

## Antireliability of noise-driven neurons

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We demonstrate, within the framework of the FitzHugh-Nagumo model, that a firing neuron can respond to a noisy driving in a nonreliable manner: the same Gaussian white noise acting on identical neurons evokes different patterns of spikes. The effect is characterized via calculations of the Lyapunov exponent and the event synchronization correlations. We construct a theory that explains the antireliability as a combined effect of a high sensitivity to noise of some stages of the dynamics and nonisochronicity of oscillations. Geometrically, the antireliability is described by a random noninvertible one-dimensional map.

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Recently, the reliability property of spiking neurons has attracted great attention [1]. The effect appears as a coincidence of responses of a single neuron subject to repeatedly applied weak input fluctuations. A similar property has been referred to in recent experiments with a noise-driven neodymium-doped yttrium aluminum garnet (Nd:YAG) laser [2] as consistency. From the theoretical viewpoint, reliability and consistency are manifestations of the synchronization of nonlinear systems by common noisy driving [3–8]. Indeed, the usual protocol in a reliability experiment, when a particular fluctuating wave form is repeatedly used to force a neuron, is equivalent to the driving of an ensemble of identical neurons by a common fluctuating force. The intrinsic noise is a source of nonidentity, and may lead to nonperfect reliability.

Reliability means that the response of a nonlinear system to the fluctuating forcing is stable. Quantitatively, this stability is measured by the largest Lyapunov exponent (LE) in the presence of noise. For a limit cycle in a smooth dynamical system one can show that a small noise results in a negative LE, thus leading to synchronization and reliability [3,5,6]. A larger noise can, however, result in a positive LE [3,9,8,7] (a positive exponent was also reported for a nonsmooth system in [5]).

In this paper we demonstrate an *antireliability*, i.e., a transition to a positive LE, for a realistic model of a neuron in an excitable state. We show that a FitzHugh-Nagumo (FHN) neuron responds to a fluctuating forcing of a certain intensity in a nonreliable manner, while reliability is observed for very small and very large intensities of the driving noise. Furthermore, we develop an analytical approach, allowing us to calculate the LE for moderate noise amplitudes. We explain the transition to antireliability geometrically as a chaotic transition due to random stretchings and foldings of the phase mapping.

The basic model we use to describe a spiking neuron is the FHN system [10]:

$$\dot{v} = \varepsilon^{-1}[(3 - v^2)v - w] + \xi(t), \quad \dot{w} = v - v_0, \quad (1)$$

where  $\varepsilon$  is a small parameter (below in the numerical simulations we fix  $\varepsilon=0.05$ ), and  $\xi(t)$  is a white Gaussian noise:  $\langle \xi(t)\xi(t') \rangle = 2\sigma^2 \delta(t')$ . For  $v_0 < -1$  the only attractor in the

noiseless system is a stable fixed point, i.e., the system is in the excitable regime, and the LE is negative. For  $v_0 > -1$  this fixed point becomes unstable, and a stable limit cycle appears. In this state of periodic spiking the LE vanishes. Due to the smallness of the parameter  $\varepsilon$  the oscillation transition is very sharp, and already for  $v_0 > -1 + O(\varepsilon^{1/2})$  the cycle takes a form characteristic for relaxation oscillations, not depending on  $v_0$ .

In the vicinity of the transition value  $v_0 \lesssim -1$  the system is mostly sensitive to external noise which evokes a spike train. The latter can be more or less regular, but here we focus on the stability properties of the dynamics, and characterize them in Fig. 1 with the largest LE. One can see that the region of moderate noise intensities, where the LE is positive, exists both when the dynamics is excitable ( $v_0 < -1$  and the LE is negative for vanishing noise) and when the system is oscillating ( $v_0 \gtrsim -1$  and the LE vanishes for vanishing noise). Only outside the vicinity of the transition (for  $|v_0 + 1| \gtrsim 0.005$ ) does the LE remain negative for all  $\sigma$ .

