Two paradigmatic scenarios for inverse stochastic resonance

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Inverse stochastic resonance comprises a nonlinear response of an oscillatory system to noise where the frequency of noise-perturbed oscillations becomes minimal at an intermediate noise level. We demonstrate two generic scenarios for inverse stochastic resonance by considering a paradigmatic model of two adaptively coupled stochastic active rotators whose local dynamics is close to a bifurcation threshold. In the first scenario, shown for the two rotators in the excitable regime, inverse stochastic resonance emerges due to a biased switching between the oscillatory and the quasi-stationary metastable states derived from the attractors of the noiseless system. In the second scenario, illustrated for the rotators in the oscillatory regime, inverse stochastic resonance arises due to a trapping effect associated to a noise-enhanced stability of an unstable fixed point. The details of the mechanisms behind the resonant effect are explained in terms of slow-fast analysis of the corresponding noiseless systems.

The effects of noise may generically be classified into two groups: on the one hand, the noise may enhance or suppress certain features of deterministic dynamics by acting on the system states in an inhomogeneous fashion, while on the other hand, it may give rise to novel forms of behavior, associated to crossing of thresholds and separatrices, or to a stability of deterministically unstable states. The constructive role of noise has been evinced in a wide range of real-world applications, from neural networks and chemical reactions to lasers and electronic circuits. The classical examples of stochastic facilitation concern the resonant phenomena, including the stochastic resonance, where the noise of appropriate intensity may induce oscillations in bistable systems that are preferentially locked to a weak periodic forcing, and the coherence resonance, where an intermediate level of noise may trigger coherent oscillations in excitable systems. Recently, a novel form of nonlinear response to noise, called inverse stochastic resonance, has been discovered while studying individual neural oscillators and models of neuronal populations. It has come to light that the noise may reduce the intrinsic spiking frequency of neuronal oscillators, transforming the tonic firing into a bursting-like activity or even quenching the oscillations. Within the present study, we demonstrate two paradigmatic mechanisms of inverse stochastic resonance, one based on biased switching between the metastable states, and the other associated to a noise-enhanced stability of an unstable fixed point. We show that the effect is robust, in a sense that it may emerge in coupled excitable and coupled oscillatory systems, and both in cases of Type I and Type II oscillators.

Noise in excitable or multistable systems may fundamentally change their deterministic dynamics, giving rise to qualitatively novel forms of behavior, associated to crossing of thresholds and separatrices, or stabilization of certain unstable structures123. The emergent dynamics may involve noise-induced oscillations and stochastic bursting1316, switching between metastable states2517 or noise-enhanced stability of metastable and unstable states512 to name but a few. In neuronal systems, the phenomena reflecting the constructive role of noise are collected under the notion of stochastic facilitation1417, which mainly comprises the resonant effects. The most prominent examples concern the coherence resonance1620, where the regularity of noise-induced oscillations becomes maximal at a preferred noise level, and the stochastic resonance21, where optimizing the signal-to-noise ratio enables the detection of weak periodic signals. Recent studies on the impact of noise in neuronal oscillators have revealed that the noise may also give rise to an inhibitory effect, which consists in reducing the intrinsic spiking frequency, such that it becomes minimal at an intermediate noise intensity14122239. This effect has been called inverse stochastic resonance (ISR), but in contrast to the stochastic resonance, it concerns autonomous rather than periodically driven systems. Apart from reports in models of neurons and neuronal populations, ISR has recently been evinced for cerebellar Purkinje cells in-vitro28, having shown how the lifetimes of the so-called UP states with elevated spiking activity and the DOWN states of relative quiescence2223 depend on the noise variance.

The studies of the mechanism behind ISR have so far mostly been focused on Type II neural oscillators with bistable dynamics poised close to a subcritical Hopf bifurcation11122125, considering Hodgkin-Huxley and Morris-Lecar models. Under the influence of noise, such systems exhibit switching between the two metastable states, derived from the periodic and the stationary attractor of the deterministic dynamics. At an
intermediate noise level, one observes that the switching rates become strongly asymmetric, with the system spending substantially more time in a quasi-stationary state. This is reflected in a characteristic non-monotone dependence of the spiking frequency on noise, which is a hallmark of ISR.

