Excitable chaos in diffusively coupled FitzHugh-Nagumo equations

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A prototypic model of three coupled FitzHugh-Nagumo oscillators is shown to exhibit spatio-temporal hyperchaos. With increasing the number of coupled units the number of positive Lyapunov exponents increases. A system in two spatial dimensions shows two types of excitable spatio-temporal (hyper-)chaos depending on which variable is chosen for the coupling. Some implications for excitable cardiac tissue are discussed.

Keywords: FitzHugh-Nagumo equation; hyperchaos; spatio-temporal chaos.

Un modelo prototípico de tres osciladores acoplados tipo FitzHugh-Nagumo muestra hipercaos espacio-temporal. Aumentando el número de unidades acopladas se aumenta el número de exponentes de Lyapunov positivos. Un sistema extendido en dos dimensiones espaciales genera dos tipos de (hiper-)caos excitable espacio-temporal dependiente de la variable de acoplamiento. Se discuten unas implicaciones para tejidos excitables cardiacos.

Descriptores: Ecuación de FitzHugh-Nagumo; hipercaos; caos espacio-temporal.

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1. Introduction

Rössler [1] and Kuramoto [2] first demonstrated how linear diffusive coupling can induce low-dimensional spatio-temporal chaos in reaction-kinetic oscillators. By "chaos" they referred to attractors of deterministic systems that possess at least one positive Lyapunov characteristic exponent (LCE). Attractors with more than one positive LCE are referred to as hyperchaos [3]. A set of **N** ordinary differential equations containing at least one nonlinear term may have attractors with up to **N**-2 positive LCEs. The concept of hyperchaos serves as a link for the stepwise transition from low-dimensional to high-dimensional irregularity in deterministic systems [4]. In the case of diffusively coupled oscillators, conditions were found under which the number of positive LCEs increases monotonically when the number of oscillators was increased [5,6]. More recently, using this approach, a system of diffusively coupled Goldbeter-Dupont-Berridge models was reported to show this phenomenon under conditions where a single oscillator is excitable [7]. None of the arguments involved depends on the specific type of reaction-kinetic functions. It is therefore probable that a similar mechanism should work in abstract excitable systems of the van der Pol type, *e.g.* the FitzHugh-Nagumo equation. Here we study linearly coupled FHN equations and show how hyperchaos found in (comparatively) low-dimensional systems leads to the discovery of new types of excitable spatio-temporal chaos in spatially extended versions.

2. Model

The FitzHugh-Nagumo model is used in the following form:

$$\frac{dX_1}{dt}=X_1(a-X_1)(X_1-1)-Y_1+I_a+D_X(X_2-X_1)$$

$$\frac{dY_1}{dt}=b(X_1-Y_1)+D_Y(Y_2-Y_1)$$

$$\frac{dX_i}{dt}=X_i(a-X_i)(X_i-1)-Y_i+I_a + D_X(X_{i-i}+X_{i+1}-2X_i)$$

$$\frac{dY_i}{dt}=b(X_i-Y_i)+D_Y(Y_{i-i}+Y_{i+1}-2Y_i) \qquad (1)$$

$$\frac{dX_N}{dt}=X_N(a-X_N)(X_N-1)-Y_N+I_a + D_X(X_{N-1}-X_N)$$

$$\frac{dY_N}{dt}=b(X_N-Y_N)+D_Y(Y_{N-1}-Y_N)$$

with $i=2,3,\ldots,N-1$. With $a=0.1$ and $b=0.015$ the isolated system ($D_X=D_Y=0$) has a stable fixed point solution for $I_a<0.0590$. At $I_a\approx 0.0590$ a supercritical Hopf bifurcation to near-harmonic oscillations occurs. As I_a is increased the amplitude of the oscillations grows first with A$\propto\sqrt{I_a-I_a^{\rm crit}}$, where $I_a^{\rm crit}$ is the critical value of the Hopf bifurcation. The amplitude then grows in an exponential fashion between $0.061<I_a<0.063$. Following this Canard region, further increase of $I_a$leads to relaxation oscillations with linearly growing amplitude.

