Theory for Inverse Stochastic Resonance in Nature

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The *inverse stochastic resonance* (ISR) phenomenon consists in an unexpected depression in the response of a system under external noise, e.g., as observed in the behavior of the mean-firing rate in some pacemaker neurons in the presence of moderate values of noise. A possible requirement for such behavior is the existence of a bistable regime in the behavior of these neurons. We here explore theoretically the possible emergence of this behavior in a general bistable system, and conclude on conditions the potential function which drives the dynamics must accomplish. We show that such an intriguing, and apparently widely observed, phenomenon ensues in the case of an asymmetric potential function when the high activity minimum state of the system is metastable with the largest basin of attraction and the low activity state is the global minimum with a smaller basin of attraction. We discuss on the relevance of such a picture to understand the ISR features and to predict its general appearance in other natural systems that share the requirements described here. Finally, we report another intriguing non-standard stochastic resonance in our system, which occurs in the absence of any weak signal input into the system and whose emergence can be explained, with the ISR, within our theoretical framework in this paper in terms of the shape of the potential function.

I. INTRODUCTION

Noise is ubiquitous in the real world, which has been a topic of significant interest in the field of science and engineering applications. Much effort have been devoted to understanding the source of noise and the emergence mechanisms of noise induced phenomena as well as their role in systems and devices. While noise was first considered to be something that should be filtered out or reduced, it is now widely accepted that noise can have a constructive role and enrich the stochastic dynamics of nonlinear systems [1-3]. A prominent example of this is stochastic resonance (SR) phenomenon in which the signal to noise ratio in a nonlinear system under the action of a weak input signal is maximized for a proper amount (not too small nor too large) of noise [4–8]. Under SR, a plot of the system response versus the ambient noise is bell shaped, indicating that the correlation between the weak signal and response is maximal around a moderate level of noise. A detailed dynamical analysis has revealed that the existence of SR in natural systems is due to the presence of kind of bistability on their driving dynamics characterized, for instance, by the existence of a potential function driving the dynamics with two minima separated by a finite energy barrier. This barrier can be overpassed – thus inducing jumps of the activity among the two minima – thanks to a strong driving force or an efficiently high level of noise. SR then occurs when, for very weak signals unable to jump, an optimal amount of noise induces jumps that are thus correlated with the weak signal [9].

The presence of such conditions of bistability during the activity of actual neurons has been widely depicted [10–12]. For instance, the pacemaker activity of the squid giant axon shows a pattern of switching on-off activity which depends on several features of a noisy input current and its fluctuations [11]. In this case, the authors illustrate a kind of bistability in which noise induces different types of neuron behavior, including repetitive firing, emergence of bursting and, even more intriguing, the complete quietness of neural activity. Following these interesting findings, a series of theoretical studies reported a new intriguing noise induced phenomenon in neural systems, in which a minimum – possibly zero – occurs in the average spiking activity of single neuron models for an optimal amount of noise [13–19]. Such a noise induced behavior has also recently been found in neuronal populations in biophysical realistic models with different network coupling schemes [20]. Following this, a *double in*verse stochastic resonance with two distinct minima has been reported in the response of a Hodgkin-Huxley model neuron that receives synaptic inputs subject to different types of short-term synaptic plasticity [21]. Since the dependence of the neuronal system response on the noise is the opposite to that in the SR mechanism, by analogy, this phenomenon has been named "inverse stochastic resonance" (ISR). These previous studies have stated that co-existence of a stable resting equilibrium and a stable spiking limit cycle during the model neuron dynamics is the key factor for the emergence of interesting noise induced effects. These theoretical findings have been complemented with the first experimental evidence for ISR in an *in vitro* preperation of cerebral purkinje cells [22]. The authors show in this work that ISR allows the Purkinje cells to operate in different functional regimes depending on the variance of the neuronal noise: the all-or-none toggle or the linear filter mode in cerebral information

processing. Furthermore, ISR might also play a critical role in computational mechanisms that require reduced firing activity without chemical inhibitory neuromodulation or, alternatively, when other computational mechanisms require on-off bursts of activity. On the other hand, apart from neural systems, a recent experimental study reported the existence of ISR in nematic liquid crystals (NLC) [23]. This work shows that a proper arrangement of colored noise intensity and its correlation time constant induces ISR in an ac-driven electroconvection in NLC.