Nevertheless, a number of important issues on the mechanism giving rise to ISR have remained unresolved. In particular, is the effect dependent on the type of neuronal excitability? Also, can there be more than a single mechanism of ISR? And finally, how does the effect depend on the form of couplings and whether it can be robust for adaptively changing couplings, typical for neuronal systems?

To address these issues, we invoke a simple, yet paradigmatic model that combines the three typical ingredients of neuronal dynamics, including excitability, noise and coupling plasticity. In particular, we consider a system of two identical, adaptively coupled active rotators influenced by independent Gaussian white noise sources

\[
\dot{\varphi}_i = I_0 - \sin \varphi_i + \kappa_i \sin (\varphi_j - \varphi_i) + \sqrt{D} \xi_i(t)
\]

\[
\dot{\kappa}_i = \varepsilon (-\kappa_i + \sin(\varphi_j - \varphi_i + \beta)).
\]

The indices \(i, j \in \{1, 2\}, i \neq j\) denote the particular units, described by the respective phases \(\{\varphi_1, \varphi_2\} \in \mathbb{S}^1\), which constitute the fast variables, and the slowly varying coupling weights \(\{\kappa_1, \kappa_2\} \in \mathbb{R}\). The scale separation between the characteristic timescales is set by the small parameter \(\varepsilon \ll 1\) that defines the adaptivity rate. The local dynamics is controlled by the excitability parameter \(I_0\), such that the SNIPER bifurcation at \(I_0 = 1\) mediates the transition between the excitable \((I_0 \lesssim 1)\) and the oscillatory regime \((I_0 > 1)\). The excitable units may still exhibit oscillations, induced either by the action of the coupling (emergent oscillations) and/or evoked by the stochastic terms (noise-induced oscillations). The noiseless coupled system is invariant with respect to exchange of the units indices, such that all the stationary or the periodic solutions always appear in pairs connected by the \(Z_2\) symmetry. Given the similarity between the active rotators and the theta neurons, which also conform to Type I excitability, system may be considered qualitatively analogous to a motif of two adaptively coupled neurons influenced by an external bias current \(I_0\) and the synaptic noise. Adaptivity is modeled in terms of phase-dependent plasticity of coupling weights, with the modality of the plasticity rule adjusted by the parameter \(\beta\). This form of plasticity has already been shown capable of qualitatively reproducing the features of some well-known neuronal plasticity rules. In particular, for \(\beta = 3\pi/2\), one recovers Hebbian learning, where synaptic potentiation promotes phase synchronization, while for \(\beta = \pi\), one finds an STDP-like type of plasticity, which favors a causal relationship between the spike times of a presynaptic and a postsynaptic neuron.

### FIG. 1. Emergent oscillations in (1) for \(I_0 = 0.95, D = 0\). (a) Variation \(\sigma_{\kappa_1}\) of the coupling weight \(\kappa_1\) in the \((\beta, \varepsilon)\) plane. (b) Dependencies \(\sigma_{\kappa_1}(\varepsilon), i \in \{1, 2\}\) for the oscillatory (thick lines) and the stationary solution (thin line). Shading indicates the \(\varepsilon\) interval admitting stable periodic solutions.

### I. INVERSE STOCHASTIC RESONANCE DUE TO A BIASED SWITCHING

The first generic scenario for ISR we demonstrate is based on biased switching between the metastable states associated to coexisting stationary and periodic attractors of the corresponding deterministic system. As an example, we consider the noise-induced reduction of frequency of emergent oscillations on a motif of two adaptively coupled stochastic active rotators with excitatory local dynamics \((I_0 = 0.95)\). To elucidate the mechanism behind the effect, we first summarize the details of the noise-free dynamics, and then address the switching behavior. A complete bifurcation analysis of the noiseless version of (1) with excitatory local dynamics has been carried out in [33,34] having shown (i) how the number and stability of the fixed points depends on the plasticity rule, characterized by \(\beta\), as well as (ii) how the interplay between \(\beta\) and the adaptivity rate, controlled by the small parameter \(\varepsilon\), gives rise to limit cycle attractors. Our focus is on the interval \(\beta \in (3.298, 4.495)\), which approximately interpolates between the limiting cases of Hebbian-like and STDP-like plasticity rules. There, the system exhibits two stable equilibria born from the symmetry-breaking pitchfork bifurcation, and has four additional unstable fixed points. For the particular case \(\beta = 4.2\) analyzed below, the two stable equilibria, given by \((\varphi_1^*, \varphi_2^*, \kappa_1^*, \kappa_2^*) = (1.177, 0.175, 0.932, -0.92)\) and \((\varphi_1^*, \varphi_2^*, \kappa_1^*, \kappa_2^*) = (0.175, 1.177, -0.92, 0.032)\), manifest excitatory behavior, such that applying a sufficiently strong perturbation may evoke either synchronized or phase-shifted spikes of individual unit.

