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Phase-sensitive excitability of a limit cycle

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The classical notion of excitability refers to an equilibrium state that shows under the influence of perturbations a nonlinear threshold-like behavior. Here, we extend this concept by demonstrating how periodic orbits can exhibit a specific form of excitable behavior where the nonlinear threshold-like response appears only after perturbations applied within a certain part of the periodic orbit, i.e., the excitability happens to be phase-sensitive. As a paradigmatic example of this concept, we employ the classical FitzHugh-Nagumo system. The relaxation oscillations, appearing in the oscillatory regime of this system, turn out to exhibit a phase-sensitive nonlinear threshold-like response to perturbations, which can be explained by the nonlinear behavior in the vicinity of the canard trajectory. Triggering the phase-sensitive excitability of the relaxation oscillations by noise, we find a characteristic non-monotone dependence of the mean spiking rate of the relaxation oscillation on the noise level. We explain this non-monotone dependence as a result of an interplay of two competing effects of the increasing noise: the growing efficiency of the excitation and the degradation of the nonlinear response. *Published by AIP Publishing*. https://doi.org/10.1063/1.5045179

The classical concept of excitability refers to a specific nonlinear response of a system to perturbations of its rest state. While for small perturbations the system reacts only with a linear relaxation directly back to the rest state, for larger perturbations above a certain threshold it reacts with a large non-linear response, called excitation. Such a behavior can be observed, for example, when a neuron in the quiescent state receives a presynaptic impulse and reacts with the emission of a spike. Until the non-linear response has terminated, the system is not susceptible to further excitations. Only after the system has again reached the rest state, can it be excited again. We study here the case where the rest state is not a stationary state but a stable periodic orbit. Then, the response of the system to perturbations may be nonuniform along the orbit. Of particular interest is the case where the non-linear response to perturbations above threshold appears only in a certain part of the periodic orbit. We call this situation phase-sensitive excitability and demonstrate that the oscillatory regime of the FitzHugh-Nagumo system can serve as an example for this type of behavior. It is well known that for other parameter values, the FitzHugh-Nagumo system has an excitable equilibrium. In this case, a perturbation above threshold induces a response in the form of a single spike. We present a completely different scenario. Perturbations are now applied to the regime of periodic spiking. If these perturbations act close to the passage near the unstable equilibrium, they may evoke a response in the form of a subthreshold oscillation and in this way prevent the system for a certain time from spiking. There are many cases where the triggering of an excitable system by noise can result in a characteristic non-monotone dependence of the system behavior on the noise intensity. This also holds for our example of the oscillatory regime of the FitzHugh-Nagumo system, where we can demonstrate that the spiking frequency becomes minimal at an intermediate noise level.

I. INTRODUCTION

In their groundbreaking work from 1946, Wiener and Rosenblueth,¹ having observed propagating contractions in the cardiac muscle, developed the fundamental concept of an excitable system: exciting a state of rest by perturbations above a certain threshold, the system reacts with a nonlinear response. Subsequently, the system needs a certain time, called the refractory period, until it can be excited again. This concept provided an extremely successful framework for understanding a large variety of real-life systems.² Beginning from biological systems, where it describes not only cardiac tissue³ but also certain functionalities of organisms,^{4,5} and behavioral aspects of individuals, or of whole populations,^{6,7} it has been translated to gene regulatory networks,8 chemical reactions,⁹ laser systems,¹⁰ and semiconductors,¹¹ and last but not least, it has become one of the key principles of theoretical neuroscience.12-16

We extend the concept of excitability by considering as the rest state of the system a stable periodic orbit rather than an equilibrium. In this case, the nonlinear threshold-like response may additionally depend on the phase of the oscillation at which the impulse acts such that an excitation may occur only if a super-threshold perturbation is applied within a certain part of the periodic orbit. We shall use the regime of relaxation oscillations in the FitzHugh-Nagumo system as an example

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FIG. 1. Phase plane for (1) with b = 0.99, $\epsilon = 0.05$, I(t) = 0: relaxation oscillation orbit (green), maximal canard (red), and nullclines (dash-dotted). Inset: region close to the unstable equilibrium. In the region of phase-sensitive excitability (green stripe), the maximal canard passes close to the relaxation oscillation orbit such that small perturbations may deviate a solution to make an extra round trip around the unstable equilibrium.