These observations compelled us to develop a general theory, which is presented in this paper, to explain the emergence of ISR in nature. Our model considers the existence of two local minima separated by an energy barrier for a potential function driving the activity of a natural system, one corresponding to a low activity state, or Down state, and the other corresponding to a high activity state, that is the Up state. In addition, we assume that the low activity state is the global minimum of the dynamics but it has a narrower basin of attraction. On the other hand, the high activity state is a metastable state but with a large basin of attraction. Note that these requirements in our model impede in practice to observe ISR in pure bistable systems with the two minima having their basins of attraction with the same depth and size. It thus follows that ISR can only appear in natural systems with metastable states.

II. MODEL AND METHOD

Consider, for simplicity, a one dimensional dynamical system whose activity or state is described by a variable x(t) (representing neural population activity, cell membrane voltage, chemical ion concentration, etc) which follows the dynamics

$$\frac{dx}{dt} = -\frac{\partial\varphi(x)}{\partial x} \tag{1}$$

where the potential function is given, for instance, by

$$\varphi(x) = a \arctan \left[b \left(x + x_0 \right) \right] + c \left(x + x_0 \right)^2 + d \left(x + x_0 \right),$$
(2)

which is a particular case of a class of familiar models for chemical kinetics [24–26]. This, which yields

$$\frac{dx}{dt} = -\frac{ab}{1+b^2 (x+x_0)^2} - 2c (x+x_0) - d, \qquad (3)$$

produces, for the indicated set of parameter values, the shape asymmetry of the local minima depicted in figure 1. This potential function depicts two locally stable minima separated by a local maximum x_m , being x_1 the low activity one or Down state, and x_2 being the high activity state or Up state, in such a way that $x_1 < x_m < x_2$. We use this particular potential since it is easy to tune between different shapes for it by changing the value of a



Figure 1. (a) Bistable potential $\varphi(x)$ with asymmetric basin of attractions defined in equation (2). Parameters are a =3.367, b = 2, c = 0.5, d = -3.357, and $x_0 = -2$. (b) The same potential $\varphi(x, c)$ for $c \in (0.3, 1)$ depicting transitions of the stability of the local minima as a function of the parameter c. Lines here correspond to c = 0.35 (purple), c = 0.5 (red, the case illustrated in panel A corresponding to an asymmetric bistable potential) and c = 0.8 (black).

few parameters, as it is depicted in figure 1(b), including the case of symmetric bistable potentials and asymmetric ones.

We are going to consider in the following the behavior of this system under the action of a source of noise, i.e., the unidimensional Langevin equation:

$$\frac{dx}{dt} = -\frac{\partial\varphi(x)}{\partial x} + \eta(t). \tag{4}$$

We assume here that the noise has the form of an additive Gaussian term, $\eta(t)$ with zero mean, $\langle \eta(t) \rangle = 0$, and autocorrelation, $\langle \eta(t)\eta(t') \rangle = 2D\delta(t-t')$.

A. Limit of small noise

Let us first consider the behavior of the system under the action of a small noise. In addition, we assume a nonbistable potential with two minima of different depth, one being the global minimum of the dynamics and the other a metastable state. First, in the absence of noise, after averaging over a number of trials with random initial conditions $x_0 \in (a, b)$, one has in the steady state that

$$\langle x \rangle = x_1 p (x_0 < x_m) + x_2 p (x_0 > x_m).$$
 (5)

Here, $p(x_0) = (b-a)^{-1}$ is the uniform distribution of random initial conditions. It then follows that

$$p(x_0 < x_m) = \frac{x_m - a}{b - a}, \quad p(x_0 > x_m) = \frac{b - x_m}{b - a}.$$
 (6)

Consider next the system in the presence of a weak noise, in such a way that, if its state at a given time is in the basin of attraction of the metastable state (Up state), it has a probability of escape during a time interval dt equal to $p_e = dt/\langle t_e \rangle$. The denominator here is the average escape time from that local minimum, i.e., the inverse of the Kramer's escape rate probability,

$$r_{K,2} = \frac{1}{2\pi} \left[\varphi''(x_2) \left| \varphi''(x_m) \right| \right]^{1/2} \exp\left(-\Delta \varphi_2 / D\right), \quad (7)$$

from the high activity x_2 to the low activity x_1 values of the minimum. $\Delta \varphi_2 \equiv \varphi(x_m) - \varphi(x_2)$ is the potential barrier the state of the system has to overpass (see for instance [27]) to escape from the metastable state. Similarly, if the state of the system is around the low value minimum x_1 it can jump to the high-value minimum x_2 with rate probability

$$r_{K,1} = \frac{1}{2\pi} \left[\varphi''(x_1) \left| \varphi''(x_m) \right| \right]^{1/2} \exp\left(-\Delta \varphi_1 / D\right), \quad (8)$$

where $\Delta \varphi_1 \equiv \varphi(x_m) - \varphi(x_1)$ is the potential barrier that the state of the system has to overpass now starting around the minimum x_1 . The expressions (7) and (8) are only valid when noise fluctuations are small so that $\Delta \varphi \gg D$ [27].