The onset of emergent oscillations, as well as the coexistence between the stable stationary and periodic solutions in the noiseless version of (1), are illustrated in Fig. 1. In regard to the former, the maximal stability region of the two \(Z_2\) symmetry-related periodic solutions is indicated in Figure 1(a), which shows the variation of the \(\kappa_1\) variable, \(\sigma_{\kappa_1} = \max(\kappa_1(t)) - \min(\kappa_1(t))\), in the \((\beta, \varepsilon)\) parameter plane. The scan was performed by the method of numerical continuation starting from a stable periodic solution, such that the initial conditions...
for an incremented parameter value are given by the final state obtained for the previous iteration step. One finds that for a given fixed $\beta$, there exists an interval $\varepsilon \in (\varepsilon_{\text{min}}, \varepsilon_{\text{max}})$ of intermediate scale separation ratios supporting the oscillations, cf. the highlighted region in Fig. 1(b). In particular, the two $Z_2$-symmetry-related branches of stable periodic solutions emanate from the fold of cycles bifurcations, whereby the associated threshold $\varepsilon_{\text{min}}(\beta)$ reduces with $\beta$. Note that the indicated $\varepsilon$ range admits multistability between the two periodic solutions and the two symmetry-related stable stationary states described above, but for simplicity, we only show a single representative for both types of solutions. It turns out that increasing the adaptivity rate affects the waveform of oscillations. While for a smaller $\varepsilon$, the corresponding profiles are rather different for the two units, around $\varepsilon \approx 0.06$ the system undergoes an inverse pitchfork bifurcation of limit cycles, such that the oscillatory solution gains the anti-phase space-time symmetry $\varphi_1(t) = \varphi_2(t + T_{\text{osc}}/2), \kappa_1(t) = \kappa_2(t + T_{\text{osc}}/2)$, where $T_{\text{osc}}$ denotes the oscillation period. In the presence of noise, the coexisting attractors of the deterministic system turn to metastable states, connected by switching dynamics induced by the noise.

Inverse stochastic resonance manifests itself as the noise-mediated suppression of oscillations, whereby the frequency of noise-perturbed oscillations becomes minimal at an intermediate noise level. For the motif of two adaptively coupled excitable active rotators, such characteristic non-monotone dependence on noise is generically found for intermediate adaptivity rates supporting multistability between the stationary and the oscillatory solutions. A family of curves illustrating the dependence of the oscillation frequency on noise variance $\langle f \rangle(D)$ for a set of different $\varepsilon$ values above the $\varepsilon_{\text{min}}(\beta)$ threshold is shown in Fig. 2(a). The angled brackets $\langle \cdot \rangle$ refer to averaging over an ensemble of a thousand different stochastic realizations, having fixed a set of initial conditions within the basin of attraction of the limit cycle attractor. Nonetheless, qualitatively analogous results are recovered if for each realization of the stochastic process one selects a set of random initial conditions lying within the stability basin of a periodic solution. The characteristic examples of the time series $\varphi_i(t)$ for the noise levels below, around and above the resonance, cf. Fig. 2(b)-(d), indicate that the noise-induced switching gives rise to a bursting-like behavior. The associated quiescent episodes correspond to the system residing in the vicinity of the quasi-stationary metastable states, and become prevalent at the noise levels above the minimum of $\langle f \rangle(D)$. For the weaker noise, the frequency of emergent oscillations remains close to the deterministic one, whereas for a much stronger noise, it increases above that of unperturbed oscillations. Note that the suppression effect of noise depends on the adaptivity rate, such that it is enhanced for faster adaptivity. Indeed, for an intermediate scale separation $\varepsilon = 0.1$, the noise is found capable of quenching the oscillations, i.e. the quasi-stationary states become effectively absorbing, such that the minimal frequency observed approaches zero. This has been established to be caused by the orbit of a limit cycle becoming more sensitive to external perturbation for faster adaptivity. At the level of coupling weights, the switching dynamics is reflected in that the corresponding stationary distributions $P(\kappa_i), i \in \{1, 2\}$ acquire a bimodal form. As expected, the noise dependence of the bimodality coefficient for the distribution $P(\kappa_1), b_{P(\kappa_1)}$, shows a pronounced maximum at the resonant noise intensity, see Fig. 2(c).

