

## Self-exciting chaos as a dynamic model for irregular neural spiking

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We introduce a nonlinear dynamical system with self-exciting chaotic dynamics. Its interspike interval return map shows a noisy Poisson-like distribution. Spike sequences from different initial conditions are unrelated but possess the same mean frequency. In the presence of noisy perturbations, sequences started from different initial conditions synchronize. The features of the model are compared with experimental results for irregular spike sequences in neurons. Self-exciting chaos offers a mechanism for temporal coding of complex input signals.

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Irregular spike sequences are the foundation of neural information processing. They occur under at least three different situations. First, as spontaneous firing under nonperturbing constant external conditions (see, e.g., [1] for recordings from afferent neurons). Second, as irregular firing with a constant mean frequency in response to a constant external stimulation. Adrian [2] and countless subsequent studies (see, e.g., [3]) observed that in repeated experiments only this mean frequency is conserved, whereas the individual spike sequences appear unrelated (see [4] for a comparison of 25 sequences). This formed the basis for the hypothesis that the specific sequence of interspike intervals is irrelevant for neural information processing and that the relevant part of the information is encoded in the mean frequency of a single neuron's firing [5]. Third, irregular spike sequences occur in response to irregular perturbation of neurons. This fact by itself is not very surprising. However, in repeated experiments where the *identical* irregular perturbation is applied repeatedly neurons respond with the same irregular spike sequence [4]. This means that complex input functions increase the reliability of the response compared to a constant external perturbation.

Excitable chaotic systems have an aperiodically oscillating “basal state” and there is no constant threshold for an external perturbation to induce a spike. Rather, the minimal perturbation required to induce a spike depends on the phase of the basal chaos. Spatially extended excitable chaotic systems do not transport a single suprathreshold perturbation through the medium but require a minimal number of properly correlated perturbations to transport waves [6]. Together with the fact that two chaotic systems can be synchronized by applying identical noisy perturbations [7], these findings suggest that excitable chaos may provide a model for the irregular spiking of nerve cells. We demonstrate how this could account for the experimental observations.

We introduce a deterministic chaotic system that is not only excitable but also spontaneously generates irregular spike sequences. Due to its deterministic origin such a system is expected to differ dynamically from a system where an excitable fixed point is perturbed by noisy fluctuations, the standard assumption to explain spontaneous irregular activity of nerve cells (see, e.g., [8] for a discussion).

The following set of kinetic rate equations is considered:

$$\begin{aligned}\dot{X} &= a(X_0 - X) - r_1 \cdot r_2 \cdot r_3 - XY/(c_4 + X) - X, \\ \dot{Y} &= a(Y_0 - Y) - r_1 \cdot r_2 \cdot r_3 - XY/(c_4 + X), \\ \dot{Z} &= a(Z_0 - Z) + r_1 \cdot r_2 \cdot r_3 - c_9 Z, \\ \dot{W} &= a(W_0 - W) + XY/(c_4 + X),\end{aligned}\tag{1}$$

where

$$\begin{aligned}r_1 &= c_1 X / [c_2 + X^3 / (W^3 + 0.001)], \\ r_2 &= Y(1 + Y)^3 / [L / (1 + c_6 W) + (1 + Y)^4], \\ r_3 &= Z^4 / (c_7 + Z^6).\end{aligned}$$

This set of equations describes a reaction of variables  $X$  and  $Y$  yielding  $Z$  under the nonlinear regulation of effector  $W$ . Details can be found in [9]. In spite of its different origin the dynamics of the subsystem  $X$ ,  $Y$ , and  $Z$  shows qualitative similarities with the excitable Hodgkin-Huxley equations. For some sets of parameters the full system (1) possesses a spontaneously spiking chaotic attractor. The dynamics is composed of sections of high-frequency, small-amplitude “basal” chaos irregularly interrupted by large-amplitude spikes (Fig. 1). The attractor has one positive Lyapunov exponent (LCE).

Self-exciting chaos results from a global bifurcation of an excitable chaotic attractor. The bifurcation creates an escape region that allows the trajectory to leave the former chaotic attractor. The size of the escape region and the escape frequency depend on the distance of a relevant bifurcation parameter from the bifurcation point. If an external stimulation modifies this parameter the strength of the stimulation is coded in the mean frequency of the spiking. Spike sequences with different initial conditions are unrelated to each other even though the mean frequency is preserved.