of this general concept of phase-sensitive excitability. In the context of neuroscience, this spiking regime can already be considered as the "excited state" of a neuron. Nevertheless, here we shall consider this periodic regime as the "rest state" in the sense of Refs. 1 and 2 and shall study its nonlinear threshold-like response to perturbations, which in this case manifests as a reduced spiking activity. Note that in Ref. 17 a similar model was considered but with the rest state given by the subtreshold oscillations and with the excited state associated to the large-amplitude oscillations. Using multiscale techniques and the canard trajectories, we shall analyze in detail the specific mechanism realizing the non-linear excitations in our system.

In Ref. 18, it has been pointed out that excitable systems can respond to noise in a specific way, showing a characteristic non-monotone dependence on the noise level. Such effects have been studied extensively and the FitzHugh-Nagumo system in the regime of an excitable equilibrium represents one of the classical examples.¹⁸⁻²⁰ There, it is the mean spiking regularity of noise-induced oscillations that shows a characteristic maximum, called coherence resonance, at an intermediate noise level. Our study of the FitzHugh-Nagumo system in the oscillatory regime will demonstrate that also the relaxation oscillation shows a non-monotone response to noise: here, however, it is the mean spiking rate that shows a characteristic minimum at an intermediate noise level. This effect is most pronounced for intermediate values of the time-scale separation ($\varepsilon \approx 0.05$), while in the singular limit $\varepsilon \to 0$, the effect disappears. This is the reason why the effect has not been observed in the detailed study of Muratov and Vanden-Eijnden,²¹ where the behavior of the FitzHugh-Nagumo system under the influence of noise has been investigated by singular perturbation techniques. We believe that our parameter regime can be adequate in the context of neuroscience and that the effect of phasesensitive excitability may be of importance both for deterministic inputs in coupled network systems and for the case of stochastic input signals.

II. THE FITZHUGH-NAGUMO OSCILLATOR

Our basic example for the mechanism of phase-sensitive excitability is the FitzHugh-Nagumo system

$$\varepsilon \dot{x} = x - x^3/3 - y,$$

$$\dot{y} = x + b + I(t).$$
 (1)

In the context of neuroscience, x and y correspond to the neuronal membrane potential and the ion-gating channels, respectively. The time-dependent input signal I(t) can be used to resemble intrinsic noise in the opening of the ion-channels.²² The smallness of the parameter ε reflects the time-scale separation between the dynamics of x and y. The system has been extensively studied as a slow-fast system, using the singular limit $\epsilon \to 0$, cf. Ref. 23 for an overview on the deterministic case and Refs. 2, 19, 20, and 24-26 for different scenarios with noise. Classical results for the case without input signal I(t) show that system (1) undergoes a supercritical Hopf bifurcation at b = 1 such that for decreasing b a branch of small-amplitude oscillations of period $\mathcal{O}(\sqrt{\varepsilon})$ appears. Then, for $b = b_c \approx 1 - \varepsilon/8$, there is a rapid transition to largeamplitude relaxation oscillations of period $\mathcal{O}(1)$.²⁷ From the neuroscience point of view, this corresponds to the transition from the quiescent state to the spiking regime via subthreshold oscillations. In order to explain the mechanism of phasesensitive excitability, we consider the slow-fast structures in the phase space for the relaxation oscillations at $b < b_c$ in the system (1). Figure 1 shows the relaxation oscillation orbit together with the nullclines of the vector field. During the passage close to the unstable equilibrium, located at the intersection of the nullclines, the relaxation oscillation orbit is excitable in the following sense: there is an exponentially thin layer of trajectories, called maximal canard, such that any perturbation large enough to elevate the state from the periodic orbit to a point above these trajectories will cause the system to make at least one loop around the unstable equilibrium before proceeding again along the relaxation oscillation orbit. Smaller perturbations or perturbations in directions below

the relaxation oscillation orbit will not give rise to such a response.