In order to elucidate the mechanism behind ISR, we have calculated how the fraction of the total time spent at the oscillatory metastable states, $T_{\text{LC}}/T$, changes with noise. Figure 3(a) shows a non-monotone dependence, indicating that the switching process around the resonant noise level becomes strongly biased toward the quasi-stationary state, even more so for a faster adaptivity. The biased switching is facilitated by the geometry of the phase space, featuring an asymmetrical structure with respect to the separatrix between the coexisting attractors, such that the limit cycle lies much closer to the separatrix than the stationary states. In this context, the nonlinear response to noise may be understood in terms of the competition between the transition processes from and to the limit cycle attractors. In Fig. 3(b)-(c) is illustrated the qualitative distinction between the noise-dependences of the transition rates from the stability basin of the limit cycle attractors to that of the stationary states $\gamma_{\text{LC} \rightarrow FP}$.
and vice versa, $\gamma_{FP\rightarrow LC}$: while $\gamma_{LC\rightarrow FP}$ displays a maximum at the resonant noise level, $\gamma_{FP\rightarrow LC}$ just increases monotonously with noise. For small noise, both types of transition events are rare, which leaves the deterministic oscillation frequency almost unperturbed. For increasing noise, the competition between the two processes is resolved in such a way that at an intermediate/large noise, the impact of $\gamma_{LC\rightarrow FP}/\gamma_{FP\rightarrow LC}$ becomes prevalent.

Though ISR is most pronounced for intermediate $\varepsilon$, it turns out that an additional subtlety in the mechanism of biased switching may be explained by employing the singular perturbation theory to the noiseless version of (1). In particular, by combining the critical manifold theorem\cite{1} and the averaging approach\cite{3}, one may demonstrate the facilitatory role of plasticity in enhancing the resonant effect, showing that the adaptation drives the fast flow toward the parameter region where the stationary state is a focus rather than a node. The response to noise in multiple timescale systems has already been indicated to qualitatively depend on the character of the stationary states, yielding fundamentally different scaling regimes with respect to noise variance and the scale-separation ratio\cite{2,3}. Intuitively, one expects that the resonant effects should be associated to the quasi-stationary states derived from the focuses rather than the nodes\cite{3}, because the local dynamics then involves an eigenfrequency.

The fast-slow analysis of (1) comprises two steps: we first address the layer problem to determine the attractors of the fast flow, and then consider the reduced problem, concerning the dynamics of the slow flow\cite{4,5}. Within the layer problem, formally obtained by setting $\varepsilon = 0$ in (1), the fast flow dynamics

$$\begin{align*}
\dot{\varphi}_1 &= I_0 - \sin \varphi_1 + \kappa_1 \sin (\varphi_2 - \varphi_1) \\
\dot{\varphi}_2 &= I_0 - \sin \varphi_2 + \kappa_2 \sin (\varphi_1 - \varphi_2),
\end{align*}$$

(2)

is considered by treating the slow variables $\kappa_1, \kappa_2 \in [-1, 1]$ as additional system parameters. Depending on $\kappa_1$ and $\kappa_2$, one finds that the fast flow dynamics is almost always monostable, exhibiting either a stable equilibrium or a limit cycle attractor. In general, the system (2) may possess two or four fixed points, and the bifurcation scenarios underlying the changes in their number and stability are described in detail in Ref.\cite{6}. The maximal stability region of the oscillatory regime, indicated by the gray shading in Fig. 4(a), is determined by the method of numerical continuation, starting from a periodic solution. The thick red lines outlining the regions boundaries correspond to the two branches of SNIPER bifurcations. Note that for each periodic solution above the main diagonal $\kappa_1 = \kappa_2$, there exists a $Z_2$ symmetry-related counterpart below the diagonal.