Figure 2(a) shows the return map of interspike intervals (ISIs), i.e., the periods of time between two successive spike maxima which neglects the small chaotic oscillations. With the exception of the sharp border for small values of ISIs (indicating a finite minimal period within which no spike is induced) this return map is remarkably structureless. The density of points is highest near the origin and decreases

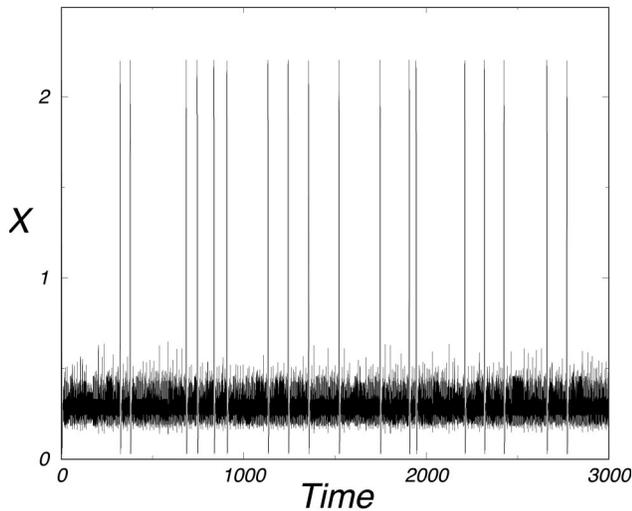


FIG. 1. Time series of spontaneous spiking from a chaotic basal state in Eq. (1). Parameters:  $a=0.675$ ,  $X_0=10.6$ ,  $Y_0=10.4$ ,  $Z_0=1.1611$ ,  $W_0=0$ ,  $c_1=33$ ,  $c_2=0.1$ ,  $c_4=0.1$ ,  $c_6=19$ ,  $c_7=0.1$ ,  $c_9=10$ , and  $L=80$ .

continuously with increasing interval length. In contrast, a return map from the maxima of the chaotic oscillations between spikes displays the one-dimensional fractal structure of chaos.

We studied the influence of noise added to all variables in Eq. (1). It was found that for increasing noise intensity the mean frequency of spikes increases. The sequence of ISIs remains irregular, however. Figure 2(b) is an ISI return map with added white noise. The plot shows a significant reduction of the ISI distribution compared to the unperturbed case. As in the unperturbed case, there is a sharp border for small ISI values. In addition, a pattern of orthogonal lines is discernible.

In order to verify correlations present in the ISI sequences we applied sensitive correlation measures from random matrix theory. The measure chosen is the nearest-neighbor spacing distribution  $P(s)$ , which is designed to detect any correlation in the temporal position of two adjacent events [10]. In order to calculate  $P(s)$  the sequence has to be unfolded to get rid of the smooth part of the spike density. Figure 3 displays the probabilities that a distance of length  $s$  occurs within the unfolded sequence. To obtain a realistic picture only 1000 events have been taken into account.

Figure 3(a) is the histogram for a spike sequence generated by Eq. (1) in the case of unperturbed self-exciting chaos [cf. Fig. 2(a)]. The histogram displays a probability hole for small time distances  $s$  reflecting the finite minimal period between two consecutive spikes. For distances  $s$  up to  $s \approx 1.2$  the histogram slightly overshoots the theoretical curve. In the asymptotic region  $s > 2$  the histogram is well-described by the theoretical curve of the Poisson distribution. We have confirmed that the match of the ISI analysis and the Poisson distribution is almost perfect for longer time series. Compare the excellent agreement with experimentally obtained histograms in [1,8].