We denote the regime with positive LE as an antireliable one, and illustrate it in Fig. 2. Here the same realization of noise drives ten uncoupled identical neurons. While for  $\lambda < 0$  a perfect synchrony of spikes is observed, for  $\lambda > 0$  one can see an alternation between the epochs of asynchro-

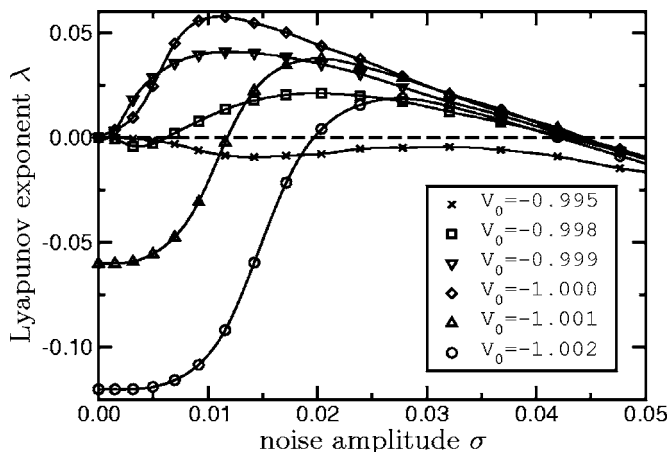


FIG. 1. The Lyapunov exponent vs the noise amplitude for the FHN system (1) for different values of  $v_0$ .

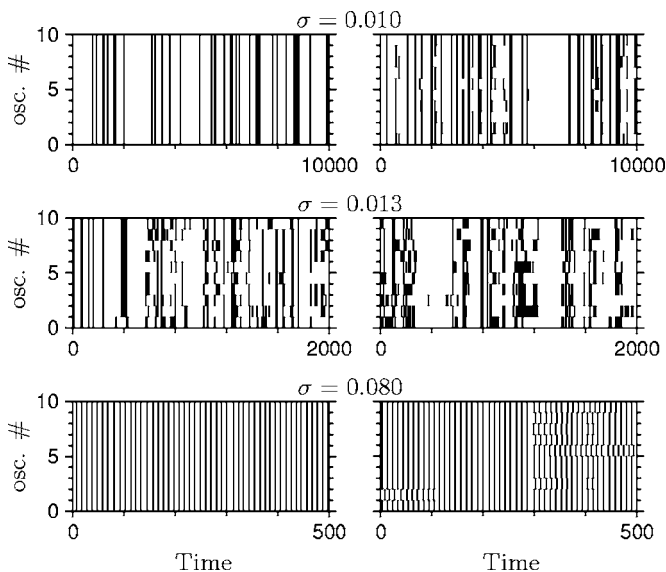


FIG. 2. Samples of firing patterns for the ensemble of ten neurons (1) driven by common noise. Each spike is depicted as a short vertical stripe, so a long vertical stripe corresponds to a synchronous, reliable firing. Left column, the neurons are perfectly identical; right column, there is small intrinsic noise with amplitude  $\sigma_{\text{int}}=5 \times 10^{-5}$ . For  $\sigma=0.01$  and  $0.08$ , the LE is negative (reliability); for  $\sigma=0.013$  the LE is positive (antireliability).

nous and relatively synchronous behavior. The latter epochs, which look in the middle row of Fig. 2 like vertical stripes, are in fact not perfectly synchronous, but slightly different in the spike timings ( $\Delta t_i \approx 0.01-0.1$ ). We will give an explanation for this intermittency below.

In real situations, the perfect synchrony (for  $\lambda < 0$ ) is distorted by small nonidentities in the oscillators or in the noisy driving (e.g., by an additional noise specific for each oscillator; in the context of neuron reliability one speaks of intrinsic noise). We illustrate this imperfect synchrony in Fig. 2, right column.

Figure 2 provides a qualitative frame for observations of antireliability in experiments, because there typically the same protocol as above and the same representation of data is used. To characterize the reliability and antireliability quantitatively, we adopt the event synchronization approach [11]. For the observed sequence of spikes, one can introduce the “reduction” function  $x^\tau(t) = c \sum_{j=1}^M [\Theta(t-t_j) - \Theta(t-t_j-\tau)]$ , where  $\Theta$  is the Heaviside function,  $t_j$  is the time of the  $j$ th firing event, and  $c$  is a normalization constant defined by  $\langle x^\tau \rangle = 1$ . The synchrony of firing events for two systems with the reduction functions  $x^\tau(t)$  and  $y^\tau(t)$  can be quantified by the event synchronization correlation function

$C_{xy}^\tau(t') = \langle x^\tau(t)y^\tau(t+t') \rangle$ . In the case of a perfect event synchrony,

$$C_{xy}^\tau(t) = \begin{cases} 1 - |t/\tau|, & |t| < \tau, \\ 0, & |t| \geq \tau. \end{cases} \quad (2)$$

We present the calculations of the event synchronization in Fig. 3. In Fig. 3(a) identical neurons are considered. One can see that the regions of perfect event synchrony [ $C^\tau(0)=1$ ] coincide with the ones of negative LE in Fig. 1. For regions of antireliability ( $\lambda > 0$ ), the event correlation function  $C^\tau(0)$  is small, but does not vanish: this is due to the intermittent synchronous epochs seen in Fig. 2. The persistence of synchrony against the intrinsic noise nonidentity may be estimated from Fig. 3(b).

