Event-triggered feedback in noise-driven phase oscillators

Justus A. Kromer,1,2 Benjamin Lindner,1,2 and Lutz Schimansky-Geier1,2

1Department of Physics, Humboldt-Universität zu Berlin, Newtonstr. 15, 12489 Berlin, Germany
2Bernstein Center for Computational Neuroscience Berlin, Germany

Using a stochastic nonlinear phase oscillator model, we study the effect of event-triggered feedback
on the statistics of interevent intervals. Events are associated with the entering of a new cycle. The
feedback is modeled by an instantaneous increase (positive feedback) or decrease (negative feedback)
of the oscillators frequency, whenever an event occurs followed by an exponential decay on a slow
timescale. In contrast to previous works, we also consider positive feedback that leads to various
novel effects. For instance, besides the known excitable and oscillatory regime, that are separated
by a saddle-node on invariant circle bifurcation, positive feedback can lead to bistable dynamics and
a change of the system’s excitability. The feedback has also a strong effect on noise-induced phe-
nomena like coherence resonance or anti-coherence resonance. Both positive and negative feedback
can lead to more regular output for particular noise strengths. Finally, we investigate serial corre-
lation in the sequence of interevent intervals that occur due to the additional slow dynamics. We
derive approximations for the serial correlation coefficient and show that positive feedback results
in extended positive interval correlations whereas negative feedback yields short-ranging negative
correlations. Investigating the interplay of feedback and the nonlinear phase dynamics close to the
bifurcation, we find that correlations are most pronounced for an optimal feedback strengths.

PACS numbers: 05.40.-a, 05.10.Gg

I. INTRODUCTION

Self-sustained oscillations occur in many physical, chemical or biological systems [1]. If variations of the
amplitude are negligible, a widely-used model in this context is the well-known dynamics for the phase φ [2]:

\[ \dot{\phi}(t) = \omega_0 - \epsilon \sin[\phi(t)]. \]  (1)

Here \( \omega_0 \) represents the oscillators frequency in the case \( \epsilon \to 0 \). Without loss of generality, we restrict our inves-
tigations on \( \omega_0 > 0 \). By rescaling \( \omega_0 \) and the timescale, \( \epsilon \) can be set to one (dimensionless units). The system can show both excitable \( (0 < \omega_0 < 1) \) or oscillatory \( (\omega_0 > 1) \) dynamics. Both regimes are separated by a saddle-node on invariant circle (SNIC) bifurcation at \( \omega_0 = 1 \), which makes the system to a good model for class I excitability [3]. Eq. (1) is known as the Adler’s equation [4] and is
often used to describe excitability in optical system [5, 6], particle motion in a tilted periodic
potential, or to study the onset of resistance in supercon-
ducting Josephson junctions [8, 9]. Generally, such oscil-
lators are studied when driven by time-dependent forces, such as noise, when subjected to time delayed feedback [10], or when they are coupled in networks.

For many applications, particular events in the phase dynamics are of foremost interest, e.g. the crossings of a
threshold value \( \phi = 2\pi \) as, for instance, associated with the generation of an action potential in a nerve cell, the
dropout of light intensity in an excitable laser, the release of a messenger by a cell, or the division of a cell. The

Statistics of the intervals between these events \( \Delta t \) (inter-
event intervals or in the following IEI) in the presence of noise have been studied intensely in the neurobiological
context for the related class of integrate-and-fire models [11, 12] (here IEIs are referred to as interspike intervals).

In some systems, the events directly influence the dynamics of the oscillator. Put differently, in these sys-
tems we find event-triggered feedback mechanisms. Generally, the oscillator’s dynamics becomes more interesting
if such feedback mechanisms are taken into account. For neurons negative feedback can arise from slow inhibitory
ionic currents that change over several IEIs. This can
lead to spike-frequency adaptation [13, 14], noise shaping
[15], and interval correlations [16, 17]. Feedback, how-
ever, can be also positive, for instance, due to variations in
the external potassium concentration, which are trig-
gered by neural spiking [18, 19] and act on a timescale
which is large compared to the individual IEIs [20]. In
some systems strong positive feedback can change the dy-
namics fundamentally, leading, for instance, to bursting behavior [21]. In laser physics positive feedback for par-
ticular modes can be used to self-mode-lock lasers [22]
and it seems to be a plausible explanation of positive
IEI correlations, reported in Ref. [23]. In cell biology, positive feedback loops occur, for instance, in the lactose
utilization network of the Escherichia coli, where the pro-
duction of lactose permease increases its expression level
and is assumed to be a reason for bistability in the lac-
tose utilization [24, 25]. However, the effect of positive
feedback, especially in the presence of noise, is so far only
poorly understood.

Analytical attempts to deal with an additional feed-
back dynamics in a pulse generator were mainly limited
to approximations of the firing rate [13, 26] and weak
feedback approximations for the IEI statistics of a very

*justuskr@physik.hu-berlin.de
simple integrate-and-fire model, the so-called perfect IF model \[27\]. Regarding the more striking feature of the feedback-induced interspike interval correlations, approximations until recently were carried out for the perfect IF model \[16\], variants that deviate only by a weak non-linearity from it \[28\], or integrate-and-fire models subjected to a weak feedback \[29\]. In \[30\], a general theory has been worked out to calculate patterns of interval correlations in multidimensional IF models. All these studies focused on a negative feedback, however, and did not address the generic phase oscillator dynamics eq. (1).

Here we study the dynamics of a phase oscillator in the vicinity of a saddle-node on invariant circle bifurcation from the excitable to the oscillatory regime, which is subject to noise and an event-triggered feedback. We consider feedback strengths that can attain both positive or negative values and derive analytic approximation for several statistical measures by considering a large timescale separation between the phase and the feedback dynamics.

Our results for negative feedback are in line with previous studies: we find suppression of low-frequency power in the power spectrum of the spike train \[31, 32\] and negative serial correlations in the series of \[N\] subsequent IEIs \[\Delta t_i, \ldots, \Delta t_N\], \[13, 33–35\]. More remarkably, we find that positive feedback causes a number of novel effects. In the deterministic system, bistability emerges in the form of the coexistence of a stable node (SN) and a limit cycle (LC) attractor. Secondly, we study the effect of noise and feedback on the system. Here we focus on the excitable and the oscillatory regime. We find anti-coherence resonance in the excitable regime - IEI variability is maximized at a finite noise intensity - and observe positive IEI correlations in both, the excitable and the oscillatory regime. Interestingly, IEI correlations for both positive and negative feedback behave non-monotonically with the feedback strength, if the system is close to the bifurcation.

Our paper is organized as follows. In section II we introduce the model and the statistics of interest. We study first, in section III the non-linear dynamics of the system without noise (including a bifurcation analysis) and explore the effects of noise and feedback on the mean frequency of the oscillator. In section IV we investigate the IEI variability and the power spectrum of the phase oscillator with feedback. Section V is devoted to IEI correlations. Finally, we conclude by summarizing our results and discussing their broader implications. All details concerning simulation techniques and analytical calculations of the serial correlation coefficient are given in Appendix A and C respectively.