3. A prototype composed of three coupled oscillators

The coupled system with N=3 is found to be prototypic for the generation of hyperchaos (see *e.g.* [4] or any textbook on nonlinear dynamics for an introduction to the technical terms used). If, for a constant value $I_a = 0.0625$, with $D_Y = 0$, D_X is slowly increased we find a sequence of bifurcations from periodic behavior in the uncoupled case to quasiperiodicity, chaos on a fractalized two-torus, and hyperchaos. Figure 1 is a bifurcation diagram of the N=3 system as a function of coupling strength. The sequence of transitions (from left to right) starts with a secondary Hopf bifurcation from periodic to quasiperiodic oscillations (exemplary value $D_X = 0.001$). Within the chaotic region there are other transitions whose generic nature has not been resolved so far (this holds in general for $N > 2$). Increasing the coupling further we obtain a sequence of reverse bifurcations to the periodic synchronized state. To characterize the degree of chaoticity we use the spectrum of LCEs. The LCEs are calculated with a modified Wolf algorithm with periodic Gram-Schmitt orthogonalization implemented by C. Knudsen, R. Feldberg and J.S. Thomsen. All values are given in bits per model time unit. The values converge in all cases and the numerical error is found to be less than 3%. The complete spectrum of 6 LCEs

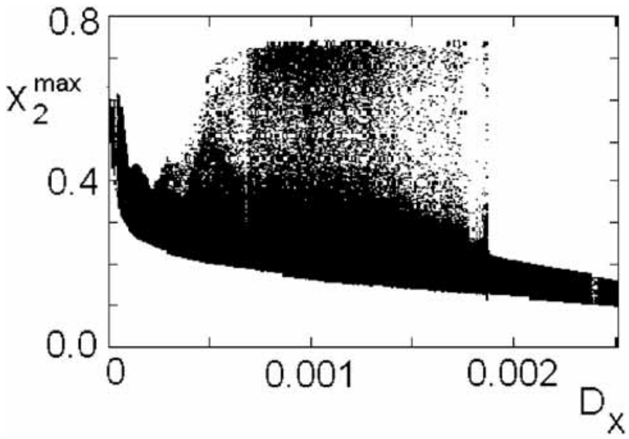

FIGURE 1. Bifurcation diagram of Eq. (1) with $N = 3$ with coupling in variable X. Maxima of variable X_2 are plotted as a function of D_X. Parameters: $a = 0.1$, $b = 0.015$, $I_a = 0.0625$, $D_Y = 0$.

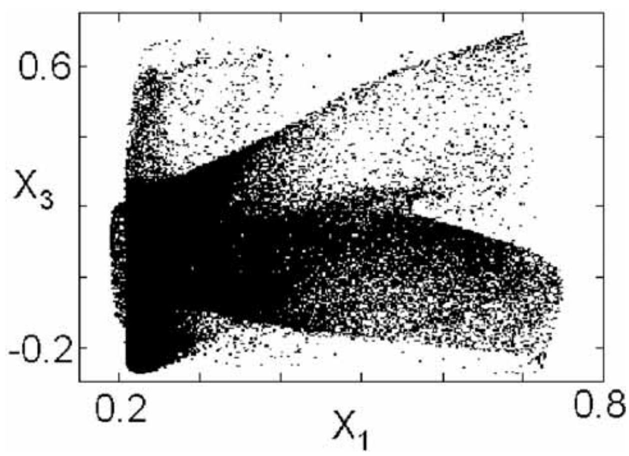

FIGURE 2. Cross-section of hyperchaotic attractor in Eq. (1) with $N = 3$, $D_X = 0.001$. Other parameters as in Fig. 1.

in the hyperchaotic case is calculated to be 0.007, 0.003, 0, -0.008, and -0.034 bps, *i.e.* two positive LCEs. Figure 2 shows a Poincaré cross-section of the attractor. The cross-section shows the multiply folded sheet structure typical of two orthogonal directions of stretching and folding in phase space.

The same equation also has diffusion-induced chaotic solutions for couplings $D_X = 0.0$, $D_Y > 0$. With all other parameters as above only one positive LCE is found, however. The cross-section is sheet-like for $D_Y = 0.015$ (implying a fractal dimension larger than 3), but this is associated with an increase in dimension in accordance with the Kaplan-Yorke conjecture [8].

