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Phase sensitive excitability of a limit cycle

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Abstract

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.

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: a system in the state of rest can be elicited to an excited state by an impulse that exceeds a certain threshold. While for sub-threshold perturbations the system displays a linear relaxation to the rest state, super-threshold perturbations induce a non-linear response, called excitation. Subsequently, the system needs a certain time, called 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 tissue [3], but also certain functionalities of organisms [4, 5], 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], semiconductors [11] and last but not least, it has become one of the key principles of theoretical neuroscience [12, 13, 14, 15].

In this letter, 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. A detailed study of the relaxation oscillation in the Fitzhugh-Nagumo system, using classical multi-scale techniques and canard trajectories, reveals that this periodic solution conforms to our general concept of phase sensitive excitability.

In [17] 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 called *coherence resonance*. This effect has been studied extensively and the FitzHugh-Nagumo system in the regime of an excitable equilibrium represents one of the classical examples. 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: the mean spiking rate shows a characteristic minimum at an intermediate noise level.

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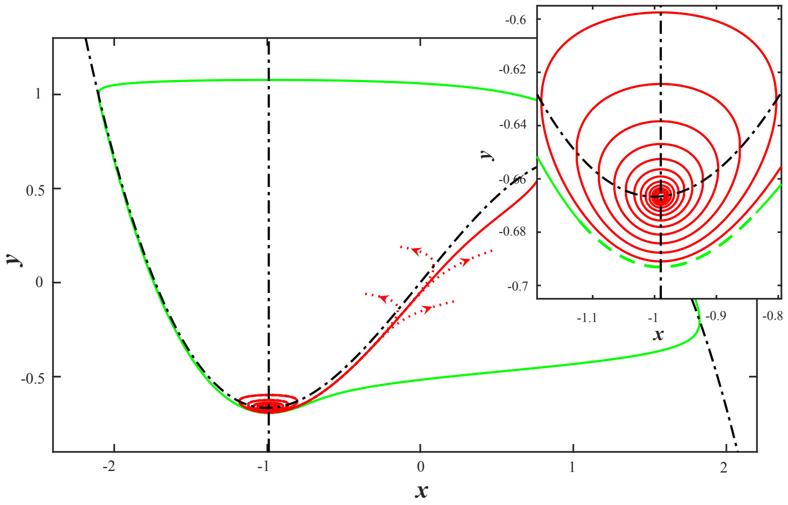

Figure 1: (color online) Phase plane for (1) with $b = 0.99$, $\epsilon = 0.05$, $I(t) = 0$: relaxation oscillation orbit (green), maximal canard (red) and nullclines (dash-dotted). Inset: region close to the unstable equilibrium. In the region of phase sensitive excitability (green stripe) the maximal 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.

The 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 studies of Muratov e.a. [23, 18], 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 the effect of phase sensitive excitability may be of importance both for deterministic inputs in coupled network systems as well as for the case of stochastic input signals.

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

$$\begin{aligned} \varepsilon\dot{x} &= x - x^3/3 - y, \\ \dot{y} &= x + b + I(t). \end{aligned} \tag{1}$$

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. 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. [20] for an overview on the deterministic case and [2, 22, 23, 24, 25, 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 $b = b_c \approx (1, 1 - \varepsilon/8)$, there is a rapid transition to large-amplitude relaxation oscillations of period $\mathcal{O}(1)$ [21]. 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 phase sensitive excitability we consider the slow-fast structures in the phase space for the relaxation oscillations at $b > b_c$ in system (1). Fig. 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 a particular trajectory, called