II. THE MODEL

In order to implement the feedback we define an event to occur whenever the phase reaches the threshold \(2\pi\), i.e., \(\phi(t_i) = 2\pi\), where \(t_i\) denotes the time of the \(i\)th event.

\[
\phi(t) = \Delta \phi(t) + \omega_0 - \sin[\phi(t)] + \sqrt{2D} \xi(t) .
\]

(2)

Combined with the reset condition

\[
\text{if } \phi = 2\pi, \text{ then } \phi \to 0.
\]

(3)

Here we also added white Gaussian noise \([\langle \xi(t) \rangle = 0 \text{ and } \langle \xi(t)\xi(t') \rangle = \delta(t-t')\]\) with a noise strength \(D\). Where \(\langle \cdot \rangle\) denotes averaging.

When an event occurs, the system perceives a kick which changes \(\Delta \omega\). This is modeled by the additional dynamics

\[
\tau \frac{d}{dt} \Delta \omega(t) = -\Delta \omega(t) + 2\pi a \, x(t),
\]

(4)

where

\[
x(t) = \sum_i \delta(t-t_i)
\]

(5)

is the sequence of kicks at the event times \(t_i\).

Eq. (4) describes the dynamics of \(\Delta \omega\) evolving on the feedback timescale \(\tau\). Due to the first term, it decays towards zero from any deviation. The second term models the feedback and alters \(\Delta \omega\) by an amount of \(2\pi a / \tau\) whenever an event occurs \((t = t_i)\). This is illustrated in fig. 1 for a positive feedback strength \(a > 0\), showing the time evolution, and in fig. 2 (center) illustrating the

Figure 1. (Color online) Time evolution of \(x(t), \phi(t), \text{ and } \Delta \omega(t)\) (from top to bottom) for \(\omega_0 = 1.1, a = 0.5, \tau = 10\), and \(D = 0.1\).

Afterwards, the phase is reset \((\phi \to 0)\). The feedback acts on the phase oscillator by increasing (positive feedback) or reducing (negative feedback) its frequency. Thus, we add a time-dependent part \(\Delta \omega(t)\) to the frequency \(\omega_0\), which accounts for the frequency adaptation due to the feedback. Consequently, eq. (1) becomes

\[
\dot{\phi}(t) = \Delta \phi(t) + \omega_0 - \sin[\phi(t)] + \sqrt{2D} \xi(t) .
\]
integration of Eqs. (2) and (4) to the eqs. (14) and (17). Parameters: $\omega \to \Delta \omega$, $\tau \to \Delta \omega$, $a > 0$, and $a < 0$.

1. phase reset $\phi \to 0$

2. increment of $\Delta \omega$ at $\phi = 2\pi$, and start with an offset of $2\pi a/\tau$ to $\Delta \omega$ after the reset. Here $\Delta \omega_{lc} := \Delta \omega_{lc} - \Delta \omega_{lc}(\Delta t_{det})$ according to the eqs. (11) and (17). Parameters: (A) $\omega_0 = 0.8$, $\tau = 50$; (B) $\omega_0 = 1.05$, $\tau = 50$, $a = \pm 0.5$; (C) $\omega_0 = 0.85$, $\tau = 50$, $a = 0.55$.

Note that putting $a = 0$, yields in the stationary case always the situation without feedback.

After some transient behavior, the rate becomes stationary and we define the oscillator’s mean firing rate, which describes the average rate at which events occur

$$r = \langle \frac{\dot{\phi}(t)}{2\pi} \rangle = \langle x(t) \rangle = \frac{1}{\langle \Delta t_i \rangle}.$$  

(6)

Here the average is taken over a time interval large compared to the individual IEs $\Delta t_i = t_{i+1} - t_i$, i.e., the time the oscillator needs to reach $\phi = 2\pi$, when started at $\phi = 0$.

By averaging eq. (4), we obtain:

$$\tau \langle \frac{d}{dt} \Delta \omega \rangle = -\langle \Delta \omega \rangle + 2\pi a \langle x(t) \rangle.$$  

(7)

In the stationary case, the left hand side should be zero and we obtain

$$\langle \Delta \omega \rangle = 2\pi a r.$$  

(8)

Using eq. (8) in the averaged eq. (2), yields

$$r = \frac{\omega_0 - \langle \sin[\phi(t)] \rangle}{2\pi(1 - a)}.$$  

(9)

Note that $\phi(t)$ is the solution of eq. (2) in the presence of feedback.

Interestingly, the limit of $a \to 1$ leads to infinite $r$ if $\omega_0 > 1$. In this case the unknown numerator is positive, since $\langle \sin[\phi(t)] \rangle \leq 1$. Here $\langle x \rangle$ denotes the left-hand limit. For such strong positive feedback, the deterministic decay of $\Delta \omega$ cannot balance the increase of $\Delta \omega$ due to the kicks after each event and the assumption of stationarity $\langle \Delta \omega \rangle = 0$ does not hold. To study the stationary regime, we therefore concentrate on $a < 1$.

### III. MEAN INTEREVENT INTERVAL

#### A. Deterministic case

At first, we concentrate on the deterministic case ($D = 0$). Here, after some transient behavior, all IEs become equal $\Delta t_i = \Delta t_{det}$ for all $i$. If no feedback is applied, $\Delta \omega$ will converge to zero and the IEs can be calculated by integrating eq. (2), which yields

$$\Delta t_{det,0} = \frac{2\pi}{\sqrt{\omega_0^2 - 1}}.$$  

(10)

Here the index 0 marks the non-feedback solution for the mean IEI. Note that positive real solutions for $\Delta t_{det,0}$ exist only in the oscillatory regime $|\omega_0| > 1$.

If, however, feedback is applied ($a \neq 0$), the dynamics becomes more complex. Here the deterministic behavior can be understood by evaluating the time-dependent frequency adaptation $\Delta \omega$. Assume, that the system evolves on a LC, and let $\Delta \omega_{lc}$ be the value of $\Delta \omega$ just before an event occurs, i.e.

$$\lim_{t/t_{lc}} \Delta \omega(t) = \Delta \omega_{lc}.$$  

(11)
can integrate eq. (3) for one IEI, resulting in
\[
\Delta \omega(t) = (\Delta \omega_c + 2\pi a/\tau) \exp\left(-\frac{t - t_k}{\tau}\right), \quad t_k \leq t < t_k + \Delta t_{det}. \tag{12}
\]

Since after one IEI \(\Delta \omega\) reaches \(\Delta \omega_c\) again, i.e.
\[
\lim_{t \to t_k} \Delta \omega(t) = \lim_{t \to t_k + \Delta t_{det}} \Delta \omega(t) = \Delta \omega_c, \tag{13}
\]
we obtain an explicit expression for \(\Delta \omega_c\):
\[
\Delta \omega_c = \frac{2\pi a}{\tau [\exp(\frac{2\pi a}{\tau}) - 1]}. \tag{14}
\]

In the following, we consider a slow feedback timescale \(\tau\), i.e., \(\tau \gg \Delta t_{det}\). In this case, we can expand \(\Delta \omega(t)\) [eq. (12)] in the small parameter \(\Delta t_{det}/\tau\). Using that \(t \in [t_k, t_k + \Delta t_{det}]\) and \(\Delta \omega_c = 2\pi a/\Delta t_{det} + o(\Delta t_{det}/\tau)\) [see eq. (14)], the zeroth order Taylor expansion for \(\Delta \omega(t)\) reads
\[
\Delta \omega(t) = \frac{2\pi a}{\Delta t_{det}} + o\left(\frac{\Delta t_{det}}{\tau}\right). \tag{15}
\]