Consider now that, at given time t, the state of the system has a probability $p(x_t < x_m) \equiv \alpha_t$ to be around the minimum at x_1 , and a probability $p(x_t > x_m) \equiv \beta_t$ to be around the minimum at x_2 , with $\alpha_t + \beta_t = 1 \forall t$. Then, it follows that $\alpha_0 = p(x_0 < x_m)$ and $\beta_0 = p(x_0 > x_m)$. One may now assume that both α_t and β_t evolve in time according to the equations $\frac{d\alpha_t}{dt} = r_{K,2}\beta_t - r_{K,1}\alpha_t$ and $\frac{d\beta_t}{dt} = r_{K,1}\alpha_t - r_{K,2}\beta_t$ due to possible escapes from one minimum to the other and vice versa. Then, one can easily solve the previous system of equations to obtain

$$\alpha_t = [r_{K,2} - (r_{K,2} - \lambda\alpha_0)e^{-\lambda t}]/\lambda$$

$$\beta_t = [r_{K,1} - (r_{K,1} - \lambda\beta_0)e^{-\lambda t}]/\lambda$$
(9)

where $\lambda = r_{K,1} + r_{K,2}$. We may compute the mean state or activity of the system at each time t, which is approximately

$$\langle x \rangle_t \approx x_1 \alpha_t + x_2 \beta_t. \tag{10}$$

At t = 0, one has that $\langle x \rangle_0 \approx x_1 \alpha_0 + x_2 \beta_0$, which coincides with (5). On the other hand, the steady state of (9) is $\alpha_{\infty} = \frac{r_{K,2}}{r_{K,1}+r_{K,2}} = p(x_{\infty} < x_m), \ \beta_{\infty} = \frac{r_{K,1}}{r_{K,1}+r_{K,2}} = p(x_{\infty} > x_m)$ which are the probability of the system to be in a state around the minimum x_1 and x_2 respectively in the steady state.

B. The limit of high noise

Alternatively, in the presence of a noise high enough to overpass the potential barrier, we can perform a different derivation to compute the mean activity of the system in the steady sate. Starting with the Langevin description (4), x(t) is a random variable with probability distribution P(x, t) that obeys the Fokker-Planck equation [28]

$$\frac{dP(x,t)}{dt} = -\frac{\partial}{\partial x}A(x)P(x,t) + D\frac{\partial^2}{\partial x^2}P(x,t).$$
 (11)

with $A(x) = -\frac{\partial \varphi(x)}{\partial x}$. The steady-state solution $P_{\infty}(x) = \lim_{t \to \infty} P(x, t)$ to this equilibrium is known to be [28]

$$P_{\infty}(x) = N e^{-\varphi(x)/D}, \qquad (12)$$

where $N = \left[\int e^{-\varphi(x)/D} dx\right]^{-1}$ is a normalization factor. We can then compute the average of $\langle x \rangle$ using such probability distribution and write it as a function of the potential parameters and the noise level D, that is,

$$\langle x \rangle = \int_{\mathbb{R}} x P_{\infty}(x) = \frac{\int_{\mathbb{R}} x e^{-\varphi(x)/D} dx}{\int_{\mathbb{R}} e^{-\varphi(x)/D} dx}.$$
 (13)

III. RESULTS

A. Inverse stochastic resonance

Within the above model one may easily understand the shape and features of the ISR curves previously reported in the literature. Figure 2 shows the level of agreement with the ISR curves computed in simulations of the Langevin equation (4) for different values of the potential parameter c (open circles), compared with the value of $\langle x \rangle$ computed with the low-noise Kramer's approximation from equation (2) and depicted in panel (a) (solid lines). The high-noise equilibrium theory using expression (13) is shown in panel (b) (solid lines) also compared with simulations of the Langevin equation (open circles). This shows that the Kramer's escape theory reproduces very well the behavior of the ISR curve for low noise while fails for large noise. The agreement for very low noise is due to the fact that in this case the noise fluctuations cannot overpass the potential barrier in finite time, so that the observed mean activity at zero noise is just the result of an initial condition effect, and it can be computed through the probabilities that the state of the system initially falls in any of the basin of attractions of each minimum. That is, the zero noise mean activity can be computed through the expression (5). Note that, in this case the asymmetry between minima in the potential function is what induces the zero noise level of the ISR curve to be higher or lower. In fact, if the basin of attraction of the low activity minimum is too narrow, then $p(x_0 < x_m) \ll p(x_0 > x_m)$ and therefore $\langle x \rangle \approx x_2$. On the other hand, if the highactivity minimum has a very narrow basin of attraction,