By averaging over the different attractors of the fast flow dynamics, one may obtain multiple stable sheets of the slow flow\cite{8,9}. The procedure consists in determining the time average $\langle \varphi_2 - \varphi_1 \rangle_t = h(\kappa_1, \kappa_2)$ by iterating (2) for each fixed set $(\kappa_1, \kappa_2)$, such that the average naturally reflects the type of attractor of the fast flow\cite{8,9}. In the second step, one substitutes these averages into the equations of the slow flow

$$\begin{align*}
\kappa_1' &= [-\kappa_1 + \sin (h(\kappa_1, \kappa_2) + \beta)] \\
\kappa_2' &= [-\kappa_2 + \sin (-h(\kappa_1, \kappa_2) + \beta)],
\end{align*}$$

(3)

where the prime refers to a derivative over the rescaled time variable $T := t/\varepsilon$. The arrows in Fig. 4(a) show the vector fields on the two stable sheets of the slow flow (\cite{10}), associated to the stationary and the periodic attractors of the fast flow. Using this framework, one may gain a deeper insight into the facilitatory role of adaptivity within the ISR. In particular, in the inset of Fig. 4(a) are extracted the time series $(\kappa_1(t), \kappa_2(t))$ which (from left to right) illustrate the switching episode from an oscillatory to the quasi-stationary metastable state. The triggering/termination of this switching event is associated to an inverse/direct SNIPER bifurcation of the fast flow. Note that for $(\kappa_1, \kappa_2)$ values immediately after the inverse SNIPER bifurcation, the stable equilibrium of the fast flow is a node. Nevertheless, for the noise levels where the effect of ISR is most pronounced, we observe that the coupling dynamics guides the system into the regions shown by the orange shading in Fig. 4(a), where the equilibrium is a stable focus rather than a node. We have verified that this feature is a hallmark of ISR by numerically calculating the conditional probability $p_F$ that the events of crossing the SNIPER bifurcation are followed by the system’s orbit visiting the $(\kappa_1, \kappa_2)$ regions featuring a focus equilibrium. The $p_F(D)$ dependencies for two characteristic $\varepsilon$ values in Fig. 4(b) indeed show a maximum for the resonant noise levels, where the corresponding frequency dependencies $f(D)$ display a minimum. The local dynamics around the focus gives rise to a trapping effect, such that the phase variables remain for a longer time in the associated quasi-stationary states than in case where the metastable states derive from the nodes of the fast flow. Small noise below the resonant values is insufficient to drive the system to the regions featuring focal equilibria, whereas for too large a noise,
the stochastic fluctuations completely take over, washing out the quasi-stationary regime. One observes that the trapping effect is enhanced for the faster adaptivity rate, as evidenced by the fact that the curve $p_F(D)$ for $\varepsilon = 0.1$ lies above that for $\varepsilon = 0.06$.

II. INVERSE STOCHASTIC RESONANCE DUE TO A TRAPPING EFFECT

As the second paradigmatic scenario for ISR, we consider the case where the oscillation frequency is reduced due to a noise-induced trapping in the vicinity of an unstable fixed point of the noiseless system. Such trapping effect may be interpreted as an example of the phenomenon of noise-enhanced stability of an unstable fixed point.\cite{[1],[2]} This mechanism is distinct from the one based on biased switching, because there the quasi-stationary states derive from the stable equilibria of the noise-free system, such that the noise gives rise to crossing over the separatrix between the oscillatory and the quiescent regime. Nevertheless, in the scenario below, noise induces "tunneling" through the bifurcation threshold, temporarily stabilizing an unstable fixed point of the deterministic system.

In particular, we study an example of a system\cite{[1]} comprised of two adaptively coupled active rotators in the oscillatory, rather than the excitatory regime, setting the parameter $I_0 = 1.05$ close to a bifurcation threshold. The plasticity parameter is fixed to $\beta = \pi$, such that the modality of the phase-dependent adaptivity resembles the STDP rule in neuronal systems. One finds that this system exhibits a characteristic non-monotone behavior, with the oscillation frequency of the phases displaying a minimum at an intermediate noise level, see Fig. 3. Similar to Fig. 2, the effect is found to depend on the adaptivity rate, becoming more pronounced for an intermediate scale separation $\varepsilon \approx 0.1$.