Note that the zeroth order term equals the time-averaged frequency adaptation in eq. (8). Using only the zeroth order in eq. (2) for \(D = 0\), leads to the solvability condition
\[
\Delta t_{det} = \frac{2\pi}{\sqrt{\omega_0^2 + (2\pi a/\Delta t_{det})^2} - 1} \tag{16}
\]

Solving the resulting quadratic equation for \(\Delta t_{det}\) yields
\[
\Delta t_{det}^{(1,2)} \approx \frac{2\pi}{\omega_0^2 - 1} (\pm \sqrt{\omega_0^2 + (a^2 - 1) - a\omega_0}), \quad \Delta t_{det} \ll \tau. \tag{17}
\]

By comparison with simulations, we found that positive real solutions \(\Delta t_{det}^{(1)}\) correspond to the cycle period of oscillations on a stable limit cycle, whereas positive real solutions \(\Delta t_{det}^{(2)}\) correspond to the cycle period of oscillations evolving on an unstable limit cycle.

In agreement with eq. (3), the solution \(\Delta t_{det}^{(1)}\) runs to zero (infinite rate) for \(a \neq 1\) when \(\omega_0 \neq 1\). However, positive solutions \(\Delta t_{det}^{(2)}\) also exist for \(a \geq 1\), if \(\omega_0 < 1\) (dashed region in fig. 4). They describe oscillations on an unstable LC which separates the basin of attraction of the stable node from a regime where the system speeds up to infinite rate.

For \(a < 1\) we find three qualitatively different regimes. Fig. 6 depicts the resulting firing rates \(r = 1/\Delta t_{det}^{(i)}\) for \(i = 1, 2\), and fig. 4 illustrates the different regimes in the \((\omega_0, a)\) parameter space. The corresponding dynamics is illustrated in fig. 2.

- (A) [Fig. 2 (top)] For \(0 < a < 1\) and \(\omega_0 < \sqrt{1 - a^2}\), and for \(a \leq 0\) and \(\omega_0 < 1\), eq. (14) has no real solution. Here the only stable equilibrium is the SN and only noisy excitations can lead to new events.
• (B) [Fig. 2 (center)]: For $a < 1$ and $\omega_0 > 1$, only $\Delta t_{(1)}^a$ is positive. Here the system possesses a stable LC for both, negative and positive feedback respectively.

• (C) [Fig. 2 (bottom)]: For $0 < a < 1$ and $\sqrt{1-a^2} < \omega_0 < 1$ eq. (13) has the two positive real solutions $\Delta t_{(1)}^a$ and $\Delta t_{(2)}^a$. Simulations of trajectories show, that positive solutions of $\Delta t_{(2)}^a$ correspond to slow oscillations on an unstable LC (dashed), which separates the basins of attraction of the stable LC, described by oscillations with period $\Delta t_{(1)}^a$ (bold), and the SN (black dot). Here bistability between the SN and the stable LC occurs.

These regimes are separated by different bifurcations, indicated by thick lines in fig. 3 that can be studied using the positions of the stable $(\phi_{stat}, \Delta \omega_{stat}) = (\arcsin |\omega_0|, 0)$, and unstable node $(\phi_{u, stat}, \Delta \omega_{u, stat}) = (\pi - \arcsin |\omega_0|, 0)$, and the linearized system of the eqs. (2) and (4) evaluated at $s = 0$.

Using the solutions for the mean IEI [eq. (17)], one can describe the effect of feedback by substituting $\omega$ by a < ω̃ and study how the event-triggered feedback affects the IEI statistics.

In the following, we will study the dynamics for $a < 1$. We will refer to the regimes as excitable (A), oscillatory (B) and bistable (C, D) according to their properties. When studying the system in the presence of noise, we concentrate on the excitable and the oscillatory regime and study how the event-triggered feedback affects the IEI statistics.

B. Finite noise strengths

In case of finite noise strengths ($D \neq 0$) the mean IEI, of long sequences $\Delta t_i$ ($N \to \infty$), in the absence of feedback is given by the mean first passage time (FPT) for the system to reach $\phi = 2\pi$ for the first time, when it was started at $\phi = 0$. For this problem, the mean FPT $(\Delta t_i)$ is given by a well-known integral formula [37] and related to the mean velocity $v$ of a Brownian particle by $(\langle \Delta t_i \rangle) = 2\pi/v$. Due to the periodicity of the sinus in eq. (2), our system in the absence of feedback is equivalent to overdamped Brownian motion in a tilted periodic potential, for which the mean FPT [39, 40] is given by

$$\frac{1}{\tau_0} = \langle \Delta t_{i,0} \rangle = \int_0^{2\pi} dx \frac{e^{\frac{\omega_0(x)}{v}}}{\frac{x}{2\pi} - x} \int_0^{\frac{\omega_0(y)}{v}} dy e^{-\frac{\omega_0(y)}{v}}.$$  

(19)

Here the index 0 marks the absence of feedback. The potential $U_0(\phi)$ is given by $U_0(\phi) = -\omega_0 \phi - \cos(\phi)$. For this potential, eq. (19) can be written in terms of modified Bessel functions [41]:

$$\langle \Delta t_{i,0} \rangle = \frac{2\pi^2}{D} \left( \frac{I_1(\omega_0)}{I_0(\omega_0)} \right)^2.$$  

(20)

Here $I_n(y)$ denotes the nth modified Bessel function of the first kind.

In order to account for the feedback, we use the approximation of slow varying $\Delta \omega$ (see above), which holds in the case of $(\Delta t_i) \ll \tau$. For such $\tau$, we can describe the effect of feedback by substituting $\omega_0 \to \omega_0 + \langle \Delta \omega \rangle$ [compare eq. (8)] in eq. (19). Applying this approximation to $U_0(\phi)$, leads to the extended potential $U(\phi) = -(\omega_0 + \langle \Delta \omega \rangle) \phi - \cos(\phi)$.

Since $(\Delta \omega)$ depends on $(\Delta t_i)$, eq. (19)
Figure 5. (Color online) Firing rate $r$ (top) and CV (bottom) in the excitable regime for $\omega_0 = 0.9$ (left), and the oscillatory regime for $\omega_0 = 1.1$ (right), both with $\tau = 100$. Insets show the IEI density (top, left) and the power spectra (bottom) for particular noise strengths. Colors denote the particular amount of feedback. Points represent data obtained from simulations. Firing rates (top): Bold lines represent the series approximation eq. (25), dashed lines show the strong noise approximation eq. (27) (see details in appendix B 1 for both approximations), and the triangles mark the deterministic firing rates $r = 1/\Delta t(1)$ obtained from eq. (17). Firing rates for $D < 0.02$ were calculated using the rare-event method presented in Ref. [42] and are shown in the double logarithmic plot fig. 11 (in appendix B 1) together with the weak noise approximation eq. (31), CV (bottom): Dashed lines indicate the strong noise approximation [eq. (37)] and bold lines (right bottom) the weak noise approximation [eq. (40)] (see appendix B 2 for details). In the excitable regime the weak noise limit is given by the Poisson process. Power spectra (bottom, insets) and IEI density (top left, inset) are obtained from simulations.