We now turn to an analytical description of the effect and to revealing its mechanism. First, we give a general argument that a positive LE cannot be explained within the one-dimensional phase approximation [12] to the oscillation dynamics (a statistical evidence of this fact has been presented in [5,6]). Indeed, a time-continuous evolution of the phase (and of any one-dimensional variable) under arbitrary forcing on a finite time interval can be reduced to a monotonic transformation of the phase. Because an attracting set of a monotonic transformation has a negative LE, a positive LE is excluded. Therefore, we have to go beyond the usual one-dimensional phase approximation for the dynamics of perturbed oscillatory systems. This makes the problem non-trivial, because in higher dimensions one cannot obtain the LE by a plain averaging. For simplicity, we assume that the noise-free system is periodic, and model the two-dimensional perturbed dynamics with the system

$$\dot{\varphi} = \omega + a(\varphi)r, \quad \dot{r} = -\gamma(\varphi)r + f(\varphi)\xi(t). \quad (3)$$

Here  $\varphi$  is the oscillation phase and  $r$  is a transversal deviation from the limit cycle (hereafter referred as an amplitude), and  $\omega = 2\pi/T$  is the oscillation frequency. We have introduced three functions:  $a(\varphi)$  describes the nonisochronicity of the system,  $\gamma(\varphi)$  is the relaxation rate of the amplitude perturbations, and  $f(\varphi)$  is the sensitivity to noise; all these functions of  $\varphi$  are  $2\pi$  periodic. We have omitted noise in the equation for the phase because of its (already mentioned) purely stabilizing effect.

For a relatively small noise the dynamics is close to the limit cycle, on which, at the noiseless limit,  $\varphi(t) = \varphi_0(t) = \varphi(0) + \omega t$  and  $r(t) = 0$ . The infinitesimally small perturbations obey linearized equations which, to the main order with respect to noise, take the form

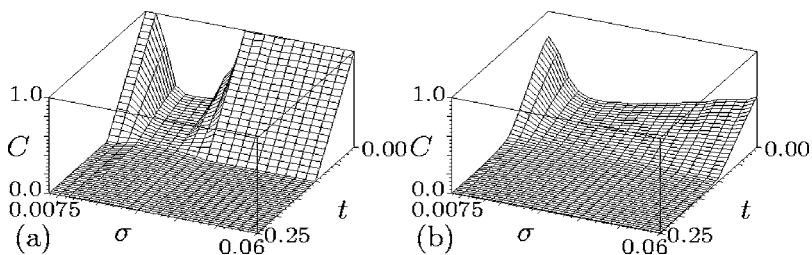


FIG. 3. The correlation function  $C_{xy}^\tau(t)$  for two FHN systems driven by (a) identical, and (b) nonidentical noise signals, with the intrinsic noise of amplitude  $\sigma_{\text{int}}=5 \times 10^{-5}$ . Parameters  $v_0=-1.001$ ,  $\tau=0.1$ .

$$\delta\dot{\varphi} = a(\varphi_0)\delta r, \quad \delta\dot{r} = -\gamma(\varphi_0)\delta r + f'(\varphi_0)\xi(t)\delta\varphi. \quad (4)$$

We now make two assumptions that are typically valid for the spiky systems under consideration. First, let us suppose that the system is especially sensitive to noise on some short part of the limit cycle near  $\varphi = \Phi$ , and neglect the effect of noise for the rest of the cycle. This means that  $f'(\varphi_0)$  is nonzero only in some interval  $[\varphi^-, \varphi^+] \ni \Phi$ . For the FHN system with  $v_0 \approx -1$  this is exactly the region near the tip of the slow branch  $v = -1$ ,  $w = -2$ . Here the trajectory slowly passes close to the unstable steady state and is highly sensitive to perturbations. The next assumption is that the relaxation rate  $\gamma$  is large at least on some pieces of the limit cycle. For the FHN system this is ensured due to the separation of slow and fast motions.