The maximal canard trajectories are characterized by the fact that they follow the whole unstable branch of the slow manifold, which in first approximation is given by the part of the nullcline $y = x - x^3/3$ lying in between the two folds, cf. Ref. 28. Already exponentially small deviations from the maximal canard cause the solutions to rapidly depart from it, traveling in either direction towards one of the stable branches of the slow manifold (dotted curves in Fig. 1). A maximal canard trajectory can readily be determined numerically by selecting an initial condition closely below the upper fold (x, y) = (1, 2/3), and from there integrating backward in time. Following one of the canard trajectories in this way, one finds a region where it passes extremely close to the relaxation oscillation orbit. Along this part of the relaxation oscillation orbit, the maximal canard acts as a threshold for perturbations such that super-threshold perturbations cause a nonlinear response with an extra excitation loop around the unstable equilibrium.

III. RESPONSE TO NOISE

Having understood the response of the system to single impact perturbations of different size, we examine now the response to Gaussian white noise

$$I(t) = D\xi(t),$$

of varying amplitude *D*. Figure 2 shows typical realizations of trajectories for three different levels of noise. The plots show that for low noise level (a), the noise-induced excitation loops occur rarely and are well confined by the spiral structure of the maximal canard. For increasing noise level (b), they become more frequent, but at the same time they get increasingly blurred by the noise. For the largest noise level (c), the prevalence of the small excitation loops decreases again since the efficiency of the confinement by the deterministic maximal canard is reduced.

To study this process in more detail, we introduce a Poincaré section at

$$x = x_0 = -0.99, \quad y < x_0 - x_0^3/3,$$
 (2)

i.e., we record passages through a vertical line extending below the unstable fixed point. In Fig. 3(a), we show the sampled return times ΔT between successive crossing events, obtained for the same noise levels as used in Fig. 2. The histograms show that for all three noise levels one can clearly distinguish between return times $\Delta T \approx T_R$ corresponding to relaxation oscillation cycles and those corresponding to excitation loops $\Delta T \approx T_E$. For the time trace shown in Fig. 3(b), we have shaded the corresponding time intervals accordingly. Panel (c) shows the corresponding variances $\sigma_{R,E}$ for each of the two separate peaks of the return time distribution, and panel (d) shows their relative size for varying noise level D. One can observe that there is a prevalence of excitation loops for intermediate values of the noise level $D \approx$ 10^{-2} . Above this value, the variances for each of the peaks start to increase, indicating an increasing degradation of the nonlinear response by noise. The excitation loops delay the



FIG. 2. Response of the relaxation oscillation to different levels of noise: (a) D = 0.003, (b) D = 0.01, and (c) D = 0.03. Left panels: noisy trajectories in the phase plane together with the deterministic relaxation oscillation orbit and maximal canard. Top panels: corresponding time traces x(t) from the panels above. Bottom panels: longer time traces indicating the prevalence of noise induced small excitation loops for the middle noise level D = 0.01.

occurrence of the next spike and thus affect the mean spiking rate of the system $\langle R \rangle$, measured as the average number of large-amplitude oscillations per time. Figure 4 shows that the spiking rate exhibits a non-monotone dependence with increasing noise level *D*, where the minimum of $\langle R \rangle$ coincides with the maximal fraction of small excitation loops shown in Fig. 3(d).

Note that this effect is most pronounced for intermediate values $\varepsilon \approx 0.05$ of the time-scale separation. This is due to the fact that the duration of the excitation loop, given to the leading order by the linearization at the unstable equilibrium, which is a weakly undamped center, scales like $O(\sqrt{\varepsilon})$. Hence, the delaying effect on the spikes and the consequent decrease of the spiking rate become small in the singular limit.

IV. EXCITATION EFFICIENCY AND DEGRADATION

The non-monotone dependence of the spiking rate $\langle R \rangle(\sigma)$ can be explained as the result of two competing effects of the increasing noise: the increasing efficiency of the excitation and the degradation of the nonlinear response. To study this competition in more detail, we consider the return times



FIG. 3. (a) Sampled return times ΔT between subsequent crossings of the Poincaré section (2) for different noise levels. The two peaks in the distributions correspond to relaxation oscillations $\Delta T \approx T_R$ (red) and noise-induced excitation loops $\Delta T \approx T_E$ (blue). (b) Time trace for D = 0.01 with respective time intervals ΔT colored accordingly. [(c) and (d)] Variances $\sigma_{R,E}$ and relative size n_E/n_R from the two separate peaks of the return time distributions for varying noise level.