becomes self-consistent:

$$\frac{1}{r} = \langle \Delta t_i \rangle = \frac{2\pi}{D(1-\exp[-2\pi(\omega_0+\langle \Delta \omega \rangle)/D])} \int_0^x dx \frac{e^{i\omega_0 x}}{x-2\pi} \frac{\int_0^{\pi(x+\langle \Delta \omega \rangle)/D} dy e^{-i\omega_0 y}}{2\pi^2 |I_{\omega_0+\langle \Delta \omega \rangle}(\pi)|^2}, \quad \langle \Delta t_i \rangle \ll \tau$$

(21)

However, for our purpose it is more advantageous to rewrite the integral in eq. (21) as the series

$$\langle \Delta t_i \rangle = \frac{2\pi}{\omega_0+\langle \Delta \omega \rangle} \sum_{k=0}^{\infty} \frac{1}{2D^k} \times \sum_{m=0}^{k} \frac{1}{m!(k-m)!} \frac{I_{k-2m}(\omega_0+\langle \Delta \omega \rangle)}{1+\frac{D(\omega_0+\langle \Delta \omega \rangle)}{\omega_0+\langle \Delta \omega \rangle}} \langle \Delta t_i \rangle \ll \tau.$$  (22)

which can be done after performing some tedious calculations, for $\omega_0 + \langle \Delta \omega \rangle \neq 0$.

Assuming a weak feedback $\langle \Delta \omega \rangle/\omega_0 \ll 1$, we can use...
a Taylor expansion and arrive at the implicit equation
\[
\frac{1}{r} = \langle \Delta t_i \rangle \approx \langle \Delta t_{i,0} \rangle - \frac{2\pi a}{\omega_0} + \frac{4\pi^2 a}{\omega_0^2} B(D, \omega_0),
\]
\[
\langle \Delta \omega \rangle \ll \omega_0, \quad \langle \Delta t_i \rangle \ll \tau
\tag{23}
\]
for the mean FPT \( \langle \Delta t_i \rangle \) in the presence of feedback. Here \( B(D, \omega_0) \) represents the series
\[
B(D, \omega_0) = \sum_{k=1}^{\infty} \frac{1}{2D^k} \sum_{m=0}^{k} \frac{1}{m!(k-m)!}
\times \frac{I_{k-2m}}{D} \frac{2(k-2m)^2}{1 + \frac{D^2}{\omega_0^2} (k-2m)^2 + (k-2m)^2} \tag{24}
\]
If \( B(D, \omega_0) \) converges, eq. \( [24] \) has the only positive solution
\[
\langle \Delta t_i \rangle \approx \langle \Delta t_{i,0} \rangle - \frac{2\pi a}{\omega_0} + \frac{4\pi^2 a}{\omega_0^2} B(D, \omega_0),
\]
\[
\langle \Delta \omega \rangle \ll \omega_0, \quad \langle \Delta t_i \rangle \ll \tau
\tag{25}
\]
This series is our final result for the mean FPT for large \( \tau \) and weak feedback. Its evaluation compared to simulations is illustrated in fig. 5. More details on its evaluation are given in appendix B.1

C. Strong noise approximation

In case of strong noise \( (D \gg 1) \), the first summand \( (k = 0) \) dominates the series [eq. \( [24] \)] and \( \langle \Delta t_i \rangle \) can be approximated by
\[
\frac{1}{r_0} = \langle \Delta t_{i,0} \rangle \approx \frac{2\pi a}{\omega_0}, \quad D \gg 1, \tag{26}
\]
in the non-feedback case.

Since the function \( B(D, \omega) \) is of order \( O(\frac{1}{D^2}) \) a similar approximation for eq. \( [26] \) leads to
\[
\langle \Delta t_i \rangle \approx \langle \Delta t_{i,0} \rangle - \frac{2\pi a}{\omega_0}, \quad D \gg 1, \quad \langle \Delta \omega \rangle \ll \omega_0, \quad \langle \Delta t_i \rangle \ll \tau
\tag{27}
\]
and, in combination with eq. \( [26] \), to
\[
\frac{1}{r} = \langle \Delta t_i \rangle = \frac{2\pi (1-a)}{\omega_0}, \quad D \gg 1, \quad \langle \Delta \omega \rangle \ll \omega_0, \quad \langle \Delta t_i \rangle \ll \tau.
\tag{28}
\]
Note that this does not depend on the noise strength, like already observed by Stratonovich in the absence of feedback [41].

D. Weak noise approximation

In the excitable regime \( (\omega_0 < 1) \), the mean IEI in the weak noise limit can be obtained from the Kramers rate theory. In the absence of feedback, the Kramers rate of generating an event
\[
r_0 = \sqrt{1 - \omega_0^2} e^{-\frac{\omega_0^2}{2\pi}}, \quad \omega_0 < 1, \quad D \ll 1.
\tag{29}
\]
Here \( DU_0 = U_{0,\text{max}} - U_{0,\text{min}} \) denotes the height of the potential barrier. \( U_{0,\text{min}} = -\sqrt{1 - \omega_0^2} - \omega_0 \arcsin(\omega_0) \) and \( U_{0,\text{max}} = -\pi \omega_0 + \sqrt{1 - \omega_0^2} + \omega_0 \arcsin(\omega_0) \) are the values of the potential at the saddle and at the stable node in the absence of feedback, respectively.

If \( \tau \) is large compared to the mean IEI, we can account for the feedback by substituting \( \omega_0 \to \omega_0 + \langle \Delta \omega \rangle \) in eq. \( [29] \). In the next step, we assume a weak feedback \( \langle \Delta \omega/\omega_0 \ll 1 \) and perform a Taylor expansion. The first order approximation for the potential barrier reads
\[
DU = DU_0 - 4\pi ar \arcsin(\omega_0),
\]
\[
\omega_0 < 1, \quad D \ll 1, \quad \langle \Delta \omega \rangle \ll \omega_0, \quad \langle \Delta t_i \rangle \ll \tau.
\tag{30}
\]
Here \( DU \) denotes the barrier of the potential \( U \) mentioned above. Consequently, the barrier height becomes rate dependent and reduces for positive feedback and increases for negative feedback.

Finally, in the presence of feedback the Kramers rate [eq. \( [29] \)] reads:
\[
r = r_0 [1 - 2\pi ar_0 \omega_0 (\frac{\omega_0}{1 - \omega_0^2} - \frac{2}{D} \arcsin(\omega_0))],
\]
\[
\omega_0 < 1, \quad D \ll 1, \quad \langle \Delta \omega \rangle \ll \omega_0, \quad \langle \Delta t_i \rangle \ll \tau.
\tag{31}
\]
In the oscillatory regime we find, using the approach of Ref. [44], that the first non-zero correction to the deterministic mean IEI [eq. \( [17] \)] is of order \( D^2 \).