As a result of these two assumptions, we can separate the dynamics of perturbations into two stages: (i) a noise-induced excitation in the vicinity of  $\Phi$ , and (ii) a relaxation. Prior to stage (i) we take a phase perturbation, i.e.,  $\delta r = 0$ ,  $\delta\varphi = \delta\varphi_0$ . During the excitation we can neglect all terms in (4) except the noisy one, which yields a perturbation in the amplitude

$$\delta r_0 = S\delta\varphi_0, \quad S = \int_{\varphi^-}^{\varphi^+/\omega} f'(\omega t)\xi(t)dt.$$

As  $\xi(t)$  is a Gaussian white noise,  $S$  is a Gaussian random variable with zero average and variance

$$\langle S^2 \rangle = \frac{2\sigma^2}{\omega} \int_{\varphi^-}^{\varphi^+} [f'(\varphi)]^2 d\varphi.$$

The next, relaxation stage, where the effect of noise can be neglected, starts with the perturbation  $\delta r_0$ ,  $\delta\varphi_0$  at the time  $t_0$ . According to Eqs. (4)

$$\delta r(t) = \delta r_0 \exp\left(-\int_{t_0}^t \gamma(\omega t')dt'\right) \approx \delta r_0 e^{-\gamma(\Phi)(t-t_0)},$$

$$\begin{aligned} \delta\varphi(t) &\approx \delta\varphi_0 + \delta r_0 \int_{t_0}^t a(\omega t') e^{-\gamma(\Phi)(t'-t_0)} dt' \\ &\approx \delta\varphi_0 + \delta r_0 \frac{a(\Phi)}{\gamma(\Phi)} (1 - e^{-\gamma(\Phi)(t-t_0)}). \end{aligned}$$

Thus, the amplitude relaxes to zero, and for the phase perturbation we obtain the mapping

$$\delta\varphi_{n+1} = \delta\varphi_n(1 + R), \quad (5)$$

where we have introduced the index  $n$  indicating repetitive passages through the noise-sensitive region. The quantity  $R = Sa(\Phi)/\gamma(\Phi)$  is a zero-mean Gaussian variable with the variance

$$V^2 = \frac{2\sigma^2 a^2(\Phi)}{\omega \gamma^2(\Phi)} \int_{\varphi^-}^{\varphi^+} [f'(\varphi)]^2 d\varphi. \quad (6)$$

The LE for the random mapping (5) is

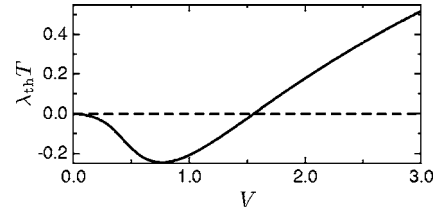


FIG. 4. The theoretical dependence  $\lambda_{\text{th}}(V)$ .

$$\lambda_{\text{th}} = T^{-1} \langle \ln|1 + R| \rangle = \frac{1}{\sqrt{2\pi TV}} \int_{-\infty}^{+\infty} \ln|1 + R| e^{-R^2/2V^2} dR. \quad (7)$$

In Fig. 4 we depict the dependence  $\lambda_{\text{th}}(V)$ . The LE changes sign at  $V \approx 1.5560$ , which corresponds to the onset of desynchronization and antireliability. According to formula (6),  $V$  is proportional to the amplitude of noise  $\sigma$ , to the sensitivity of the dynamics to the noise, which is proportional to  $[f'(\varphi)]^2$ , and to the nonisochronicity of the oscillations  $a$ , and inversely proportional to the relaxation rate  $\gamma$ .

Above we have assumed that the neuron is in the oscillating regime, and that there is no noise acting directly on the phase in (4). A violation of both these conditions leads to an additional contraction of the phase (which is, of course, much stronger for a neuron in an excitable state with small noise, because there the trajectory spends a lot of time in the vicinity of the stable fixed point). Thus, the resulting curve in Fig. 4 should be shifted down. It becomes then similar to the numerically observed dependencies of Fig. 1. The negative LE for very large noise intensities, observed in Fig. 1, cannot be explained by the theory above, as the underlying assumptions are not valid for strong noise.

