Effective phase dynamics of noise-induced oscillations in excitable systems

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We develop an effective description of noise-induced oscillations based on deterministic phase dynamics. The phase equation is constructed to exhibit correct frequency and distribution density of noise-induced oscillations. In the simplest one-dimensional case the effective phase equation is obtained analytically, whereas for more complex situations a simple method of data processing is suggested. As an application an effective coupling function is constructed that quantitatively describes periodically forced noise-induced oscillations.

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Complex dynamics of self-sustained oscillating systems lies in the focus of nonlinear science. Prominent physical examples include lasers, electronic circuits, chemical autokatalitic reactions but also many biological processes, such as firing neurons, oscillating genetic networks, rhythmic heartbeats, and circadian rhythms, can be attributed to this class although one can hardly derive corresponding mathematical models from first principles. Many phenomena characteristic for oscillatory systems, such as synchronization [1,2] are common for all these examples. The theoretical and experimental description of oscillatory dynamics relies heavily on the notion of *phase*, which is a starting point for the treatment of deterministic and noisy dynamics [1–3].

Many oscillating systems (the best example are neurons) are not autonomous but excitable: they posses a stable steady state but being adequately perturbed they perform a stereotypical large-amplitude oscillation before they relax back to the stable state. In the presence of an appropriate periodic or noisy perturbation such a system may demonstrate persistent oscillations, as it never stays long enough close to the stable steady state. If the perturbation is noisy, the observed dynamics is termed *noise-induced oscillations* (see review [4,5]). In some situations noise-induced oscillations can be rather coherent, this is often called *coherence resonance* [6]. In many aspects noise-induced oscillations behave similar to the self-sustained ones: they can demonstrate synchrony when coupled in ensembles [7] and can be controlled by a time-delayed feedback [8]. While a qualitative similarity between noise-induced and self-sustained oscillations is quite obvious, an extension of theoretical and analytical tools suitable for self-sustained dynamics on the excitable case is problematic. Indeed, the basic tool in the study of self-sustained noisy oscillators, the introduction of phase, cannot even perturbatively be applied to excitable oscillators because phase cannot be defined for a system residing on a stable steady state.

In this paper we propose to describe noise-induced oscillations via an *effective phase* dynamics, where we define an invariant phase in a nonperturbative way (as opposed to typical perturbative approaches to noisy dynamics of self-sustained oscillators [3]). Therefore, our definition of phase inherently depends on the noise intensity, and correspondingly all derived characteristics such as coupling functions as well. We present the theoretical framework by the example of noise-induced oscillations in one dimension, for which we also construct an effective coupling function describing a periodic forcing. Finally, we consider periodically driven noise-induced oscillations in a prototypic example of excitable dynamics, the FitzHugh-Nagumo system, and construct its effective phase description.

Although presented in this context, the approach is not restricted to a particular class of excitable systems or to realm of computational neuroscience but is applicable as a theory for a wide class of excitable systems, e.g., in chemical physics, biology etc. (see examples in [5]). Furthermore, the theoretical description of effective coupling functions may lead to additional insight concerning potential pitfalls for bivariate data analysis [9].

Our basic model is a noise-driven oscillator described by a 2π-periodic variable θ called hereafter *protophase* [10] governed by the Langevin equation

$$\dot{\theta} = h(\theta) + g(\theta)\xi(t), \quad \langle \xi(t)\xi(t')\rangle = 2\delta(t-t'). \qquad (1)$$

In the excitable case the deterministic system $\dot{\theta}=h(\theta)$ has two steady states, one stable and one unstable, but in the presence of noise one observes nearly monotonic growth of θ with a mean frequency ω and a smooth probability density $P(\theta)$. Therefore, we model the dynamics as that of an "effective" autonomous oscillator by approximating the equation for the protophase as

$$\dot{\theta} = H(\theta). \qquad (2)$$

We impose following conditions on the *effective velocity* H: (i) the oscillation frequency should coincide with ω and (ii) the distribution density of the protophase should be equal to $P(\theta)$. To meet these requirements we draw a correspondence between the Fokker-Planck equation to the noise-driven oscillator [Eq. (1)] given by

$$\partial_t P = -\partial_\theta h P + \partial_\theta g \partial_\theta g P, \qquad (3)$$

and the Liouville equation to the model [Eq. (2)] given by $\partial_t P = -\partial_\theta H P = -\partial_\theta J$. In the stationary case the flux J is related to the frequency by $\omega = 2\pi J$. Thus, the effective velocity can be expressed in terms of its frequency and distribution density by