E. Results obtained from simulations

Fig. 5 (top) shows the analytical results in the weak noise limit [eq. \( [17] \)], for a strong noise [eq. \( [24] \)], as well as the series approximation [eq. \( [24] \)] in the excitable (left) and in the oscillatory (right) regime, respectively. A double logarithmic plot of the weak noise regime in eq. (29) is of order approximation for the potential barrier reads
\[
DU = DU_0 - 4\pi ar \arcsin(\omega_0),
\]
\[
\omega_0 < 1, \quad D \ll 1, \quad \langle \Delta \omega \rangle \ll \omega_0, \quad \langle \Delta t_i \rangle \ll \tau.
\tag{30}
\]
Here \( DU \) denotes the barrier of the potential \( U \) mentioned above. Consequently, the barrier height becomes rate dependent and reduces for positive feedback and increases for negative feedback. Finally, in the presence of feedback the Kramers rate [eq. \( [29] \)] reads:
\[
r = r_0 [1 - 2\pi ar_0 \omega_0 (\frac{\omega_0}{1 - \omega_0^2} - \frac{2}{D} \arcsin(\omega_0))],
\]
\[
\omega_0 < 1, \quad D \ll 1, \quad \langle \Delta \omega \rangle \ll \omega_0, \quad \langle \Delta t_i \rangle \ll \tau.
\tag{31}
\]
In the excitable regime we find, using the approach of Ref. [44], that the first non-zero correction to the deterministic mean IEI [eq. \( [17] \)] is of order \( D^2 \).

Fig. 5 (top) shows the analytical results in the weak noise limit [eq. \( [17] \)], for a strong noise [eq. \( [24] \)], as well as the series approximation [eq. \( [24] \)] in the excitable (left) and in the oscillatory (right) regime, respectively. A double logarithmic plot of the weak noise regime in eq. (29) is of order approximation for the potential barrier reads
\[
DU = DU_0 - 4\pi ar \arcsin(\omega_0),
\]
\[
\omega_0 < 1, \quad D \ll 1, \quad \langle \Delta \omega \rangle \ll \omega_0, \quad \langle \Delta t_i \rangle \ll \tau.
\tag{30}
\]
Here \( DU \) denotes the barrier of the potential \( U \) mentioned above. Consequently, the barrier height becomes rate dependent and reduces for positive feedback and increases for negative feedback. Finally, in the presence of feedback the Kramers rate [eq. \( [29] \)] reads:
\[
r = r_0 [1 - 2\pi ar_0 \omega_0 (\frac{\omega_0}{1 - \omega_0^2} - \frac{2}{D} \arcsin(\omega_0))],
\]
\[
\omega_0 < 1, \quad D \ll 1, \quad \langle \Delta \omega \rangle \ll \omega_0, \quad \langle \Delta t_i \rangle \ll \tau.
\tag{31}
\]
we find a similar agreement, except that the series does not fit the simulations for strong positive feedback in the range of low and intermediate noise strengths. Here, the assumption of weak feedback \((\Delta \omega \ll \omega_0)\) does not hold anymore. Note that since \((\Delta \omega)\) depends on the mean IEI, the series approximation leads to better results for low firing rates, i.e., in the excitable regime or for a negative feedback. In general an increasing noise strength decreases the mean IEI, down to a constant value given by eq. (25).

**IV. EFFECT OF FEEDBACK ON OUTPUT VARIABILITY**

In order to study the variability in a series of IEIs two different measures can be used. The first one is the coefficient of variation (CV)

\[
C_v = \frac{\sqrt{\langle (\Delta t_i - \langle \Delta t_i \rangle)^2 \rangle}}{\langle \Delta t_i \rangle},
\]

(32)

in which the standard deviation of the \(\Delta t_i\) is compared to its mean. Therefore, \(C_v = 0\) corresponds to the most regular sequence and, consequently, to the most coherent one, whereas \(C_v = 1\) is obtained for a completely random spike train, in which all spikes are independent of each other (Poisson process).

As a second measure of spike train regularity, one can study the power spectrum \[S(f) = \int_{-\infty}^{\infty} dt' \langle x(t)x(t+t') \rangle e^{2\pi ift'},\]

(33)

which measures the spectral components of \(x(t)\). In the power spectrum, a narrow peak (possibly accompanied by more peaks at higher harmonics) indicates more coherent sequences of \(\Delta t_i\).

In order to calculate the CV of \(\Delta t_i\), its mean and its standard deviation \(\sqrt{\langle (\Delta t_i - \langle \Delta t_i \rangle)^2 \rangle}\) are needed. We first calculate the variance \(\text{Var}(\Delta t_i)\) of \(\Delta t_i\). In the absence of feedback, \(\Delta \omega\) will approach zero and we can apply the formula from Ref. [40], which was derived for \(\Delta \omega = 0\) in the excitable regime, where the IEI statistics is Poisson-like (\(C_v \approx 1\)), and the oscillatory regime, where the results of Ref. [14] can be applied. In the latter case, i.e. for \(\omega_0 > 1\) and in the absence of feedback, the first order approximation for the variance reads

\[
\text{Var}(\Delta t_i,0) \approx 2D \int_0^{2\pi} d\phi \frac{D}{(\omega_0 - \sin(\phi))^3},
\]

(38)

and a Taylor expansion with respect to the strength of the feedback \((\Delta \omega/\omega_0)\), yields the first order correction to the variance

\[
\text{Var}(\Delta t_i) \approx \text{Var}(\Delta t_i,0)
\]

\[
\times \left(1 + \frac{2\pi a}{\langle \Delta t_i,0 \rangle} - \frac{3}{\omega_0} + \frac{2D^2}{\text{Var}(\Delta t_i,0) \omega_0} C(D, \omega_0) \right),
\]

(35)

Here \(\text{Var}(\Delta t_i,0)\) denotes the variance in the absence of feedback \((a = 0)\) and \(C(D, \omega_0)\) is a infinite series.

**1. Strong noise approximation**

Fortunately, \(C(D, \omega_0)\) vanishes in the strong noise limit \(D \to \infty\). Therefore, we can derive the analytical approximation for the variance

\[
\text{Var}(\Delta t_i) \approx \text{Var}(\Delta t_i,0)\left(1 - \frac{2\pi a}{\langle \Delta t_i,0 \rangle} \frac{3}{\omega_0}\right),
\]

(36)

\[D \gg 1, \langle \Delta \omega \rangle \ll \omega_0, \langle \Delta t_i \rangle \ll \tau.\]

for the strong noise regime. In this regime, the variance decreases for positive and increases for negative feedback.

Using the eqs. (32) and (27), we obtain the first order correction to the CV

\[
C_v \approx C_{v,0} \left(1 - \frac{\pi a}{\omega_0 \langle \Delta t_i \rangle}\right),
\]

(37)

\[D \gg 1, \langle \Delta \omega \rangle \ll \omega_0, \langle \Delta t_i \rangle \ll \tau.\]

for the strong noise and weak feedback. Here \(C_{v,0}\) denotes the CV for \(a = 0\). Therefore, positive feedback decreases the CV, whereas negative feedback leads to higher variability in the strong noise regime. Comparing the strong noise approximation [eq. (32)] to simulation [fig. 5 (bottom)], we find that it fits the numerical results well for \(D > 1\).