Figure 3(b) shows the result for a time series with added white noise [cf. Fig. 2(b)]. In contrast to Fig. 3(a) the distribution now is accumulated around the mean event distance

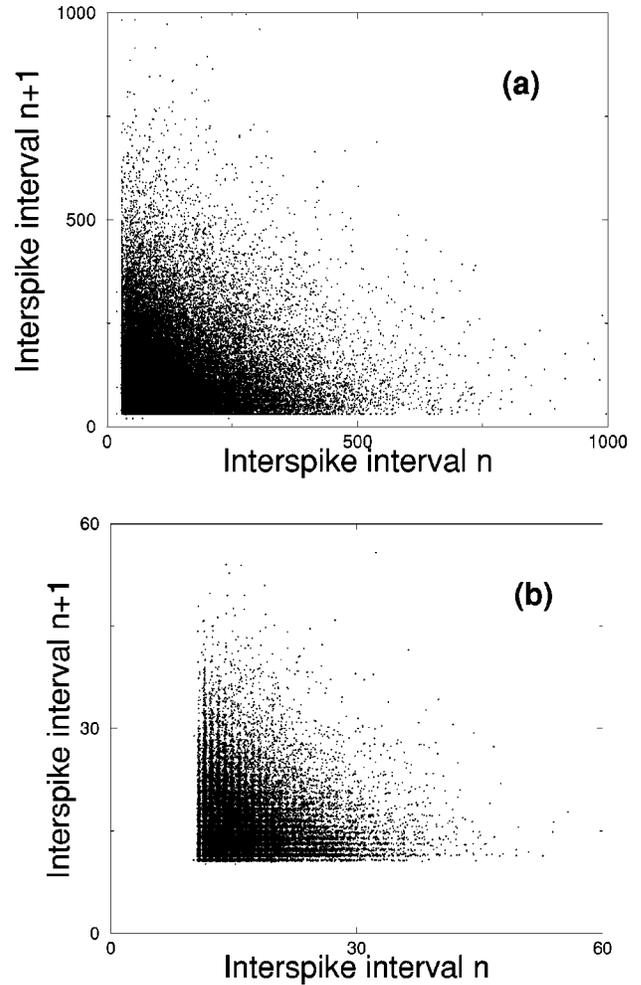


FIG. 2. Return map with 40 000 interspike intervals of large spikes in the system of Fig. 1. Only maxima larger than 1.5 were used to determine spike timing. (a) Without noise; (b) with noise added to all four variables (zero mean Gaussian noise, intensity 0.18).

$s=1$ . In this case the system possesses a distinct mean frequency for the occurrence of spikes. With high probability the interval between two adjacent spikes is close to 1 on the unfolded time scale. The probability to observe smaller or larger ISIs decreases rapidly to zero.

An important question in neural spiking is the repeatability of certain spike trains to a repeatedly applied non-constant perturbation [4]. If two simulations of Eq. (1) in the absence of any perturbation are run from different initial conditions, the spiking occurs at uncorrelated times due to the dependence of the chaotic trajectory on the choice of initial conditions. A plot of the differences in one variable between two such time series therefore continuously varies between limits given by  $+X_{max}$  and  $-X_{max}$  [Fig. 4(a)]. The small-amplitude oscillations are uncorrelated as well. The addition of Gaussian white noise changes this result dramatically. If two simulations are subject to the identical perturbation they produce irregular yet synchronized spike sequences [Fig. 4(b)]. There is an optimal value of noise amplitude for this synchronization to occur. The average duration of desynchronization between two signals decreases for small values of noise amplitude, then reaches a minimum

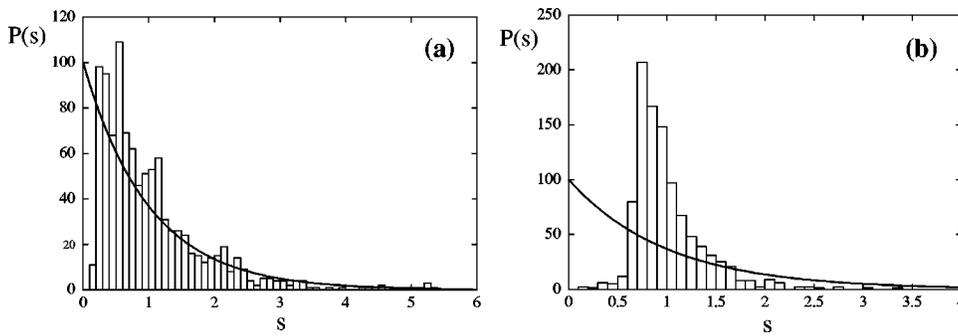


FIG. 3. Nearest-neighbor spacing distribution in Eq. (1). (a) Without noise; (b) with noise as in Fig. 2(b). Included is the analytical result for a Poisson distribution.