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$$\dot{\theta} = H(\theta) = \frac{\omega}{2\pi P(\theta)}. \quad (4)$$

Conditions (i) and (ii) are fulfilled exactly if ω and $P(\theta)$ are given by the corresponding stationary solutions of Eq. (3), which are well known [2,11,12]. Then, using Eq. (3) the effective velocity can be written as $H=h(\theta)-\tilde{h}(\theta)=h(\theta)-gg'-g^2\partial_\theta \ln P$. Additionally to the deterministic velocity h there appears a noise-induced velocity $\tilde{h}$ which can be called *osmotic* [13].

From the protophase of the effective model we define the *phase* φ by the transformation

$$\varphi = S(\theta) = 2\pi\int_0^\theta P(\eta)d\eta. \quad (5)$$

The phase satisfies the properties $P(\varphi)=1/2\pi$ and $\dot{\varphi}=\omega$. Thus, we have constructed an invariant effective phase dynamics of noise-induced oscillations.

By a simple modification we may extend the effective model to account for the random component of noise-induced oscillations. We introduce an *effective fluctuating force* to the dynamics of φ:

$$\dot{\varphi} = \omega + \sqrt{D}\eta(t), \quad \langle \eta(t)\eta(t')\rangle = 2\delta(t-t'). \quad (6)$$

For any coefficient D of the noise term, the distribution of φ is uniform and the mean frequency is ω, thus the conditions (i) and (ii) above remain fulfilled. Therefore, we are free to choose D, and we choose it from the condition: (iii) the diffusion constant of the effective phase (mapped on the real line), which is D, should be the same as in the original oscillator [Eq. (1)]. It is given by $D=\lim_{t\to\infty}\langle[\theta(t)-\omega t]^2\rangle/2t$. Fortunately, one can get an exact expression for D following [14]:

$$D = \frac{\frac{1}{2\pi}\int_0^{2\pi}\frac{d\psi}{g(\psi)}\left[\int_{\psi-2\pi}^{\psi}\frac{d\phi}{g(\phi)}r(\phi,\psi)\right]^2\int_{\psi}^{\psi+2\pi}\frac{d\phi}{g(\phi)}r(\psi,\phi)}{\left[\frac{1}{2\pi}\int_0^{2\pi}\frac{d\psi}{g(\psi)}\int_{\psi-2\pi}^{\psi}\frac{2d\phi}{g(\phi)}r(\phi,\psi)\right]^3},$$

where $r(\theta,\phi)=\exp[-\int_\theta^\phi \frac{h(\eta)}{g^2(\eta)}d\eta]$. Inverting the transformation to the phase φ, we obtain the effective model with noise [Eq. (6)] in terms of the protophase θ:

$$\dot{\theta} = H(\theta) + \frac{\sqrt{D}}{\omega}H(\theta)\eta(t). \quad (7)$$

We see that the effective model is fully determined by the distribution density $P(\theta)$ and the mean frequency ω, and knowing the diffusion constant D also random effects can be taken into account, effectively. These quantities can be estimated from synthetic (numerical) or experimental observations $\theta(n\Delta t)=\theta_n$ by a straightforward analysis. If the sampling rate $1/\Delta t$ is sufficiently large it may be easier to estimate the effective velocity $H(\theta)$ instead of $P(\theta)$. This is done via averaging of central differences as

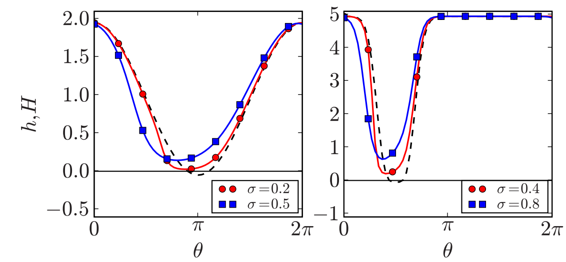

FIG. 1. (Color online) Functions h (dashed) together with effective velocities H (solid) for model A (left) at $a=0.95$ and model B (right) at $c=-0.05$. Noise intensities are as indicated.

$$H(\theta) \approx \left.\frac{\langle\theta_{n+1}-\theta_{n-1}\rangle}{2\Delta t}\right|_{\theta_n=\theta} \quad (8)$$

(while forward differences $\theta_{n+1}-\theta_n$ provide the deterministic part $h(\theta)$ only, see [15] for details).