**2. Weak noise approximation**

In the weak noise limit, we distinguish between the excitable regime, where the IEI statistics is Poisson-like \((C_v \approx 1)\), and the oscillatory regime, where the results of Ref. [14] can be applied. In the latter case, i.e. for \(\omega_0 > 1\) and in the absence of feedback, the first order approximation for the variance reads

\[
\text{Var}(\Delta t_i,0) \approx 2\pi D \left[1 - \frac{2\omega_0}{(\omega_0^2 - 1)^{5/2}}\right], \quad \omega_0 > 1, \ D \ll 1.
\]

(38)
Using this in the CV and the weak noise approximation for the mean IEI, yields

\[ C_{V,0} \approx \sqrt{\frac{D}{2\pi v}} \left(1 + \frac{1 + 2\omega_0^2}{(\omega_0^2 - 1)^{3/2}}\right), \quad \omega_0 > 1, \ D \ll 1. \quad (39) \]

Using the substitution \( \omega_0 \to \omega_0 + \langle \Delta \omega \rangle \), we can account for the feedback in case of a slow feedback timescale \( \langle \Delta t_i \rangle \ll \tau \). By assuming a weak feedback \( \langle \Delta \omega \rangle \ll \omega_0 \), we obtain the \( C_v \) up to first order in \( D \):

\[ C_v \approx C_{V,0}[1 - \frac{\pi a}{\langle \Delta t_i \rangle_0} \frac{\omega_0^2(1 + 2\omega_0^2)}{(\omega_0^2 - 1)(1 + 2\omega_0^2)}], \quad \omega_0 > 1, \ D \ll 1, \ \langle \Delta \omega \rangle \ll \omega_0, \ \langle \Delta t_i \rangle \ll \tau. \quad (40) \]

Consequently, the CV decreases for positive feedback and increases for negative feedback and hence, qualitatively, the effect of the feedback in the oscillatory regime is similar at weak and strong noise [cf. eq. (44)].

Figure 5 (left bottom) shows the Poisson limit \( C_v = 1 \). However, for slightly larger \( D \) the CV varies strongly with the feedback strength. This variation is due to the dynamics of \( \Delta \omega \) (see below) and cannot be described by our approach for a slow feedback timescale. In the oscillatory regime [fig. 5 (right bottom)] the weak noise approximation [eq. (40)] fits the data well for negative feedback and \( D < 0.05 \). For the positive feedback \( a = 0.3 \), however, the weak-feedback approximation seems to break down and, as a consequence of this eq. (40) produces slightly negative CVs. However, we find that for a weaker feedback with \( a = 0.15 \) the approximation fits the numerical results well (data not shown).

A. Excitable regime

In excitable systems increasing the noise strength does not necessarily result in higher spike train variability. Instead there exists a minimum variability at a finite noise level. This phenomenon is known as coherence resonance (CR) and becomes apparent by a local minimum in the CV or by a pronounced peak in the power spectrum attained at an optimal value of the noise intensity. CR can occur in excitable systems due to an interplay of at least two different timescales [16, 17], and has been observed in the noisy Adler’s equation without feedback [3, 18] and experimentally in laser systems [14, 51], an electric circuit [51], a chemical reaction system [52], and electrochemical systems [53, 54].

Fig. 5 shows the CV (left, bottom) and the power spectrum (left bottom, inset) in the excitable regime for a slow feedback timescale \( \tau = 100 \). Here, CR can be observed for intermediate noise strengths, where the \( C_v \) possesses a local minimum, already in the absence of feedback \( (a = 0) \). In the presence of negative feedback \( (a < 0) \), the \( C_v \) slightly increases in those regions but reduces for lower noise strengths. Consequently, it increases the region of low \( C_v \) towards lower noise strengths. Positive \( a \), however, affect \( C_v \) in the opposite direction. Such feedback improves CR for intermediate noise levels. Note that the CV in our model in the excitable regime is always above 1/\( \sqrt{3} \approx 0.577 \). This is similar to a quadratic integrate-and-fire model with noise (but without feedback) and is in marked contrast to the range of CV observed in a stochastic leaky integrate-and-fire model [53]; for differences in signal transmission properties of these models, see [56].

Interestingly, it also leads to an local maximum of the \( C_v \) at a low noise level \( (D \approx 0.02 - 0.03) \). Such a maximum indicates anti-coherence resonance (ACR) [57] or incoherence resonance [51] and has been observed in models as a consequence of either damped subthreshold oscillations [57], or due to a finite refractory period [17]; for an experimental verification, in a laser system, see [58].

For large noise strength the behavior of the \( C_v \) can be directly understood from the analytical result eq. (39) and is a consequence of the increased or decreased distance to the point \( (\omega_0 + \langle \Delta \omega \rangle) = 1 \) [17], where the system can pass the maximum of the \( \phi \)-nullcline.

The behavior in the weak noise regime, however, results from the dynamics of \( \Delta \omega \), which is illustrated in fig. 6 and leads, in contrast to the oscillatory regime, to a qualitatively different behavior of the CV in the strong and in the weak noise regime, respectively. For positive feedback, trajectory enter new cycles with positive \( \Delta \omega \). Since the \( \Delta \omega \)-dynamics is usually slower than the \( \phi \)-dynamics, the system reaches the \( \phi \)-nullcline above the stable node and then relaxes slowly toward the stable fixed point. During the relaxation, however, the system can escape the stable node’s basin of attraction much
V. FEEDBACK-INDUCED CORRELATIONS

The dynamics of $\Delta \omega$ also causes correlations of subsequent IEIs. A measure to quantify correlations of IEIs of lag $n$ is the serial correlation coefficient (SCC) \[59\]

$$\rho_n = \frac{\langle (\Delta t_i - \langle \Delta t_i \rangle)(\Delta t_{i+n} - \langle \Delta t_i \rangle) \rangle}{\text{Var}(\Delta t_i)}.$$ \hspace{1cm} (41)

If correlations are positive ($\rho_n > 0$), longer $\Delta t_i$ are, on average, followed by longer $\Delta t_{i+n}$ (and/or shorter $\Delta t_i$ by shorter $\Delta t_{i+n}$). Negative correlations between adjacent intervals ($\rho_1 < 0$) could be caused by an alternation between short and long intervals. The low frequency limit of the power spectrum is also connected to the SCCs. It holds \[59\]:

$$\lim_{f \to 0} S(f) = rC_v^2(1 + 2\sum_{k=1}^{\infty} \rho_k).$$ \hspace{1cm} (42)

Consequently, cumulative IEI correlations can be also studied using the power spectrum.
If the regime of ACR. This can be understood as follows: If positive feedback (a > 0) is applied, a fast escape from the stable node, on average, will lead to higher ∆t-det, which reduces the probability for fast escapes (small ∆t-det), and, therefore, causes positive IEI correlations. However, for negative feedback, the opposite behavior occurs. Here a fast escape (short ∆t-det) leads, on average, to lower ∆ω for subsequent cycles and, therefore, further reduces the probability for short ∆t-det, which leads to negative IEI correlations.

Analyzing the sum of the first N SCCs [fig. 8 (top right)], we find that correlations possess a maximum in the regime of ACR. This can be understood as follows: If D is small, the mean IEI is larger than the feedback timescale τ, therefore, perturbations of ∆ω are already relaxed when the system can escape the SN, leading to less correlated IEIs. However, if D is large, noise dominates the dynamics and leads to less correlations in the sequence, too. Close to the local maximum of the SCCs, however, we find strong positive (for a > 0) and strong negative (for a < 0) serial correlations. Combining these findings with eq. (42) and using that Cv is of order 1, we find that the increase in the power at low frequencies [see fig. 5 (left bottom, inset)] reflects these correlations.