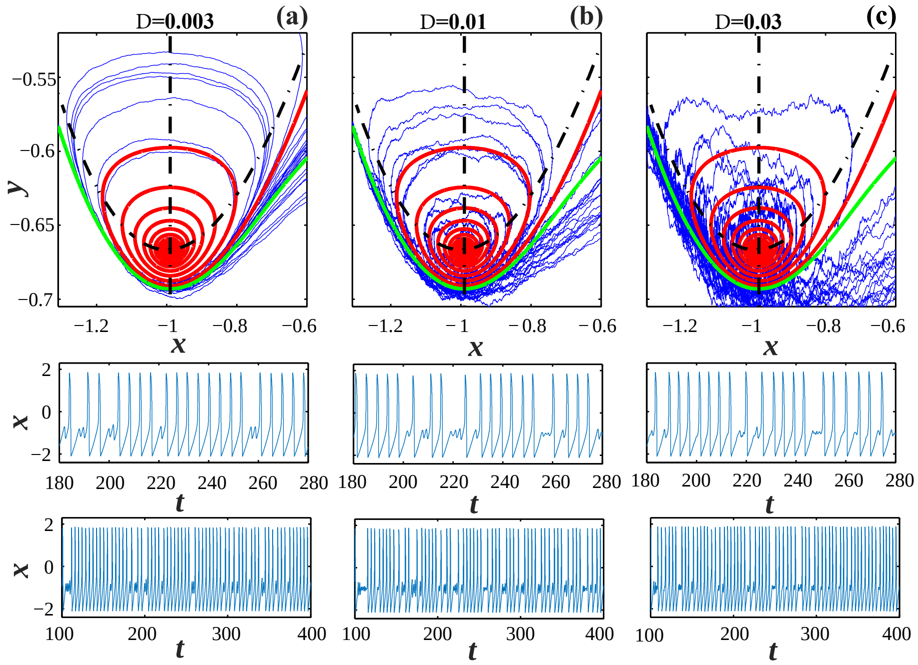

Figure 2: (color online) Response of the relaxation oscillation to different levels of noise: (a) $D = 0.003$, (b) $D = 0.01$, and (c) $D = 0.03$. Upper panels: noisy trajectories in the phase plane together with the deterministic relaxation oscillation orbit and maximal canard. Middle panels: corresponding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

the *maximal canard*, such that any perturbation large enough to elevate the state from the periodic orbit to a point above this trajectory 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: This trajectory is characterized by the fact that it follows 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. 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). The maximal canard 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 the canard trajectory, there is 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 loop around the unstable equilibrium.

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. Fig. 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

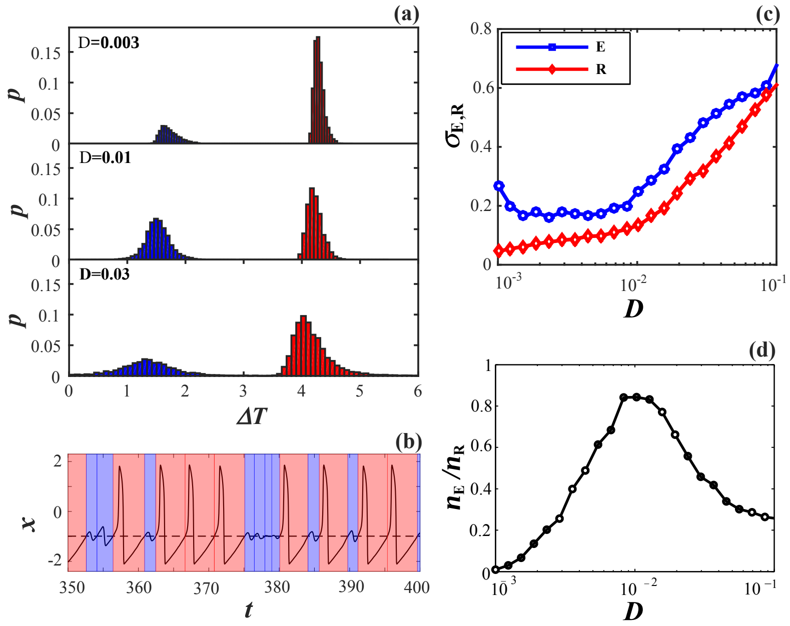

Figure 3: (color online) (a) Sampled return times ΔT between subsequent crossings of the Poincare section (2) for different noise levels. The two peaks in the distributions correspond to relaxation oscillations $\Delta T \approx T_R$ (red) and noise-induced excitation loops $\Delta T \approx T_E$ (blue). (b) Time trace for $D = 0.01$ with respective time intervals ΔT colored accordingly. (c), (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 D.

confinement by the deterministic maximal canard is reduced. To study this process in more detail, we introduce a Poincare section at

$$x = x_0 = -0.99, \quad y < x_0 - x_0^3/3, \tag{2}$$

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 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. Fig. 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).

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 $\Delta\tilde{T}$, associated to the Poincare 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

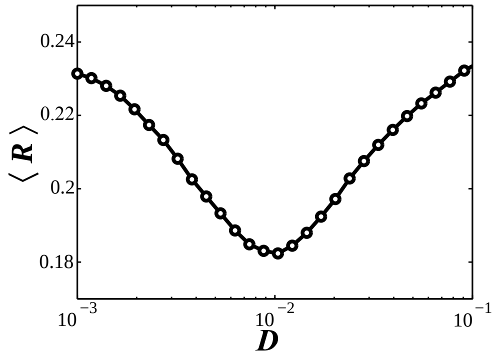

Figure 4: Non-monotone response to noise of a phase sensitive excitable periodic orbit: mean spiking rate $\langle R\rangle$ of the relaxation oscillations of (1) shows a characteristic minimum at an intermediate noise level $D \approx 10^{-2}$.

