curves (isochrons) of the asymptotic phase for $N_{\text{tot}} = 25$ (red), $N_{\text{tot}} = 100$ (black), and $N_{\text{tot}} = \infty$ (blue; deterministic case). The thick lines indicate the locations of the phase jump by $2\pi$, which have been adjusted to coincide for the three cases. Isochrons are marked in equal increments of $2\pi/20$. Nullclines as in (A).

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oscillators by studying the effects of weak noise on a deterministically defined phase [19–23]. We generalize the classical asymptotic phase to the stochastic case in terms of the eigenfunctions of the backward operator describing the evolution of densities with respect to the initial time. As with the stochastic phase defined via the MFPT [7–9], the backward-looking asymptotic phase is well defined whether or not the underlying deterministic system has a well defined phase. However, if the classical phase exists, in the absence of noise, our asymptotic phase has a well-defined phase. However, if the classical phase time. As with the stochastic phase defined via the evolution of densities with respect to the initial point $x$ to a given surface obeys an inhomogeneous partial differential equation involving the same adjoint operator $L_x^*$, an eigenfunction of which defines our asymptotic phase. Thus, the relationship between Schwabedal and Pikovsky’s phase description of stochastic oscillators and our asymptotic phase remains an appealing topic for future research.

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[1] G.B. Ermentrout and D.H. Terman. Foundations Of Mathematical Neuroscience. Springer, 2010.
[2] A.J. Ijspeert. Neural Netw., 21:642, 2008.
[3] D.W. Jordan and P. Smith. Nonlinear Ordinary Differential Equations. Oxford University Press, 4th edition, 2007.
[4] G.B. Ermentrout and N. Kopell. SIAM J. Math Anal, 15:215, 1984.
[5] A. Pikovsky, M. Rosenblum, and J. Kurths. Synchronization: A universal concept in nonlinear sciences. Cambridge University Press, 2001.
[6] Examples include spontaneous oscillations of hair bundles in inner ear organs [P. Martin, D. Bozovic, Y. Choe, and A. J. Hudspeth. J. Neurosci., 23(11):4533, 2003], stochastic oscillations of the intracellular calcium concentration [U. Kummer et al. Biophys. J., 89:2005], and subthreshold membrane oscillations [D. Schmitz, T. Govei, J. Behr, T. Dugladze, and U. Heinemann. Neurosci., 85(4):999, 1998; J.A. White, R. Klink, A. Alonso, A.R. Kay. J. Neurophys., 80:262, 1998.].
[7] J.T.C. Schwabedal and A. Pikovskiy. Phys Rev E, 81:046218, 2010.
[8] J.T.C. Schwabedal and A. Pikovskiy. Eur. Phys. J., 187:63, 2010.
[9] J.T.C. Schwabedal and A. Pikovskiy. Phys. Rev. Lett., 110:4102, 2013.
[10] K.M. Shaw, Y.-M. Park, H.J. Chiel, and P.J. Thomas. SIAM J. Appl. Dyn. Sys., 11:350, 2012.
[11] In the plot we omit points around $X_1 = X_2 = 0$ (for which a reliable estimation of the phase was difficult) and added a small off-set to the remaining points for better visibility. Relative numerical error between theory and simulations is below 5% for both noise levels.
[12] E.M. Izhikevich. Dynamical Systems in Neuroscience. Computational Neuroscience. MIT Press, Cambridge, Massachusetts, 2007.
[13] C. Morris and H. Lecar. Biophys. J., 35:193, 1981.
[14] J. Rinzel and G.B. Ermentrout. In C. Koch and I. Segev, editors, Methods in Neuronal Modeling. MIT Press, second edition, 1989.
[15] Applied current $I_0 = 60\mu A/cm^2$, passive leak current $I_L = g_L(V - V_L)$ with $g_L = 1mS/cm^2$ and $V_L = -78mV$, “persistent sodium” current $I_{NaP} = g_{NaP}m_{\infty}(V)(V - V_{NaP})$ with $g_{NaP} = 4mS/cm^2$, $V_{NaP} = 60mV$ and voltage dependent activation $m_{\infty}(v) = 1/(1 + \exp((-30 - v)/T)))$; potassium current $I_K = (g_K/N_{tot})(V - V_K)$ with $g_K = 4mS/cm^2$, $V_K = -90mV$, and open channel number $0 \leq N \leq N_{tot}$. Membrane capacitance is $C = 1 \mu F/cm^2$. Per capita transition rate for channel opening is $\alpha(v) = 1/(1+\exp((-45-v)/5))$ and for closing is $\beta(v) = 1 - \alpha(v)$.
[16] D.F. Anderson, B. Ermentrout, and P.J. Thomas. J. Comput. Neurosci., 2014. In press.
[17] J.M. Newby, P.C. Bressloff, and J.P. Keener. Phys. Rev. Lett., 111:128101, 2013.
[18] K. Pakdaman, M. Thieullen, and G. Wainrib. Adv. Appl. Prob., 42:761, 2010.
[19] L. Calembach, P. Hägg, S.J. Linz, J.A. Freund, and L. Schimansky-Geier. Phys Rev E, 65:051110, 2002.
[20] J.A. Freund, L.Schimansky-Geier, and P. Hägg. Chaos, 13:225, 2003.
[21] G.B. Ermentrout, R.F. Galán, and N.N. Urban. Phys. Rev. Lett., 99:248103, 2005.
[22] R.F. Galán, G.B. Ermentrout, and N.N. Urban. Phys. Rev. Lett., 94:138101, 2005.
[23] G.B. Ermentrout, B. Beverlin, T. Troyer, and T.I. Netoff. J. Comput. Neurosci., 31:185, 2011.