4. Spatio-temporal hyperchaos in more than 3 coupled oscillators

Increasing the number of coupled oscillators we find an increasing maximal number of positive LCEs: with $N = 5$ there are 3 positive LCE with parameters $I_a = 0.064$, $D_X = 0.004$, and with $N = 10$ there are 7 positive LCE (0.008, 0.006, 0.005, 0.003, 0.003, 0.002, 0.001, 0.0 bps) with the same set of parameters. Decoupling variable X ($D_X = 0$) and coupling in variable Y yields 4 positive LCEs with parameters $I_a = 0.0635$, $D_Y = 0.01$ (numerical values 0.005, 0.003, 0.001, 0 bps) confirming that this coupling is also able to induce hyperchaos albeit with a smaller number of positive LCEs at a given N than in the case of X-coupling.

Before jumping to systems of many coupled oscillators a few instances of small networks with coupling to 4 and six nearest neighbors were examined with respect to chaos-hyperchaos transitions. The picture outlined so far holds in all cases whether the boundary conditions are chosen zero-flux or periodic. Only slight adjustments in parameters D_X, D_Y and/or I_a are required. For example, the numerical values of the largest LCEs in a net of cubically arranged 3×3 oscillators with zero flux-boundaries and parameters $I_a = 0.0625$, $D_X = 0.001$ are 0.004, 0.003, 0.002, 0.002, 0.001, 0.0005, and 0 bps, *i.e.* six positive LCEs. Coupling to more than two nearest neighbors does not hamper the evolution of multiple direction of exponential divergence.

Common to all cases is that as long as the system is restricted to small-amplitude near-harmonic oscillations it preserves the feature of excitability. That is, a short suprathreshold stimulus induces one large-amplitude oscillation of relaxation type. In all cases where the chaos is composed only of small-amplitude oscillations (*i.e.* where it is not self-exciting) it is also excitable.

5. The case of two spatial dimensions

Following the hypothesis (first introduced by Rössler [1] and later supplied with numerous examples [5,6]) that diffusion-induced chaos in low-dimensional systems is a generic building block for spatially extended models, we present results obtained with a system of 50×50 coupled FHN subunits. Boundary conditions are zero-flux and both hexagonal and cubic net geometries were used to confirm the independence of the results from the particular geometry of coupling. The initial conditions were chosen randomly in a neighborhood of the excitable fixed point of the system. Given the parameters obtained from the low-dimensional systems $N = 3$ and $N = 10$ it is straightforward to find parameters for spatio-temporally chaotic solutions.