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 $k = 0, 1, 2, 3\dots$ counts the number of excitation loops between two successive Poincare 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 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 Poincare cross-section, 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 excitability response.

Discussion and Outlook: Note that the fact that a periodic orbit emerges by a transition from an excitable equilibrium, as it happens in the Fitzhugh-Nagumo system, is by no means sufficient for the periodic orbit to show phase sensitive excitability. A similar scenario is known for the active rotator

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

where at $b = 0$ a saddle-node infinite period (SNIPER) bifurcation 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). At the other hand, the excitable behavior and non-monotone dependence can be observed similarly for the FitzHugh-Nagumo system with the noise term $\sqrt{D/\varepsilon}\xi(t)$ in the x dynamics resembling the action of synaptic noise [19], see Fig. 6(b). 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 [27] about space-time patterns in a coupled network of Fitzhugh-Nagumo oscillators seem to be based on the phase sensitive excitability of the relaxation oscillation. The phenomena reported in [28] can be interpreted as caused by a phase sensitive excitability of the small amplitude oscillations appearing in the FitzHugh-Nagumo in a very small parameter range directly above the Hopf-bifurcation before the canard-transition to the large amplitude relaxation oscillations. Also the alternating behavior reported in [29] could possibly be an effect of

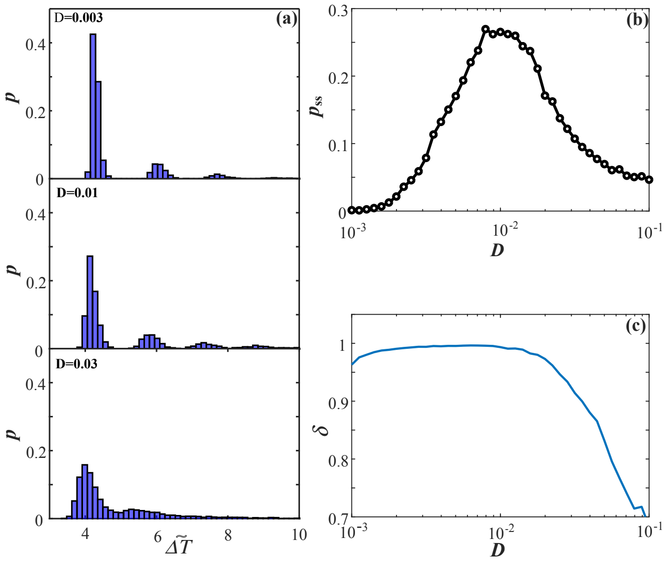

Figure 5: (color online) (a) Histograms of first return times $\Delta\tilde{T}$ to a Poincare section (2) with $x_0 = -0.2$. (b) Relative frequency of two successive excitation loops. (c) Correlation coefficient between number of excitation loops in a relaxation oscillation cycle and its duration $\Delta\tilde{T}$.

phase sensitive excitability. These examples may underline the importance of the abstract concept as such, offering a general framework and an unifying view for a variety of closely related phenomena.

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

(ii) non-monotone response to noisy inputs of increasing amplitude.

We demonstrate this general principle by studying the relaxation oscillation in the FitzHugh-Nagumo system, where the slow fast structure can be used to identify maximal canard trajectory as the excitation threshold. However, the effect is found to be most pronounced for intermediate values $\varepsilon \approx 0.05$

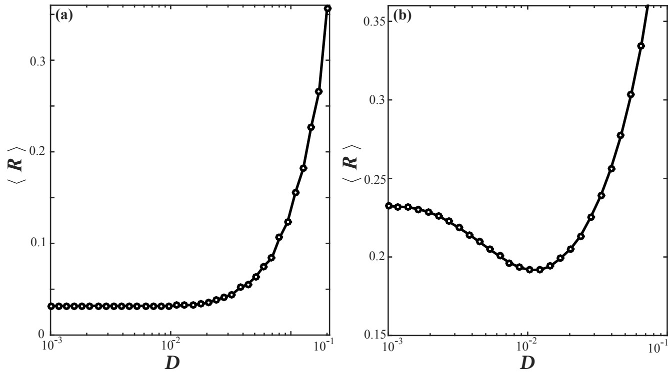

Figure 6: (a) Non-monotone mean spiking rate $\langle R \rangle$ of the relaxation oscillations of (1) with $I(t) = 0$ and instead adding noise of varying levels to the fast variable. (b) Monotone mean spiking rate of the active rotator (3)

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 $\mathcal{O}(\sqrt{\varepsilon})$. Hence, the delaying effect on the spikes and the consequent decrease of the spiking rate become small in the singular limit.

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