Although model [Eq. (7)] captures many essential properties of noise-induced oscillations, it fails to describe the Lyapunov exponent properly. The exponent vanishes in the effective model with noise [Eq. (7)], while in the original system [Eq. (1)] it is generally negative, corresponding to synchronization of oscillators by a common external noise (see [16] and references therein).

We illustrate the above theory in Fig. 1 with two examples, both with an additive noise $g(\theta)=\sigma$. Model A is a simplified theta-model (cf. [17]) used in the description of excitable neurons: $h(\theta)=a+\cos\theta$. Model B is constructed to mimic an excitable oscillator that demonstrates a pronounced coherence resonance: $h(\theta)=5\tanh^2[5(1-\sin\theta)]+c$. The effective velocities H heavily depend on the noise intensity σ, especially at the region around the stable equilibrium. For large σ the effective velocity converges to the constant function $H(\theta)=\omega$.

Next, we extend the effective model [Eq. (4)] to describe *periodically driven* noise-induced oscillations described by

$$\dot{\theta} = h(\theta) + g(\theta)\xi(t) + f[\psi(t),\theta], \quad (9)$$

with a 2π-periodic driving phase $\psi=\Omega t$. We want to obtain an effective phase description including an effective coupling. As above, the principle of correspondence between the flux of the Liouville equation and the θ component of the probability flux

$$J = [h(\theta) + f(\psi,\theta) - g\partial_\theta g]P(\theta,\psi) \quad (10)$$

is applied that yields the driven effective dynamics

$$\dot{\theta} = H(\theta,\psi) = \frac{J}{P} = h - gg' - g^2\partial_\theta \ln P + f. \quad (11)$$

It is essential to rewrite H as a sum of a ψ-independent *marginal effective velocity* $H_m(\theta)$ and an *effective coupling* $F(\theta,\psi)$. The former is obtained in terms of the marginal probability density $P_m(\theta)=\int_0^{2\pi}P(\theta,\psi)d\psi$ by integrating Eq. (10) over ψ:

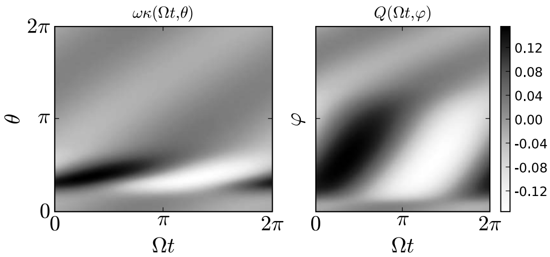

FIG. 2. A comparison of effective coupling functions for the protophase (left panel) and the phase (right panel) for the model B with $c=-0.05$, $\sigma=0.8$, $k=0.1$, and $\Omega=3.4$.

$$H_m(\theta)=\frac{\omega}{2\pi P_m(\theta)}=h-gg'-g^2\partial_\theta \ln P_m+\int_0^{2\pi} f\frac{P}{P_m}d\psi.$$

Rearranging $H=H_m+F$, we find the effective coupling

$$F(\psi,\theta)=f-\int_0^{2\pi} f\frac{P}{P_m}d\psi-g^2(\theta)\partial_\theta \ln\frac{P(\theta,\psi)}{P_m(\theta)}. \tag{12}$$

As for the effective velocity, the first two terms represent the deterministic part of the coupling, while the last term, proportional to the noise intensity, represents the osmotic part. Combining effective coupling and velocity, the local effect $\kappa(\psi,\theta)=F(\psi,\theta)/H_m(\theta)$ can be defined serving as a natural quantification of coupling strength in terms of the protophase.

For the driven effective model, we introduce a phase variable φ by transformation [Eq. (5)] using the marginal density. By this, we have $P_m(\varphi)=1/2\pi$ (this definition of phase slightly differs from the one presented in [10]). Transforming Eq. (11) in this way we get

$$\dot{\varphi}=\omega+2\pi P_m[S^{-1}(\varphi)]F[\psi,S^{-1}(\varphi)]=\omega+Q(\psi,\varphi). \tag{13}$$

Equation (13) provides the effective phase dynamics of the periodically driven noise-induced oscillations in a standard form with an effective coupling function Q that heavily depends on the noise intensity. For example, the amplitude of $Q(\psi,\varphi)$ is severely enhanced for small noise at values of φ where $P_m[S^{-1}(\varphi)]$ sharpens.