There also exists a lower boundary on the adaptivity rate below which the nonlinear response to noise can no longer be observed, see the curve $(f(D))$ for $\varepsilon = 0.02$.

To elucidate the mechanism behind ISR, we again invoke the fast-slow analysis of the corresponding noise-free system. Prior to this, we briefly summarize the results of the numerical bifurcation analysis for the noiseless system in the case of finite scale separation. First note that selecting a particular plasticity rule $\beta = \pi$ confines the dynamics of the couplings to a symmetry invariant subspace $\kappa_1(t) = -\kappa_2(t) \equiv \kappa(t)$. Due to this, the noiseless version of the original system\cite{[1]} can be reduced to a three-dimensional form

\begin{align*}
\dot{\phi}_1 &= I_0 - \sin \phi_1 + \kappa \sin (\phi_2 - \phi_1) \\
\dot{\phi}_2 &= I_0 - \sin \phi_2 + \kappa \sin (\phi_2 - \phi_1) \\
\dot{\kappa} &= \varepsilon (-\kappa - \sin (\phi_2 - \phi_1)).
\end{align*}

(4)

We have numerically verified that (4) possesses no stable fixed points, but rather a pair of saddle nodes and a pair of saddle foci. It can be shown that the maximal real part of the eigenvalues of the foci displays a power-law dependence on the scale separation, tending to zero in the singular limit $\varepsilon \to 0$. Concerning the oscillatory states, we have numerically determined that (4) exhibits multistability between three periodic solutions, whereby two of them are characterized by the non-zero couplings and a constant phase-shift between the fast variables, whereas the third solution corresponds to a case of effectively uncoupled units ($\kappa(t) = 0$) and the fast variables synchronized in-phase.

A deeper understanding of the ingredients relevant for the trapping mechanism can be gained within the framework of fast-slow analysis, considering the layer problem

\begin{align*}
\phi_1 &= I_0 - \sin \phi_1 + \kappa \sin (\phi_2 - \phi_1) \\
\phi_2 &= I_0 - \sin \phi_2 + \kappa \sin (\phi_2 - \phi_1).
\end{align*}

(5)

Treating $\kappa \in [-1,1]$ as an additional system parameter, we first look for the stationary and periodic attractors of the fast flow. It is convenient to apply the coordinate transformation $(\phi_1, \phi_2) \mapsto (\Phi, \delta \varphi) = (\frac{\phi_1 + \phi_2}{2}, \frac{\phi_1 - \phi_2}{2})$, rewriting (5) as

\begin{align*}
\dot{\delta \varphi} &= -\sin \delta \varphi \cos \Phi \\
\dot{\Phi} &= I_0 - \cos \delta \varphi (\sin \Phi + 2\kappa \sin \delta \varphi).
\end{align*}

(6)

From the second equation, one readily finds that the fast flow cannot possess any fixed points on the synchronization manifold $\delta \varphi$ because $I_0 > 1$, such that the stationary solutions derive only from the condition $\cos \Phi = 0$. A numerical analysis shows that, depending on $\kappa$, the fast flow for $I_0 \gtrsim 1$ can exhibit two or no fixed points. For the particular value $I_0 = 1.05$, one finds that two fixed points, namely a saddle and a center, exist within the interval $\kappa \in [-0.1674, 0.1674]$. The appearance of a center point is associated to the time-reversal symmetry of the fast flow (5). Indeed, one may show that the fast flow is...
FIG. 6. Typical dynamics of the fast flow for $I_0 = 1.05$ below ($\kappa = -0.8$) and above the saddle-center bifurcation ($\kappa = -0.08$) are illustrated in (a) and (b), respectively. In (a), the system possesses two unstable fixed points, a saddle (SP) and a center (CP), and exhibits three types of closed orbits: a limit cycle attractor (orange), homoclinic connections to SP (blue and green), and subthreshold oscillations around the center (purple). In (b), the system exhibits bistability between two oscillatory states, shown in orange and blue.

invariant to a symmetry-preserving map $R$ of the form

$$R = \begin{cases} 
\varphi_1 \to \pi - \varphi_2, \\
\varphi_2 \to \pi - \varphi_1, \\
t \to -t
\end{cases} \quad (7)$$

Note that in case of the finite scale separation, the counterpart of the center point of the fast flow is a weakly unstable focus of the complete system.