Figure 2. (a) ISR curves obtained in simulations (open circles) compared with the theory for low noise based in our Kramer's type theory (solid lines), for different values of the potential function parameter c. (b) ISR curves obtained in simulations (open circles) compared with the equilibrium theory for high noise (solid lines), also for different values of the potential function parameter c. Other model parameters as in figure 1.

then $p(x_0 < x_m) \ll p(x_0 > x_m)$ and therefore $\langle x \rangle \approx x_1$, which will impede the appearance of ISR, since there is not a raising of the ISR curve toward a higher value for very low noise.

When the noise increases but still remaining small. then there is a non-zero probability, according with the Kramer's theory, that the state of the system being initially in the basin of attraction of the high-activity minimum could overpass the potential barrier due to noise fluctuations and fall into the basin of attraction of the low activity minimum. In this case, to reproduce the lowering of the level of $\langle x \rangle$ for such noise levels, it is also important that the low-activity minimum is deeper than the high-activity one, in such a way that, for the same level of noise fluctuations, is easy for the state of the system to overpass the potential barrier from the high to the low activity minimum and harder the opposite. In such conditions, system states being initially around x_2 could be trapped around x_1 and, therefore, the $\langle x \rangle$ decreases as simulations of ISR depict. Note that for this small

non-zero level of noise fluctuations, the behavior of $\langle x \rangle$ is mainly determined by the rate probabilities for escaping from the potential minima, and it can be computed through expression (10). In this case, the asymmetry of the potential with reference to the depth of the minima is what determines the behavior of $\langle x \rangle$ as a function of the fluctuations intensity. In fact, such asymmetry implies that $r_{K,2} \gg r_{K,1}$ and therefore $\alpha_t \gg \beta_t$, which makes $\langle x \rangle$ to reach a minimum value, that is, the minimum of the ISR curve.

For increasing values of the noise level, the expression (10) can approximately explain the rising of $\langle x \rangle$ from the minimum of the ISR curves since the probability to be trapped in the low-activity minimum decreases. This occurs due to the fact that escapes from such low-activity minimum to the high-activity one can also occur, so both $r_{K,1}$ and $r_{K,2}$ increase and therefore β_t also increases and become comparable with α_t . However, for large values of noise such tendency fails. This is because the non-validity of the Kramer's theory which is based on the assumption of non-negligible small current probability through the potential barrier between the two minima, and for large noise such current probability is negligible due to large size stochastic jumps ($\Delta \varphi \ll D$). In such a case, we can consider that the system quickly reaches an equilibrium condition where the state of the system is randomly exploring its entire phase space. We then need to compute the steady-state probability $P_{\infty}(x)$ to evaluate $\langle x \rangle$ using the expression (13). Figure 2(b) clearly illustrates that such equilibrium theory can exactly reproduce the shape of the ISR curves for large noise values and any value of the potential parameter c. However, the equilibrium theory incorrectly predicts, for low noise values the lower value for the mean activity of the system $\langle x \rangle \approx x_1$. The reason is that such minimum x_1 corresponds to the global minimum of the dynamics and in steady-state conditions the system is in equilibrium around such minimum. However, the equilibrium theory does not account for the possibility that, for small noise and for some initial conditions, the state of the system can be trapped during a long time (that increases as the noise fluctuations decrease) around the metastable high-activity minimum, which is the responsible for the rising of $\langle x \rangle$ for small noise in the ISR curve in simulations.

One can account for both theoretical results – that is the small noise and high noise previous theories – assuming that there is a validity crossover between both theories. Therefore, one can assume for all levels of noise that the mean activity of the the system is given by

$$\langle x \rangle = \langle x \rangle_L [1 - \xi(D)] + \xi(D) \langle x \rangle_H \tag{14}$$

where the labels L and H indicate, respectively, the theories for low and high noise, and $\xi(D) = \frac{1}{2} + \frac{1}{2} \tanh[10(D-D_0)]$. This is function of noise such that, for $D > D_0$, $\xi(D) \approx 1$ indicating that the high noise theory becomes the important one while for $D < D_0$, $\xi(D) \approx 0$ so that the low-noise theory is the important one. Figure 3 depicts the behavior of $\langle x \rangle$ as a function of