In the following examples we use the periodic force $f[\psi(t),\theta]=k\sin(\Omega t-\theta)$ with driving frequency Ω and coupling strength k. First, we illustrate with Fig. 2 the difference between the coupling in terms of the protophase $\omega\kappa$ and the phase coupling function Q, all for the model B. The function $\kappa(\psi,\theta)$ is concentrated around a vicinity of the stable steady state $\theta_s\approx\pi/2$, as this value is apparently most sensitive to external forces. However, around θ_s the evolution of θ is slow, and thus this region is significantly extended when transformed to the phase φ. Correspondingly, the sensitive region of θ transformed to the phase φ is stretched.

Second, we consider the important case of weak coupling. Here, an averaged (over period of forcing) coupling function provides an adequate description of the dynamics. By averaging Eq. (13) over the period 2π of the external phase ψ, the equation for the phase difference $\Delta\varphi=\varphi-\Omega t$ is obtained in the standard Adler form [2]

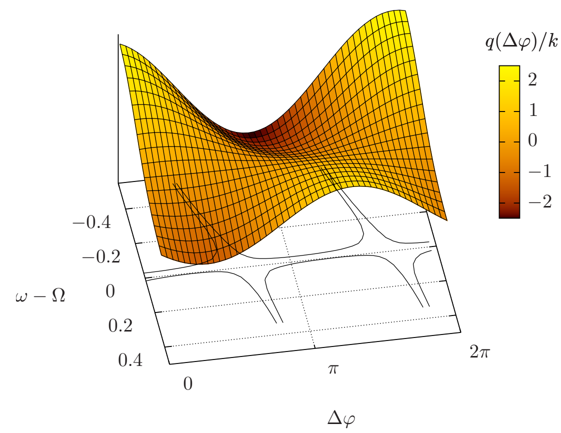

FIG. 3. (Color online) Averaged coupling function $q(\Delta\varphi)$ [Eq. (14)] divided by the coupling strength k for model A at parameters $a=0.95$, $k=0.01$, and $\sigma=0.5$ where $\omega\approx0.436$. q/k is drawn for several values of Ω. Additionally contour lines for $q/k=\pm0.1$ indicate where q vanishes.

$$\frac{d\Delta\varphi}{dt}=\omega-\Omega+q(\Delta\varphi),$$

$$q(\Delta\varphi)=\frac{1}{2\pi}\int_0^{2\pi}Q(\Delta\varphi+\psi,\psi)d\psi. \tag{14}$$

Again, there is a deterministic and an osmotic contribution to q, and they are in general of the same order of magnitude, but typically have opposite signs.

The case where the external frequency Ω is close to the natural frequency ω of noise-induced oscillations is of special interest. From Eq. (14) and the form of Q as shown in the example it could be expected that the oscillator would enter a synchronization regime where the phase is completely locked and $\Delta\varphi(t)$ remains bounded. However, for a stochastic oscillator [Eq. (9)] with $g\neq0$, such a perfect synchronization with the external forcing is in general impossible. In the effective model [Eq. (14)] the riddle is resolved by the fact, that as Ω approaches ω, an *masking* of the deterministic by the osmotic part of the averaged coupling function occurs. In this way, the oscillator does not "feel" the driver on average. We illustrate this phenomenon in Fig. 3, where the averaged coupling function $q(\Delta\varphi)$ is shown for different values of Ω. As $\omega-\Omega$ approaches zero, the osmotic and the deterministic part cancel such that the average effective coupling vanishes. From the standpoint of bivarate data analysis of coupled oscillators the effect of masking may lead to a biased detection of coupling.