The structure of the fast flow is organized around the saddle-center bifurcation, which occurs at $\kappa = \kappa_{SC} = -0.1674$. Here, the two fixed points get annihilated as a homoclinic orbit associated to the saddle collapses onto the center. To gain a complete picture of the dynamics of the fast flow, we have shown in Figures 6(a) and 6(b) the illustrative examples of the phase portraits and the associated vector fields for $\kappa < \kappa_{SC}$ and $\kappa > \kappa_{SC}$, respectively. For $\kappa \in [-1, \kappa_{SC})$, the fast flow possesses a limit cycle attractor, essentially derived from the local dynamics of the units, cf. the orbit indicated in red in Fig. 6(a). Apart from an attracting periodic orbit, one observes two additional types of closed orbits, namely the homoclinic connections to the saddle point (SP), shown by blue and green, as well as the periodic orbits around the center point (CP), an example of which is indicated in orange. For $\kappa > \kappa_{SC}$, the fast flow exhibits bistability between two oscillatory solutions, such that there is a coexistence of a limit cycle inherited from the local dynamics of units, and the limit cycle associated to the former homoclinic orbits, cf. Fig. 6(b).

In the presence of noise, the described attractors of the fast flow turn to metastable states. Nevertheless, in contrast to the case of two adaptively coupled excitable units, the slow stochastic fluctuations here do not involve only switching between the metastable states, but also comprise the subthreshold oscillations derived from the periodic orbits around the center point. These subthreshold oscillations provide for the trapping effect, which effectively leads to a reduced oscillation frequency. An example of the time series $\kappa_i(t)$ and $\varphi_i(t), i \in \{1, 2\}$ obtained for an intermediate $\varepsilon = 0.035$ in Fig. 7(a)-(b) indeed shows three characteristic episodes, including visits to two distinct oscillatory metastable states and an extended stay in the vicinity of the center, cf. the stochastic orbits $(\varphi_1(t), \varphi_2(t))$ and the vector field of the fast flow in Fig. 7(c). In the case of finite scale separation, the trapping effect is manifested as the noise-enhanced stability of an unstable fixed point. The prevalence of subthreshold oscillations changes with noise in a non-monotone fashion, becoming maximal around the resonant noise level where the frequency dependence on noise exhibits a minimum, cf. Fig. 8 and Fig. 9.

FIG. 7. (a) and (b) show the time traces of $\kappa_i(t)$ and $\varphi_i(t)$ corresponding to an episode where the system remains in vicinity of an unstable fixed point. The parameters are $I_0 = 1.05, \varepsilon = 0.035, \beta = \pi, D = 10^{-4}$. (c) The orbits corresponding to two metastable states associated to large-amplitude oscillations of the phase variables are shown in red and blue, while the subthreshold oscillations are indicated in green. Superimposed is the vector field of the fast flow, corresponding to the limit $\varepsilon \to 0$.

FIG. 8. Numerically estimated fraction of time spent in vicinity of the unstable fixed point $T_{up}/T_{tot}$ as a function of noise for $\varepsilon \in \{0.035, 0.06\}$. Note that the positions of the maxima coincide with the corresponding resonant noise levels from Fig. 5.
In terms of the robustness of the effect, the examples we presented concern coupled Type I units, whose local dynamics is close to a SNIPER bifurcation, be it in the excitable or the oscillatory regime. Nevertheless, the onset of ISR and the specific mechanisms of the phenomenon do not depend on the excitability class of local dynamics. In particular, we have recently demonstrated that a single Type II Fitzhugh-Nagumo oscillator shows the same type of non-monotone dependence on noise with the mechanism involving subthreshold oscillations that follow the maximal canard of an unstable focus. In that case, it has been established that the trapping effect and the related subthreshold oscillations are triggered due to a phase-sensitive excitability of a limit cycle. Moreover, we have verified that the same model of neuronal dynamics, set to different parameter regimes, may exhibit two different scenarios of ISR. In particular, by an appropriate selection of the system parameters, the Morris-Lecar neuron model

\[
\frac{dv}{dt} = -g_{fast}m(v)(v - E_{Na}) - g_{slow}W(v - E_{K}) - g_{leak}(v - E_{leak}) + I
\]

\[
\frac{dv}{dt} = \phi \frac{W_{\infty}(v) - W}{\tau(v)}
\]

\[
m(v) = 0.5[1 + \tanh \left(\frac{v - \beta_m}{\gamma_m}\right)]
\]

\[
W_{\infty}(v) = [1 + \tanh \left(\frac{v - \beta_w}{\gamma_w}\right)]
\]

\[
\tau(v) = \frac{1}{\cosh \left(\frac{v - \beta_w}{2\gamma_w}\right)}
\]