We now compare the theoretical predictions with the numerics. To check the mapping for the phase perturbations (5), we fix a region on the branch of slow motions of the system near  $v_* \approx -\sqrt{3}$ ,  $w_* \approx 0$ . Here, due to the strong contraction of the fast variable  $v$ , only perturbations along the slow branch are present. We characterize these perturbations with their projection on coordinate  $v$ . In Fig. 5 we present the histograms of the derivatives  $dv_{n+1}/dv_n$  for pieces of trajectories starting at  $(v_*, w_*)$  and returning to its vicinity. These quantities, which are the multipliers for infinitesimal perturbations, according to the theory above correspond to the quan-

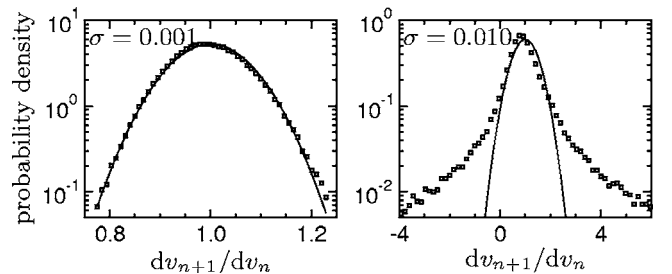


FIG. 5. Samples of the distribution of the derivatives  $dv_{n+1}/dv_n$  for the FHN system at  $v_0 = -0.998$ . The squares present results of numerical simulation, the solid line fits them with a Gaussian distribution.

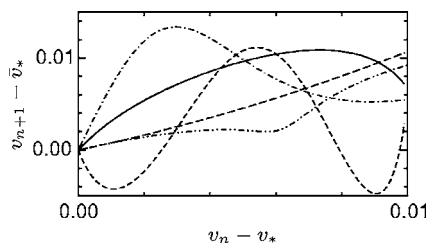


FIG. 6. Sample mappings  $v_n \rightarrow v_{n+1}$  for finite segments of the slow branch for  $v_0 = -0.998$ ,  $\sigma = 0.01$  (positive LE). The offset on the vertical axis is arbitrary.

ties  $1+R$  in Eq. (5). One can see that the distribution of these multipliers is nearly symmetric around  $dv_{n+1}/dv_n \approx 1$ . For small noise the Gaussian distribution fits very well, while for larger noise one observes “heavy tails” [ $\propto (dv_{n+1}/dv_n - 1)^{-2}$ ], which are presumably due to violations of the assumptions used in the derivation of (5).

In order to clarify the geometric nature of the transition to a positive LE, we have followed the evolution of finite but small segments of the slow branch, starting in the vicinity of  $(v_*, w_*)$ . All the points evolve under the same realization of noise for a fixed time interval  $\approx T$ . The resulting mappings of the segment are shown in Fig. 6. Of course, the mapping is random, therefore we have different realizations that depend on the noise wave form. The crucial point is that many of these mappings are not one to one. This reveals the geometrical mechanism of the production of chaos: during the evolution, the segments of the cycle are stretched and folded, so that the resulting mapping is nonmonotonic.

The distribution of multipliers Fig. 5 allows us also to explain the intermittent character of the antireliability. According to Eq. (5) and Fig. 5, there is a finite probability to observe a vanishing multiplier  $d\varphi_{n+1}/d\varphi_n$  (geometrically,

these events correspond to extrema of the random mapping Fig. 6). If such an event happens, the states of different identical neurons become very close to each other; thus they fire nearly simultaneously. Only after a certain number of cycles with large multipliers  $|d\varphi_{n+1}/d\varphi_n| > 1$  do the close states diverge, and the difference in the responses of identical neurons to the common noise becomes visible.

Summarizing, we have shown, within the framework of the noise-driven FitzHugh-Nagumo model, that identical neurons can respond antireliably to the noisy driving. Antireliability, which manifests itself as a noncorrelation of spikes, is observed when the neurons are close to the transition excitability-oscillations, where the dynamics is mostly sensitive to perturbations. Quantitatively, the antireliability is characterized as a state with a positive largest Lyapunov exponent. The latter is purely noise induced, as the noiseless FitzHugh-Nagumo system does not possess even a transient chaos. We explain the transition to antireliability within the approximate analytical theory for small noise-induced deviations from the deterministic trajectory, which goes beyond the one-dimensional phase approximation. This is crucial, because only due to transversal to trajectory perturbation, can the stretchings and foldings that lead to chaos, occur. The final formulas (6) and (7) give an explicit dependence of the LE on the physical properties of the neuron, such as nonisochronicity and sensitivity, thus guiding an experimental search for the effect. The theoretical expression for the random multiplier of phase deviations explains also the intermittent character of the antireliable state: during the epochs where the multiplier is close to zero, a temporarily synchronous firing of neurons is observed.

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