After a throughout treatment of one-dimensional oscillators, we demonstrate how to construct an effective phase model for a general noise-driven excitable system, which contrary to the one-dimensional example above, does not allow an analytic treatment. To illustrate this construction, based on the observations of the oscillations, we take a noise-driven FitzHugh-Nagumo model as a paradigmatic example of an excitable system:

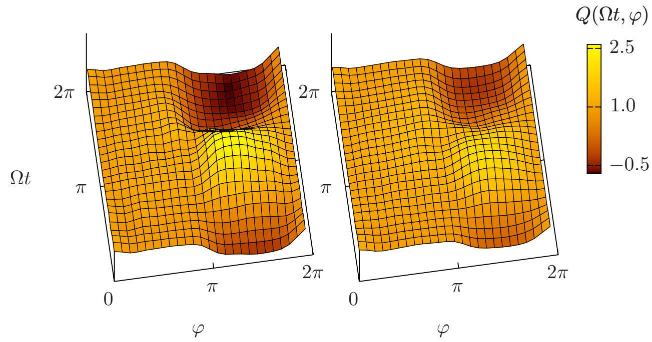

FIG. 4. (Color online) Coupling functions $Q(\psi,\varphi)$ for the noise-induced oscillations in the FitzHugh-Nagumo model [Eq. (15)] for $b=0.1$ and two different values of noise: at $\sigma=0.08$ (left panel, here the mean frequency is $\omega\approx 0.62$), and at $\sigma=0.11$ (right panel, $\omega\approx 0.95$).

$$\epsilon\frac{dx}{dt}=x-\frac{x^3}{3}-y,$$

$$\frac{dy}{dt}=x+a+\sigma\xi(t)+b\cos\Omega t. \qquad (15)$$

Together with a noisy force $\sigma\xi(t)$ that in the chosen excitable case $a=1.1$, $\epsilon=0.05$ induces oscillations, we have incorporated a periodic force for which we determine the effective phase coupling.

Although we do not have analytical expressions for the mean frequency and the probability density, these characteristics can be straightforwardly obtained from numerical simulations. Adopting the simplest choice for the protophase $\theta=\arctan(y/x)$ and calculating ω and $P_m(\theta)$, we perform a transformation to the phase φ according to Eq. (5). With long enough time series φ_n and ψ_n at hand, we determine the effective coupling function $Q(\psi,\varphi)$. For this we use a least square fit to approximate the dependence of the central difference [Eq. (8)] on ψ and φ with a double Fourier series (see [10] for details). Both effects, the increase in effective coupling for vanishing noise and the masking of coupling, were observed in numerically obtained effective coupling functions for driven noise-induced oscillations of the FitzHugh-Nagumo model. With Fig. 4, we want to present an interesting case in order to illustrate certain pitfalls that may arise in the interpretation of effective coupling functions. Here, the effective coupling function was computed for two noise intensities corresponding to $\omega\approx 0.62$ and 0.95, whereas the driving frequency was chosen as $\Omega=1.3$. One can see in Fig. 4 that the amplitude of Q decreases with increasing noise intensity. The change in amplitude may have been related to a more pronounced masking of coupling induced by the frequency shift (cf. Fig. 3) or to the generic decrease in effective coupling for stronger noise because of flattening of P_m. For an exploration of the extent to which the two effects participate, it is necessary to reconstruct the deterministic or osmotic part from data [15]. However, we will not discuss the related problems of data analysis in the scope of this article.

In summary, we have presented an effective phase dynamics description of autonomous and driven noise-induced oscillations. For oscillators based on one-dimensional dynamics many features of the effective dynamics can be found analytically. For complex oscillating processes, where an analytical treatment is not possible, we propose to determine an effective phase dynamics from synthetic or experimental observations of the system under analysis, this method is exemplified with the FitzHugh-Nagumo system. Furthermore, the method can be easily applied to real experimental data provided a long enough detailed time series is available.

The main feature of the effective phase dynamics is that it intrinsically depends on the noise intensity and on the regime observed. Thus, the effective dynamics obtained from one observation generally cannot be used for a prediction of the dynamics at other noise intensities, forcing amplitudes, or driving frequencies. In a general context of noisy oscillating systems, the effective phase approach gives a tool of reductional analysis where noise is not treated perturbatively. Thereby it can be applied to systems where the noise is not just an additional small factor but changes the dynamics qualitatively, such as excitable systems. In this paper we restricted our attention to single and periodically driven noise-induced oscillators. While in the former case it is of methodological relevance, as it provides another description of stochastic coherence in excitable systems, in the latter case it goes far beyond a standard numerical approach by yielding a well-defined coupling function that gives further inside for modeling and data analysis. Easily, the approach can be extended to the case of several coupled oscillators; this study will be presented elsewhere.

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