(8)

where \(v\) and \(W\) respectively denote the membrane potential and the slow recovery variable, can be placed in vicinity of a supercritical or a subcritical Hopf bifurcation with the external bias current \(I\) being the bifurcation parameter. In the first case, obtained for \(E_{Na} = 50\) mV, \(E_{K} = -100\) mV, \(E_{leak} = -70\) mV, \(g_{fast} = 20\) mS/cm\(^2\), \(g_{slow} = 20\) mS/cm\(^2\), \(g_{leak} = 2\) mS/cm\(^2\), \(\phi = 0.15\), \(C = 2\) µF/cm\(^2\), \(\beta_m = -1.2\) mV, \(\beta_w = -13\) mV, \(\gamma_m = 18\) mV, \(\gamma_w = 10\) mV, the model is monostable under the variation of \(I\), and the ISR is observed slightly above the Hopf bifurcation \((I = 43\mu A/cm^2)\) due to a noise-enhanced stability of an unstable fixed point, cf. Fig. 9(a)-(b). In the second case, conforming to the parameter set \(E_{Na} = 120\) mV, \(E_{K} = -84\) mV, \(E_{leak} = -60\) mV, \(g_{fast} = 4.4\) mS/cm\(^2\), \(g_{slow} = 8\) mS/cm\(^2\), \(g_{leak} = 2\) mS/cm\(^2\), \(\phi = 0.04\), \(C = 20\) µF/cm\(^2\), \(\beta_m = -1.2\) mV, \(\beta_w = 2\) mV, \(\gamma_m = 18\) mV, \(\gamma_w = 30\) mV, the model displays bistability between a limit cycle and a stable equilibrium in a range of \(I\) just below the Hopf threshold. There, ISR emerges due to a mechanism based on biased switching, see the bifurcation diagram \(V(I)\) in Fig. 9(c) and the dependence of the oscillation frequency on noise for \(I = 95\) µA/cm\(^2\) in Fig. 9(d).

Given that ISR has so far been observed at the level of models of individual neurons, the motifs of units with neuron-like dynamics and neuronal populations, it stands to reason that the phenomenon should be universal to neuronal dynamics, affecting both the emergent oscillations and systems of coupled oscillators. The explained

**III. DISCUSSION AND OUTLOOK**

Considering a model which involves the classical ingredients of neuronal dynamics, such as excitable behavior and coupling plasticity, we have demonstrated two paradigmatic scenarios for inverse stochastic resonance. By one scenario, the phenomenon arises in systems with multistable deterministic dynamics, where at least one of the attractors is a stable equilibrium. Due to the structure of the phase space, and in particular the position of the separatrices, the switching dynamics between the associated metastable states becomes biased at an intermediate noise level, such that the longevity of the quasi-stationary states substantially increases or they may even turn into absorbing states. In the other scenario, an oscillatory system possesses a weakly unstable fixed point, whose stability is enhanced due to the action of noise. The latter results in a trapping effect, such that the system exhibits subthreshold oscillations, whose prevalence is noise-dependent and is found to be maximal at the resonant noise level. Both the scenarios involve classical facilitatory effects of noise, such as crossing the separatrices or stochastic mixing across the bifurcation threshold, which should warrant the ubiquity of ISR.
mechanisms appear to be generic and should be expected in other systems comprised of units with local dynamics poised close to a bifurcation threshold. Inverse stochastic resonance should play important functional roles in neuronal systems, including the reduction of spiking frequency in the absence of neuromodulators, the triggering of stochastic bursting, i.e. of on-off tonic spiking activity, the suppression of pathologically long short-term memories, the generation of UP-DOWN states, characteristic for spontaneous and induced activity in cortical networks, and most notably, may contribute to generation of UP-DOWN states, characteristic for spontaneous and induced activity in cortical networks.

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