**B. Approximation for a slow feedback timescale in the oscillatory regime**

If the system evolves on a limit cycle, the SCC in the weak noise limit can be expressed by a product of the form

$$\rho_n = (\eta V)^{n-1} \rho_1, \quad n \geq 1, \quad \omega_0 > 1, \quad D \ll 1.$$  \hspace{1cm} (43)

This result was derived for the perfect integrate-and-fire neuron 10 and for a general integrate-and-fire neuron 30, both subjected to an adaptation current (negative feedback), respectively. It can be generalized to positive feedback as long as a limit cycle exists.

The first correlation coefficient ρ1 is given by:

$$\rho_1 = -\eta(1-V) \frac{1 - \eta^2 V}{1 + \eta^2 - 2\eta^2 V}.$$ \hspace{1cm} (44)

Here η is determined by the deterministic IEI ∆t-det [eq. (17)]

$$\eta = \exp(-\frac{\Delta t_{det}}{\tau})$$ \hspace{1cm} (45)

and the term V reads

$$V = 1 - \frac{\Delta \omega_c + 2\pi a}{\tau} \Theta,$$ \hspace{1cm} (46)

where Θ is accessible by the phase response curve (PRC) Z(t) 30

$$\Theta = -\int_0^{\Delta t_{det}} dt Z(t)e^{-\frac{t}{\tau}}.$$ \hspace{1cm} (47)

These formulas have been developed for a perfect 10 or general multidimensional integrate-and-fire models 30 with a spike-triggered linear dynamics for a negative feedback. We have verified that the approach of Ref. 30 also applies to the case of positive feedback as long as a steady state exists, i.e. for a < 1.

For our system, the PRC can be approximated for a slow feedback timescale (∆t-det ≪ τ) (see Appendix C). In this limit, Θ reads:

$$\Theta = -\frac{(1 - e^{-\frac{\Delta t_{det}}{\tau}})}{\tau} \frac{1 + \tau + \tau^2(\omega_0 + (\Delta \omega)^2)}{(\omega_0 + \Delta \omega_c) + 1 + \tau^2((\omega_0 + (\Delta \omega)^2 - 1)}.$$ \hspace{1cm} (48)

Figures 8. (Color online) SCC over several lags (top left) for D = 0.04, the sum of the first N = 100 SCCs plotted over noise strength (top right) in the excitable regime (ω0 = 0.9) (top), and SCC over several lags in the oscillatory regime (ω0 = 1.1) (bottom). Excitable regime (top): All results are obtained from simulation. Oscillatory regime (bottom): Numerical results (sim.) are shown together with the analytical approximation eq. (43). Parameter: τ = 100.
Figure 9. (Color online) Influence of the distance to the bifurcation on the SCC at lag 1 for $a < 0$ (left) and $a > 0$ (right). The theory eq. (43) (lines) is compared to simulations for a very low noise level $D = 0.001$ (points). Close to the bifurcation ($\omega = 1.01$), $\rho_1$ behaves non-monotonically, possessing a local minimum for negative feedback and a local maximum for positive feedback, respectively. If the distance to the bifurcation is increased ($\omega = 1.05$, $\omega = 1.3$), the local minimum moves to stronger negative feedback. For positive feedback, however, the local maximum vanishes in a large distance to the bifurcation. Please consider the difference of the total range of $a$ and $\rho_1$ in the two panels. Parameters: $\tau = 100$.

Here, $\Theta$ is always negative and $\eta$ is close, but smaller than one. Consequently, $V$ is larger than one for $a > 0$ and smaller than one for $a < 0$. This causes $\rho_1$ to have the same sign as $a$ (compare eq. (11) for $\eta \lesssim 1$).

C. Comparison of theory and numerical results in the oscillatory regime

1. Distance to the bifurcation

Figure 9 shows the analytical results eq. (11) for $\rho_1$ compared to those obtained from simulations for different distances to the saddle-node bifurcation at $\omega_0 = 1$. Interestingly, maximal positive correlations (for $a > 0$) become stronger, whereas maximal negative correlations (for $a < 0$) become weaker by approaching the bifurcation. Note that close to the bifurcation or for strong negative feedback, $\Delta t_{det}$ becomes comparable to $\tau$ [see fig. 3] and the assumption of a slow feedback timescale ($\Delta t_{det} \ll \tau$) does not hold anymore. For this reason the approximation fails quantitatively for large negative values of $a$.

2. Non-monotonic behavior

Another interesting observation can be made in fig. 9: stronger feedback does not necessarily increase $\rho_1$. Instead, the SCC at lag one possesses a minimum for negative feedback and a maximum when positive feedback is applied. The maximum for positive feedback, however, vanishes if the distance to the bifurcation is increased.

In order to understand how stronger feedback can lead to smaller $\rho_1$, it is helpful to consider the particular trajectories, shown in fig. 2 (center). Suppose that the system evolves on the limit cycle and highly negative feedback is applied. In that case, its trajectory looks like the lower one in fig. 2 (center). Such trajectories spend the main part of the IEI close to the stable branch of the $\phi$-nullcline. The system slowly evolves along the $\phi$-nullcline until $\omega_0 + \Delta \omega > 1$. Close to the bifurcation ($\omega_0 \gtrsim 0$), however, this requires $\Delta \omega$ to approach small values. Consequently, information on perturbations, for instance, due to prior longer (or shorter) IEIs is reduced, which decreases $\rho_1$ for strong negative feedback. In the case of positive or weak negative feedback this effect acts in the opposing direction, since $\Delta \omega$ does not have to increase to pass the maximum of the $\phi$-nullcline. Here, slightly higher $\Delta \omega(t_i)$ lead to disproportional shorter IEIs $\Delta t_{i+1}$, whereas initially slightly lower $\Delta \omega(t_i)$ lead to much longer $\Delta t_{i+1}$, if the system is close to the bifurcation point. Consequently, strong positive correlation between subsequent lags occur. However, for highly positive feedback, the limit cycle is far from the $\phi$-nullcline (see fig. 2 center). Here these non-linear effects disappear and $\rho_1$ decreases again.

3. Influence of the feedback timescale

In fig. 10 we show $\rho_1$ as a function of the feedback strength for different $\tau$. Here, interestingly, smaller $\tau$ may lead to stronger correlations for $a > 0$, whereas $\rho_1$
VI. SUMMARY AND DISCUSSION

We have studied the effect of event-triggered feedback on the dynamics and output statistics of a noise-driven phase oscillator.

Analytical results for the mean IEIs were derived, which show besides the emergence of a bistable regime, that positive feedback leads to a change the bifurcation structure of the system and the excitability class. Investigating the influence of the feedback on the output statistics in the excitable regime, we observed that whereas coherence resonance can be observed even without any feedback, only positive feedback leads to anti-coherence resonance at low noise strengths.