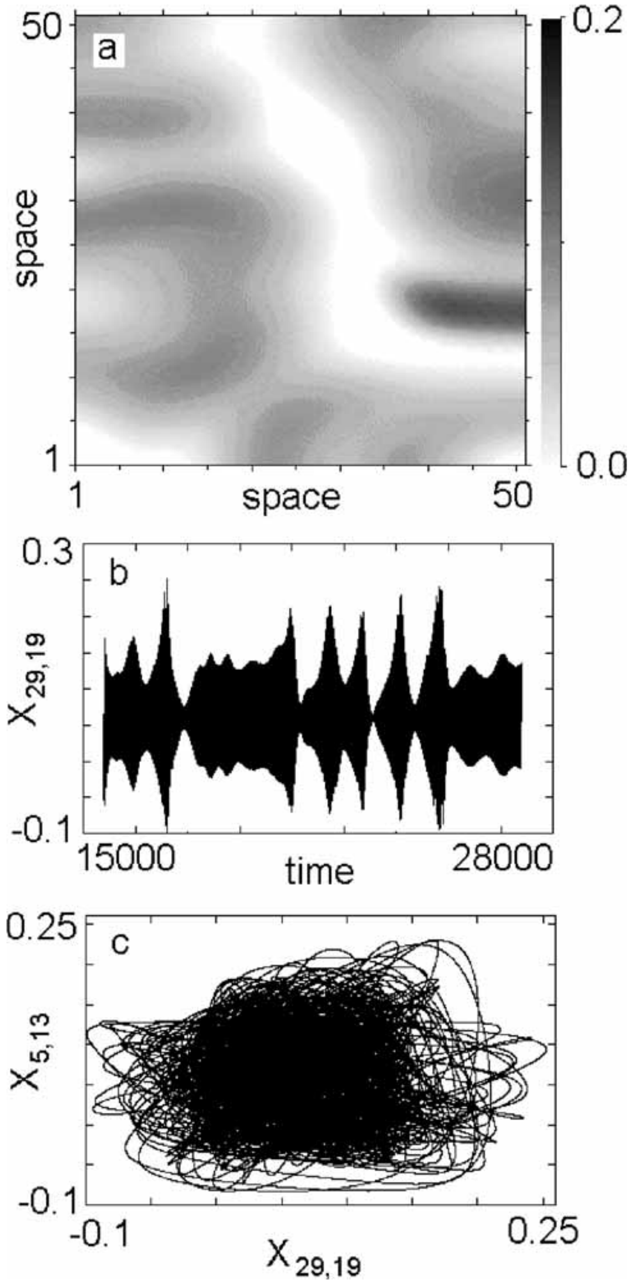

FIGURE 3. Chaotic pattern in the autonomous 2D system of 50x50 oscillators with coupling in variable X. $I_a = 0.062$, $D_X = 0.02$, $D_Y = 0$. Other parameters as in Fig. 1. a) Snapshot of the net after transients have died out. Grey coding of variable X. b) Time series of oscillator (29,19). c) Attractor projection from oscillators (29,19) and (5,13).

Figure 3a shows a snapshot of the system with diffusive coupling restricted to variable X. The distribution of all variables varies irregularly in space and time. Occasionally, a region reaches values typical of an excitation but no traveling waves are induced. The time series of an individual oscillator (Fig. 3b) shows oscillations with chaotic amplitude-modulation. The mean amplitude varies between near-harmonic and occasional relaxation oscillations. The attractor projection on a plane due to its high dimensionality does not possess any perceivable structure (Fig. 3c). The spatial homogeneity is broken yielding oscillating patterns of irregular size with all sets of initial conditions tested. This spatio-temporal chaos appears to be the only asymptotic solution.

Figure 4a is a snapshot with coupling in variable Y. Similar as in the case of Fig. 3 we see irregularly amplitude-modulated oscillations in part of the coupled units. Here, however, some units spontaneously grow to create large-amplitude columns that remain unchanged in the course of time. They can be seen as black spots in the figure. In contrast to X-coupling described in the previous paragraph here the time series of individual oscillators depends crucially on their position in the net. They can be hyperchaotic as shown in Fig. 4b, bottom, for an oscillating unit of the net or they can be quasi-fixed points if the tip of the stable column is picked as in (Fig. 4b, top). If the coupling D_Y is further increased the asymptotic solution is a temporally invariant pattern of spots (a Turing pattern with short wavelength) distributed evenly over the whole net.

6. Discussion

The principle of a chaotic hierarchy for the generation of high-dimensional asymptotic solution out of simple nonlinear units [9] is found to apply for prototypic excitable systems. Diffusion-induced instabilities of periodic orbits generically lead to quasiperiodicity, fractalized tori and eventually to chaos with more than one positive LCE. The maximal number of positive LCEs depends on the number of coupled units as expected. The bifurcation diagrams of diffusively coupled units that do not allow chaotic solutions when isolated (due to their restricted phase space) thus are characteristically different from those reported for linearly coupled chaotic units where the coupling strength causes stepwise decrease in complexity (see *e.g.* [10] for systems of coupled non-invertible maps and [11] for coupled continuous systems).

The spatio-temporal hyperchaos in Fig. 3 bears resemblance to the solutions found in spatially extended reaction-kinetic systems [5] but to our knowledge has not been reported in equations of the van-der-Pol-Bonhoeffer type so far. Thus the restrictions imposed by mass-action kinetics can be omitted and the behavior is generic to the class of equations that is commonly used to model excitable biological systems like cardiac, pancreatic, and neural tissue with their charac-