and decreases for large values. At the suboptimal value of noise intensity chosen in Fig. 4(b) the synchronization is not perfect. Occasionally a burst of desynchronized activity occurs after which the synchronization is recovered again. In purely deterministic simulations an increase in noise level [as compared to Fig. 4(b)] is sufficient to allow perfect synchronization for a long time. In the realistic situation where in addition to the identical perturbation an independent noise term of small mean amplitude is added (to mimic unavoidable experimental noise) synchronization is observed for a broad range in the intensity of the identical irregular perturbation.

A surprising feature of self-exciting chaos is the qualitative difference between an ISI return map and any return

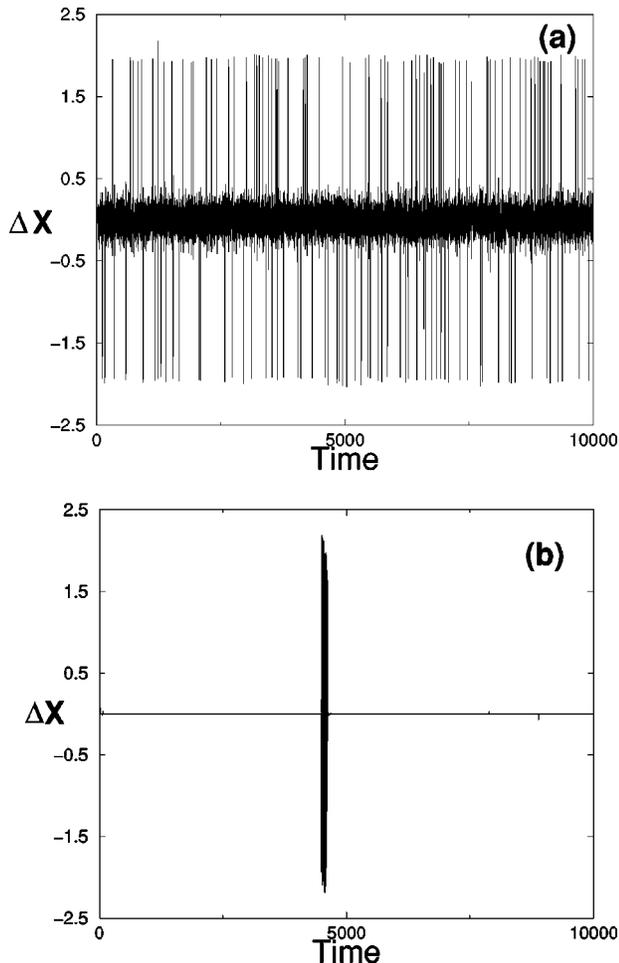


FIG. 4. Differences  $X_2 - X_1$  between two time series started with different sets of initial conditions in Eq. (1). (a) Without noise; (b) with noise as in Fig. 2(b).

map generated from the small-amplitude chaos. The ISI return map is structureless and appears high-dimensional even though it is generated from a low-dimensional chaotic attractor [Fig. 2(a)]. The reason for this is the loss of autocorrelation during the small-amplitude chaotic oscillations. Due to the positive LCE the autocorrelation function of a chaotic signal decays to zero within a finite time. If the mean interval between spikes is larger than this time, the average ISI will no longer be correlated to its predecessor and the ISI distribution will resemble that of an uncorrelated (Poisson) process.

We are not aware of reports describing excitable chaos in Hodgkin-Huxley types of equations. From the investigation of our model and several related equations we infer that the nonlinear modulation of the strength of both autoinhibition and autocatalysis [realized by variable  $W$  in Eq. (1)] is a crucial requirement. In neurons this would translate into a self-regulatory modulation of the ion channel characteristics.