 $\Delta \tilde{T}$, associated to the Poincaré section (2) with $x_0 = -0.2$. In this case, the excitation loops do not lead to additional crossing events and the corresponding return time $\Delta \tilde{T}$ measures the round trip time of each relaxation oscillation together with the included excitation loops. For small noise, the corresponding histograms in Fig. 5(a) show distributions with well separated peaks centered around $\Delta \tilde{T} \approx T_R + kT_E$, where $k \in \{0, 1, 2, 3, ...\}$ counts the number of excitation loops between two successive Poincaré events. We observe that for $D < 10^{-2}$ there is not only an increasing number of such excitation loops, cf. Fig. 3(d) but also an increasing number of multiple successive excitation loops. This can be seen from the corresponding probabilities of successive loops for varying noise intensity D given in Fig. 5(b). It underlines the increasing efficiency of the excitation process, driven by



FIG. 4. Non-monotone response to noise of a phase-sensitive excitable periodic orbit: mean spiking rate $\langle R \rangle$ of the relaxation oscillations of (1) shows a characteristic minimum at an intermediate noise level $D \approx 10^{-2}$.

noise in the subcritical range $D < 10^{-2}$. Above this value, the degradation effect takes over, which consists in the loss of correlation between the number of included excitation loops and the total duration of the corresponding relaxation oscillation cycle.

In order to quantify the degradation effect, we have calculated the noise-dependence of the correlation coefficient δ between the number k of small loops the unit performs between the two successive passages of the Poincaré crosssection, and the first return time $\Delta \tilde{T}$ being in the corresponding interval $[T_R + (k - \frac{1}{2})T_E, T_R + (k + \frac{1}{2})T_E]$. Evaluating numerically this correlation coefficient, we see the onset of a strong decay above the critical noise level of $D < \approx$ 10^{-2} , indicating the degradation of the nonlinear response, see Fig. 5(c). Similar effects have been described in Refs. 29 and 30 as noise-induced linearization.

V. DISCUSSION AND OUTLOOK

It is important to remark that a periodic orbit emerging in a transition from an excitable equilibrium, as it happens in the FitzHugh-Nagumo system, does not necessarily inherit phasesensitive excitability from the excitability of the preceding equilibrium. This can be seen, e.g., for the active rotator

$$\theta = 1 + b - \sin\theta + D\xi(t), \quad \theta \in \mathbb{R}/2\pi\mathbb{Z}, \tag{3}$$

where a saddle-node infinite period (SNIPER) bifurcation at b = 0 mediates a transition from excitable to oscillatory behavior. However, the periodic solution at b = 0.02 shows no phase-sensitive excitability, and the dependence of the spiking rate on the noise level is monotone, cf. Fig. 6(a). On the other hand, for the FitzHugh-Nagumo system with a noise term $\sqrt{D/\varepsilon}\xi(t)$ added to the fast variable x so to resemble the



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FIG. 5. (a) Histograms of first return times $\Delta \tilde{T}$ to a Poincaré section (2) with $x_0 = -0.2$. (b) Relative frequency of two successive excitation loops. (c) Correlation coefficient between the number of excitation loops in a relaxation oscillation cycle and its duration $\Delta \tilde{T}$.

action of synaptic noise,²² the excitable behavior and the nonmonotone dependence can be observed in a similar way, cf. Figs. 4 and 6(b).

The presented concept of phase-sensitive excitability establishes a natural extension of the classical concept of excitability of equilibria to periodic orbits, offering a general framework for describing certain nonlinear effects in driven or interacting oscillatory systems. It resembles the main properties of the classical case:

- (i) nonlinear threshold-like response to perturbation impulses and
- (ii) non-monotone response to noisy inputs of increasing amplitude.