Figure 3. Emerge of ISR in an asymmetric non bistable potential. Lines corresponds to the theory in this paper and open circles correspond to simulations of the Langevin equation (4) for several values of the parameter c controlling the deep and asymmetry of the potential function $\varphi(x)$. In all cases $D_0 = 0.15$. Other model parameters as in figure 1.

noise level D as given by the expression (14). This shows good agreement between the full theory (solid lines) and simulations of the Langevin equation (4) for different values of the potential parameter c. The figure also clearly depicts that only for c > 0.5 ISR emerges. This corresponds to situations in which the system is not bistable and the low activity minimum becomes the global minimum of the dynamics with the high activity one becoming a metastable state. For $c \leq 0.5$, the ISR behavior is lost since the global minimum is the high activity one while the low activity minimum becomes a metastable state in such a way that, for any value of the noise, the probability of the state of system to be around such minimum is very low and, therefore, $\langle x \rangle$ becomes large for all values of D.

B. Non-standard stochastic resonance or noise induced activity amplification

Our theory also predicts a non-standard stochastic resonance (NSSR) in our system, that is, the mean activity $\langle x \rangle$ may present a maximum as a function of noise level even in the absence of a weak signal in the right-hand side of equation (4). The only requirement for this is to have dynamics (4), as before, with a potential function with two minima, but now with the low-activity one being the metastable state and with the larger basin of attraction and the high activity one being the global minimum of the dynamics with a narrower basin of attraction, as depicted in figure 4(a). The resulting behavior of $\langle x \rangle$ as a function of noise parameter D is depicted in figure 4(b), where a maximum in the mean activity is observed at intermediate values of the noise parameter. This is quite similar to the typical stochastic resonance curves widely reported in the literature. Note, however, that the mech-



Figure 4. Emergence of noise induced activity amplification or non-standard stochastic resonance. (a) This shows the asymmetric potential $\varphi(x)$ with two minima with different depth and size of the basin of attraction for each minimum. Here, the low activity minimum is a metastable sate with a large basin of attraction, and the high activity one is the global minimum of the dynamics and has a small basin of attraction. Potential function parameters are a = 4.367, b = -1.28, c = 0.327, d = 2.79 and $x_0 = -5.78$. (b) Behavior of the $\langle x \rangle$ as a function of the noise parameter D, for the case of the potential function illustrated in panel A. The graph depicts an amplification of the observed mean activity for intermediate values of the noise parameter, which resembles stochastic resonance. In this case $D_0 = 0.15$. The solid line corresponds to our theory and data points (open circles) to simulations of the Langevin equation (4).

anism responsible for this behavior differs from that of the typical SR behavior, where there is enhancement of the correlation between the activity of a nonlinear system and a weak external input (see for instance [9]).

IV. FINAL DISCUSSION

In this paper, we present a simple and general theory to explain the emergence of ISR in a variety of natural situations. Our theory predicts that ISR will occur in any natural system whose dynamics can be interpreted as following from some potential function with two minima, one of them being metastable (the one corresponding to the higher activity) and the other being the global minimum (i.e., corresponding to the lowest activity). In addition, a requirement for the appearance of ISR is that the high activity minimum must have the larger basin of attraction while the low activity one must be the global minimum of the dynamics. We predict that any natural system that meets these requirements is a potential candidate in which ISR should perhaps be observed.

The theory presented here also predicts the existence of a non-standard stochastic resonance phenomenon if the global minimum of the dynamics corresponds to the higher activity one whereas the local or metastable minimum corresponds to the lower activity one. The resulting stochastic resonance is a non-standard one in the sense that the dynamics does not need a weak signal input to induce a maximum in the average activity of the system. In fact the observed maximum in the average activity does not indicate here a correlation between system input and output response. Thus, it can be considered as an activity amplification phenomenon induced by a

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proper arrangement of the noise. We predict that this type of non standard SR can emerge in any biological or other natural system that meets the basic requirements as explained above.

Summing up, due to the simplicity and the generality of the theory presented here, our study, firstly, can be easily extended to include other types of noise, e.g. colored noise, to analyze their influence on ISR features and, secondly, it can be useful to further explore the possible implications that both ISR or non-standard SR could have in the behavior of many different natural and physical systems.

V. ACKNOWLEDGMENTS

We acknowledge the Spanish Ministry for Science and the "Agencia Española de Investigación" (AEI) for financial support under grant FIS2017-84256-P (FEDER funds). We also thank fruitful comments from P. L. Garrido.

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