If a noisy perturbation is added to the self-exciting chaos the mean spiking frequency is increased and distinct patterns appear in the ISI return map [Fig. 2(b)]. The points then tend to be arranged along a multitude of horizontal and vertical lines. This reflects that spikes always arise from a similar phase of a small-amplitude oscillation. Thus the number of oscillations between spikes induces a certain discreteness in the escape times. This discreteness implies that the spike sequence has a preference for certain ISIs and for certain ISI sequences (motifs). The preference for motifs makes it likely that certain ISI sequences can easily be induced by external perturbations, whereas other sequences would rather suppress spiking. By these means the system can act as a filter to recognize distinct input patterns (i.e., different pieces of information). As an application, excitable chaos was used to detect hidden short-term correlated events in noisy human EEG [11].

Figure 3 shows that noise induces correlations immanent in the system. The qualitative differences between the unperturbed and the noise-perturbed case are remarkable even with the arbitrarily chosen poor statistics. This is of importance for the analysis of experimental results, where long stationary time series may be difficult to obtain. In particular, in addition to the purely geometric impression created by the return maps in Fig. 2, the distribution  $P(s)$  permits a more quantitative description of correlations within strongly irregular time series from comparatively short ISI sequences.

Irregular perturbations with zero mean increase the probability for spikes to generate a reliable sequence of ISIs [Fig. 4(b)]. This is in accordance with experiments performed with neurons in brain slice preparations [4]. It was shown that the

response of neocortical neurons to a noisy perturbation is much more reliable than the response to a constant parameter offset. In accordance with our numerical observations this increase in reliability is accompanied by an increased spiking frequency. Furthermore, the measurements of irregular spiking activity under constant conditions clearly show short-term correlations between experiments after externally forced synchronization (see Fig. 1a in Ref. [4]). This is also observed in our model after synchronization by a sudden jump in parameter  $Z_0$ . It is a typical feature of deterministic chaotic systems but unlikely in noise-driven excitable fixed point systems.

From an experimental point of view collecting the ISIs from a spontaneously firing neuron is not sufficient to obtain information about the mechanism generating the spike sequence. Even extremely long stationary time series with only a small level of (unavoidable) intrinsic noise would produce

noiselike results and not show the distinct fingerprints of chaos. Our simulations suggest that attention should be paid to any high-frequency oscillations between spikes. With low levels of experimental noise, analysis of the interspike behavior could indicate a chaotic process. In neurophysiology these high-frequency events are often considered pure noise and therefore filtered or ignored. However, e.g., Stern *et al.* have identified a distinct high-frequency component of possibly deterministic origin during irregular spiking of rat corticostriatal cells [12]. Evidence for the existence of unstable periodic orbits (implying low-dimensional chaos) within noisy ISI return maps in neural spiking was obtained for data from rat hippocampal slices by So *et al.* [13]. Self-exciting chaos offers an explanation both of the high- and the low-dimensional properties of irregular spike sequences in the absence and in the presence of external input.

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- [1] D. Robertson and G.A. Manley, *J. Comp. Physiol.* **91**, 363 (1974).
- [2] E.D. Adrian, *The Basis of Sensation: The Action of Sense Organs* (W.W. Norton, New York, 1928).
- [3] H. Noda and W.R. Adey, *Brain Res.* **18**, 513 (1970).
- [4] Z.F. Mainen and T.J. Sejnowski, *Science* **268**, 1503 (1995).
- [5] E.D. Adrian, *J. Physiol. (London)* **61**, 47 (1926).
- [6] G. Baier, S. Sahle, J.-P. Chen, and A.A. Hoff, *J. Chem. Phys.* **110**, 3251 (1999).
- [7] A.S. Pikovsky, *Phys. Lett. A* **165**, 33 (1992).
- [8] F. Rieke, D. Warland, R. de Ruyter van Steveninck, and W. Bialek, *Spikes—Exploring the Neural Code* (MIT Press, Cambridge, MA, 1998).
- [9] G. Baier, H. Ørnsnes, and H. Degn (unpublished).
- [10] M.L. Mehta, *Random Matrices* (Academic Press, New York, 1991).
- [11] G. Baier, R. Leder, and P. Parmananda, *Phys. Rev. Lett.* **84**, 4501 (2000).
- [12] E.A. Stern, A.E. Kincaid, and C.J. Wilson, *J. Neurophysiol.* **77**, 1697 (1997).
- [13] P. So, J.T. Francis, T.I. Netoff, B.J. Gluckman, and S.J. Schiff, *Biophys. J.* **74**, 2776 (1998).