The nature of the non-monotone dependence on the noise level for phase-sensitive excitability in the regime of relaxation oscillations of the FitzHugh-Nagumo system is qualitatively distinct from the two classical cases concerning the FitzHugh-Nagumo model where the rest state is given by an excitable equilibrium or conforms to the regime of subthreshold oscillations before the canard explosion ($b > b_c \approx 1 - \epsilon/8$). In both the classical examples, the excited state conforms to a relaxation oscillation (spike), and the applied noise affects the *regularity* of noise-induced oscillations such that it becomes maximal for the optimal noise intensity.^{17–20} The qualitative similarity between these two cases is to be expected because the subthreshold oscillations become indistinguishable from an equilibrium in the



FIG. 6. (a) Monotone mean spiking rate $\langle R \rangle$ of the active rotator (3). (b) Non-monotone mean spiking rate of the relaxation oscillations of (1) with I(t) = 0 and adding instead noise of varying levels to the fast variable.

singular limit $\epsilon \to 0$. As opposed to that, our scenario of phase-sensitive excitability involves the regime of relaxation oscillations as the rest state, the subthreshold oscillations conform to the excited state, and the applied noise affects the *mean spiking frequency* such that it becomes minimal at an intermediate noise level.

In the context of neuroscience, the resonant effect consisting in a reduction of the spiking frequency of neural oscillators within a certain range of intermediate noise levels has been referred to as inverse stochastic resonance. Such an inhibitory action of noise has been observed experimentally³¹ and has also been discussed in several model studies, concerning the impact of external or intrinsic noise on single^{32–34} or coupled neurons.^{35,36} The effect has been suggested as a potential paradigm for computational tasks that either require reducing the neuronal spiking frequency without chemical neuro-modulation or involve generating episodes of bursting activity in neurons that are not endogenously bursting. The generic mechanism behind the effect has typically been linked to bistability of the underlying deterministic dynamics, which exhibits coexistence between an equilibrium and a stable limit cycle. For such a scenario, the noise induces a switching between the corresponding metastable states, with the spiking frequency decreasing at a certain range of intermediate noise levels where the transition rate from the quasi-stationary to oscillatory state becomes much smaller than the one in the opposite direction. The noise-driven effect reported here is based on a qualitatively distinct mechanism, because the deterministic dynamics is monostable, and the excitations off the limit cycle emerge due to phase-sensitive excitability of the associated orbit, derived from the multi-scale structure of the system.

Revisiting earlier work on coupled oscillator systems, one can find instances where effects that could be explained as a result of phase-sensitive excitability have been reported. Indeed, some of the results in Ref. 37 about space-time patterns in a coupled network of FitzHugh-Nagumo oscillators seem to be based on the phase-sensitive excitability of the relaxation oscillations. Also, the alternating behavior reported in Ref. 38 could possibly be an effect of phase-sensitive excitability. These examples may underline the importance of the abstract concept as such, offering a general framework and a unifying view for a variety of closely related phenomena.