For both kinds of feedback, we found serial correlations in the sequence of IEIs, which can be approximated analytically in the oscillatory regime for a weak noise and a large timescale separation between the phase and the feedback dynamics, which can be found in cases of spike-triggered feedback due to slow inhibitory currents or slow decaying variations in external ion concentrations in neural systems. Close to the bifurcation from the excitable to the oscillatory regime, we find a non-monotonic behavior of the correlation between adjacent IEIs and the feedback strength, which indicates that maximal correlations occur at an optimal feedback strength.

Our general approach can be used to understand the role of individual slow processes on the IEI statistics in neurons, excitable lasers, or other pulse-generating systems, that operate close to a saddle-node on invariant circle bifurcation (class I excitability), or to identify the source of serial correlations in the IEI sequence. Our results illustrate that event-triggered feedback can be used to reduce (or increase) the output variability. This is particularly interesting in information processing systems, in which this variability is the limiting factor for a reliable signal transmission.

Appendix A: Simulation techniques

All simulations were performed, using the Euler method for the numerical integration of the system eqs. (2) and (11). The integration time step was chosen to be $10^{-4}$ for $D < 1$ and $10^{-6}$ for larger $D$. After an equilibration time of $100\tau$, IEIs were recorded up to an ensemble of $10^6$ IEIs. From this series of $\Delta t_i$, the mean firing rate, the CV, the power spectrum, and the SCC was calculated.

In the excitable regime, the firing rate becomes very low, especially for low noise levels. For such weak noise ($D < 0.02$), we used the rare event method presented in Ref. [42]. Here the parameters, named according to the notation in the reference, read: borders of the simulated area: $L^\phi_0 = -\pi/2$, $L^-_\phi = -2\pi$, $L^-_\omega = -\omega_0$, $L^+_\omega = 1.5$; walkers per box: $N = 2$; size of a time step $h = 0.1$; box size in $\phi$-direction $\Delta \phi = 0.1\sqrt{2Dh}$; box size in $\omega$-direction $\Delta \tau = 1/(2\tau)$. Simulation were performed for a time $T_{\text{sim}} = 20000$. After entering the stationary regime, the probability current through absorbing boundary at $\phi = 2\pi$ was recorded and, finally, averaged to get the mean firing rate.

Appendix B: Details of figure 5

1. Firing rates

The series approximation was calculated by using eq. (24). For $B(D,\omega_0)$ the terms ($k = 1, 2, \ldots, 500$) were evaluated with high numerical precision. $\langle \Delta t_{i,0} \rangle$ was obtained from eq. (20). For large $D$ fewer terms are needed to approximate the firing rate well. However, for $D \approx 0.01$ a few hundred terms are needed and must be calculated with high precision. For even smaller values of $D$ the computation time becomes too large. Therefore, the series approximation in fig. 4 (top) is shown for $D \geq 0.01$.

The strong noise approximation is given by eq. (21). Here $\langle \Delta t_{i,0} \rangle$ was obtained from eq. (20), too.

The weak noise approximation eq. (31) was evaluated using eq. (23) for $r_0$ and is illustrated in fig. 11 together with results from simulations.

2. Coefficient of variation

The strong noise approximation was calculated from eq. (37), where the eqs. (20), (34) and (32) were used for $\langle \Delta t_{i,0} \rangle$ and $C_{v,0}$.

The weak noise approximation in the oscillatory regime was obtained from eq. (40), where the eqs. (20) and (33) were used for $\langle \Delta t_{i,0} \rangle$ and $C_{v,0}$.

VII. ACKNOWLEDGMENTS

This paper was developed within the scope of IRTG 1740/TRP 2011/50151-0, funded by the DFG / FAPESP an by the BMBF (FKZ: 01GQ1001A).
In order to calculate the PRC, we first solve eq. \( \text{(C1)} \) for the non-feedback case and account for feedback by substituting \( \omega_0 \to \omega_0 + \langle \Delta \omega \rangle \) afterwards. In the non-feedback case, \( \phi_{lc}(t) \) can be obtained by integrating eq. \( \text{(1)} \), considering \( \phi_{lc}(0) = 0 \) and the smoothness of \( \phi_{lc}(t) \) in the interval \( t \in [0, \Delta t_{det}] \). This yields:

\[
\phi_{lc}(t) \simeq 2 \arctan \left( \frac{1}{\omega_0} \tan \left( \arctan \left( \frac{1}{\Omega_0} \right) - \frac{\Omega_0 t}{2} \right) \right). 
\]  

(C2)

Here \( \Omega_0 := \sqrt{\omega_0^2 - 1} \) and \( \simeq \) denotes equality modulo \( 2\pi \). Putting \( \phi_{lc}(t) \) into eq. \( \text{(C1)} \), the PRC in the non-feedback case can be calculated. After some tedious steps, we get:

\[
Z(t) = Z_{ev}(\Delta t_{det})(1 + \frac{1 + \Omega_0 \sin(\Omega_0 t) - \cos(\Omega_0 t)}{\Omega_0^2}). 
\]  

(C3)

The result for \( \Theta \) can be obtained from eq. \( \text{(47)} \). This yields:

\[
\Theta = -(1 - e^{-\Delta t_{det}})Z_{ev}(\Delta t_{det}) \frac{1 + \tau + \tau^2(\omega_0 + \langle \Delta \omega \rangle)^2}{1 + \tau^2(\omega_0^2 - 1)}. 
\]  

(C4)

Finally, we account for the feedback by substituting \( \omega_0 \to \omega_0 + \langle \Delta \omega \rangle \), which yields

\[
\Theta = -(1 - e^{-\Delta t_{det}}) \frac{\tau}{(\omega_0 + \langle \Delta \omega \rangle)^2} \frac{1 + \tau + \tau^2(\omega_0 + \langle \Delta \omega \rangle)^2}{1 + \tau^2(\omega_0^2 + \langle \Delta \omega \rangle)^2 - 1}, 
\] 

\( \tau \gg \Delta t_{det} \)  

(C5)

Expanding this for large \( \tau \gg 1 \), the zeroth order term reads

\[
\Theta \approx -\frac{\Delta t_{det} (\omega_0 + \langle \Delta \omega \rangle)}{(\omega_0 + \langle \Delta \omega \rangle)^2 - 1}, \quad \tau \gg \Delta t_{det}. 
\]  

(C6)

Appendix C: Calculation of \( \Theta \) using the phase response curve

We can calculate \( \Theta \), using eq. \( \text{(47)} \), i.e., by calculating the PRC. In our case the PRC is given by \( \text{(31)} \):

\[
Z(t) = Z_{ev}(\Delta t_{det}) \exp \left[- \int_0^{\Delta t_{det}} dt' \cos(\phi_{lc}(t')) \right]. 
\]  

(C1)

Here \( Z_{ev}(\Delta t_{det}) = 1/(\omega_0 + \omega_{lc}) \) is the inverse \( \phi \)-velocity when an event occurs, if the system evolves on the deterministic limit cycle and \( \phi_{lc}(t) \) is the corresponding \( \phi \)-solution.

Figure 11. (Color online) The firing rate in the excitatory regime obtained from simulations (points) for a weak noise compared to the analytic approximation eq. \( \text{(31)} \) (lines). Note the double logarithmic scale. Simulations for \( D \leq 0.01 \) were performed using the rare-event method presented in Ref. \[42 \].

Parameters: \( \omega_0 = 0.9, \tau = 100. \)