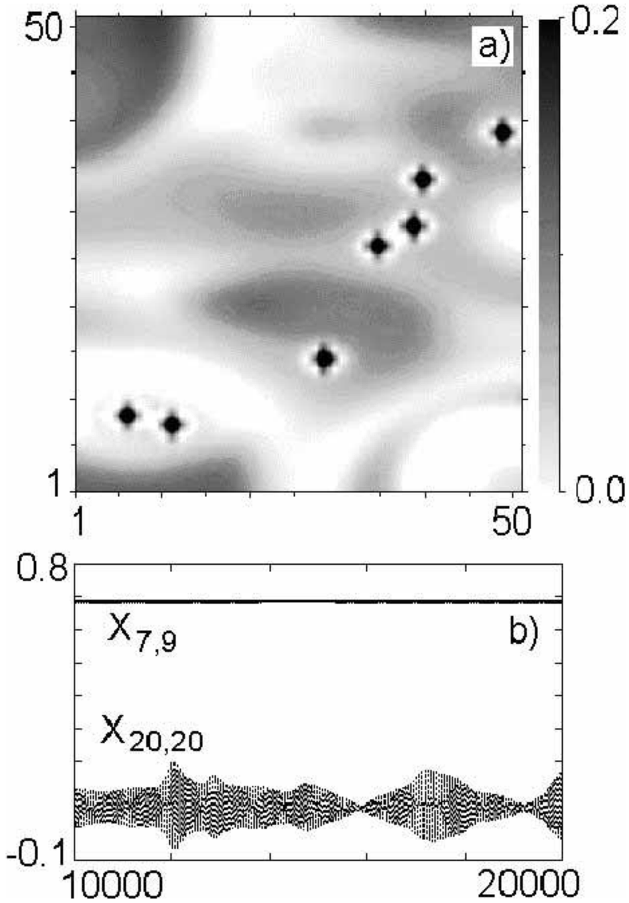

FIGURE 4. a) Snapshots of mixed chaotic pattern in the 2D system of 50×50 oscillators with coupling in variable Y. b) Time series of two oscillators in the net shown in a). $I_a = 0.062$, $D_X = 0$, $D_Y = 0.01$. Other parameters as in Fig. 1.

teristic and hitherto not well-understood order-disorder transitions [12].

Remarkably, the spontaneous small-amplitude oscillations prohibit the evolution of spirals or broken spirals typical of FHN media with subcritical Hopf bifurcation in the isolated oscillator [13]. The reason is that the small-amplitude chaos prevents the propagation of excitation waves, be they target patterns or spirals. We find that the transition from global to local excitability is continuous, *i.e.* there exists a region that allows both propagation waves and spatio-temporal chaos for nearby parameters. As one consequence, a shift of the parameters from subcritical to supercritical Hopf bifurcation in an excitable system offers a new dynamic mechanism to explain temporal incapacity of a spatially extended excitable system to support traveling waves.

The generation of deterministic chaos in diffusively coupled FHN-type oscillators has been suggested as an explanation of the dynamic transition to fibrillatory states in cardiac tissue [13,14]. In these studies fibrillation is considered as an example of a hyperchaotic spatio-temporal dynamics that often occurs without obvious external stimulus. Dynamic mechanisms are of importance when trying to understand sudden breaking of the normally regular excitation waves in the heart that cannot be attributed to permanent alterations of the tissue (see [15] for a discussion of the role of dynamic explanations). In this context, heart cell cultures obtained from mammals or chicken offer an experimental system where the present results can be tested. In particular, with mouse heart cells it was possible to prepare clusters of different size that showed a transition from regular to synchronized irregular and finally to desynchronized irregular excitations at either low potassium or high calcium concentration in the medium [16]. In such a set-up it is possible to study the degree of chaoticity as a function of the number of connected cells either by electrophysiologic techniques or recordings of the spatio-temporal dynamics of voltage-dependent dyes.

The stable Turing patterns for strong coupling of variable Y are well-known solutions of partial differential equations of the activator-inhibitor type with inhibitor coupling [17]. The pattern in Fig. 4 can therefore be understood as a chaotic mixture of the Hopf instability (breaking the temporal symmetry) and the Turing-like pattern instability (breaking the spatial symmetry). In the classical Hopf-Turing mixed mode chaos however, the Turing patterns are temporally unstable and unpredictably appear and disappear [18,19]. The fact that hyperchaotic oscillations coexists with quasi-steady-states in the same net has previously only been reported for systems with parameter gradients [20]. The dynamic reason for the quasi-unperturbed fixed point behavior of the spot tips is that they show center-surround characteristics [21]. That is, each excitation spots is surrounded by a ring of cells that are hyperpolarized and thereby successfully dampen the oscillations of the neighborhood. This is not only a surprising finding in itself but also an intriguing feature when thinking of *e.g.* the transition to fibrillation: in the case of Y-coupling the perfectly homogeneous system *dynamically* generates obstacles that may help to explain the break-up of pace-maker-induced excitation waves. In contrast to the generally supposed ischemia (organic damage that can be considered constant on the time scale of individual excitations) this would allow switching from regular to tachycardic to fibrillatory behavior on the short time scales often observed in cardiology (see *e.g.* [22] for references).

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