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- ¹N. Wiener and A. Rosenblueth, Arch. Inst. Cardiol. Mex. **16**, 205 (1946), available at https://www.ncbi.nlm.nih.gov/pubmed/20245817.
- ²B. Lindner, J. Garcia-Ojalvo, A. Neiman, and L. Schimansky-Geier, Phys. Rep. **392**, 321 (2004).
- ³S. Alonso and M. Bär, Phys. Rev. Lett. **110**, 158101 (2013).
- ⁴J. D. Murray, *Mathematical Biology* (Springer, Berlin, Heidelberg, New York, 1993).
- ⁵J. P. Keener and J. Sneyd, *Mathematical Physiology* (Springer, New York, 2009).
- ⁶I. Farkas, D. Helbing, and T. Vicsek, Nature 419, 131 (2002).
- ⁷S. P. Borgatti, A. Mehra, D. J. Brass, and G. Labianca, Science **323**, 892 (2009).
- ⁸Y. Chen, J. K. Kim, A. J. Hirning, K. Josić, and M. R. Bennett, Science **349**, 986 (2015).
- ⁹A. S. Mikhailov and K. Showalter, Phys. Rep. 425, 79 (2006).
- ¹⁰S. Wieczorek, B. Krauskopf, T. B. Simpson, and D. Lenstra, Phys. Rep. 416, 1 (2005).
- ¹¹A. M. Yacomotti, P. Monnier, F. Raineri, B. B. Bakir, C. Seassal, R. Raj, and J. A. Levenson, Phys. Rev. Lett. 97, 143904 (2006).
- ¹²E. M. Izhikevich, Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting (MIT Press, Cambridge, 2007).
- ¹³J. White, J. Rubinstein, and A. Kay, Trends Neurosci. 23, 131 (2000).
- ¹⁴I. Franović, K. Todorović, N. Vasović, and N. Burić, Phys. Rev. E 87, 012922 (2013).
- ¹⁵I. Franović, K. Todorović, N. Vasović, and N. Burić, Phys. Rev. Lett. **108**, 094101 (2012).
- ¹⁶I. Franović, K. Todorović, N. Vasović, and N. Burić, Chaos 22, 033147 (2012).
- ¹⁷ V. A. Makarov, V. I. Nekorkin, and M. G. Velarde, Phys. Rev. Lett. 86, 3431 (2001).
- ¹⁸A. S. Pikovsky and J. Kurths, Phys. Rev. Lett. 78, 775 (1997).
- ¹⁹R. E. Lee DeVille, E. Vanden-Eijnden, and C. B. Muratov, Phys. Rev. E 72, 031105 (2005).
- ²⁰C. B. Muratov, E. Vanden-Eijnden, and E. Weinan, Physica D 210, 227 (2005).
- ²¹C. B. Muratov and E. Vanden-Eijnden, Chaos 18, 015111 (2008).
- ²²A. Destexhe and M. Rudolph-Lilith, *Neuronal Noise* (Springer, New York, 2012).
- ²³C. Kuehn, *Multiple Time Scale Dynamics*, (Springer International Publishing, Switzerland, 2015).
- ²⁴I. Franović, K. Todorović, M. Perc, N. Vasović, and N. Burić, Phys. Rev. E 92, 062911 (2015).
- ²⁵J. M. Newby and M. A. Schwemmer, Phys. Rev. Lett. 112, 114101 (2014).
- ²⁶N. Berglund and D. Landon, Nonlinearity **25**, 2303 (2012).
- ²⁷S. M. Baer and T. Erneux, SIAM J. Appl. Math. 46, 721 (1986).
- ²⁸M. Krupa and P. Szmolyan, SIAM J. Math. Anal. 33, 286 (2001).
- ²⁹N. G. Stocks, N. D. Stein, H. E. Short, R. Mannella, D. G. Luchinsky, and P. V. E. McClintock, in *Fluctuations and Order: The New Synthesis* (Springer, Berlin, 1996), pp. 53–67.
- ³⁰E. Hunsberger, M. Scott, and C. Eliasmith, Neural Comput. 26, 1600 (2014).
- ³¹D. Paydarfar, D. B. Forger, and J. R. Clay, J. Neurophysiol. **96**, 3338 (2006).
- ³²H. C. Tuckwell, J. Jost, and B. S. Gutkin, Phys. Rev. E **80**, 031907 (2009).
- ³³M. Uzuntarla, J. R. Cressman, M. Ozer, and E. Barreto, Phys. Rev. E 88, 042712 (2013).
- ³⁴M. Uzuntarla, J. J. Torres, P. So, M. Ozer, and E. Barreto, Phys. Rev. E 95, 012404 (2017).
- ³⁵B. S. Gutkin, J. Jost, and H. C. Tuckwell, Europhys. Lett. 81, 20005 (2008).
- ³⁶M. Uzuntarla, E. Barreto, and J. J. Torres, PLoS Comput. Biol. 13, e1005646 (2017).
- ³⁷G. Ansmann, K. Lehnertz, and U. Feudel, Phys. Rev. X 6, 011030 (2016).
- ³⁸N. Semenova, A. Zakharova, V. Anishchenko, and E. Schöll, Phys. Rev. Lett. **117**(1), 014102 (2016).