

Fluctuating excitability: A mechanism for self-sustained information flow in excitable arrays

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Accepted 16 November 2005

Communicated by Prof. Mohamed Saladin El Naschie

Abstract

We show that the fluctuating excitability of FitzHugh–Nagumo neurons, constituting a diffusively coupled excitable array, can induce phase slips that lead to a symmetry break yielding a preferred spreading direction of excitatory events, thus enabling persistent self-sustained and self-organized information flow in a periodic array long after a localized stimulus perturbation has sized. Possible oscillation frequencies of the information-carrying signal are expressed analytically, and necessary conditions for the phenomenon are derived. Our results suggest that cellular diversity in neural tissue is crucial for maintaining self-sustained and organized activity in the brain even in the absence of immediate stimuli, thus facilitating continuous evolution of its mechanisms for information retrieval and storage.

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1. Introduction

Excitability is a fundamental property of several biological and artificial systems, ranging from neural and cardiac tissue to chemical reaction systems and laser optics, which allows robust and immutable information transmission in time and space [1,2]. Characteristically, weak perturbations acting upon the stable steady state of an excitable system evoke nontrivial spike-like responses, which after a system-typical refractory time fade towards the steady state. Weak perturbations can be delivered by stochastic and/or deterministic signals, whereby one can observe fascinating phenomena such are, for example, stochastic and coherence resonance in temporal [3–8] and spatially extended systems [9–14], self-sustained activity [15] and fast coherent responses [16] in small-world networks, or persistency of noise-induced spatial periodicity [17], spatial decoherence [18,19], and noise-enhanced phase synchronization [20] in excitable media.

A particularly interesting property that can greatly influence the collective dynamics of diffusively or small-world coupled arrays is the heterogeneity of excitable units that constitute it. Recently, it has been reported that heterogeneity enhances coherence resonance in an excitable array [21]. Importantly, the consideration of heterogeneity is especially relevant when studying the dynamics of neural networks since it encompasses cellular diversity that is acknowledged

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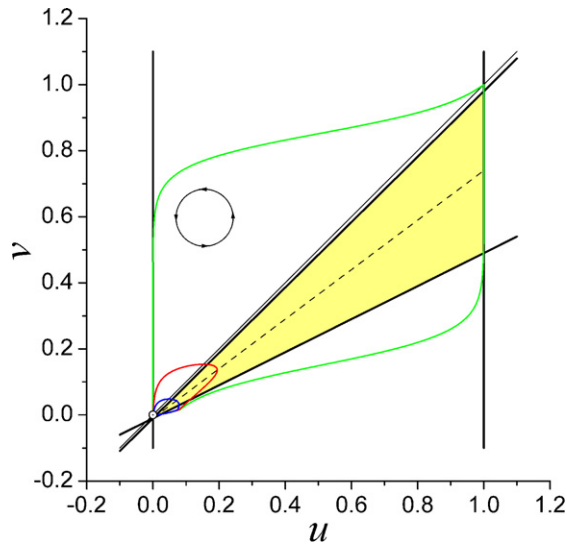


Fig. 1. (colour online) Phase space analysis of feasible excitable steady states constituting the array. The thin solid line shows the nullcline of variable v , whilst thick solid lines, together with the colour shading, present nullclines of variable u for $a_i \in (0.5, 1.0)$ (thin dashed line specifically depicting $a = 0.75$). Trajectory loops originating from $u = v = 0$ present responses of the system to a single pulse with amplitude $\chi = 0.14$ and duration $d = 0.5$ for various values of a . The circle with arrows indicates the direction of the flow.

to be universally present throughout the nervous apparatus [22–25]. Moreover, cell heterogeneity plays a decisive role also in cardiac tissue, where it was taken into account to model experimentally observed spiral wave generation and global organization of dynamics [26,27].

Although arrays consisting of heterogeneous units are widely acknowledged to represent more faithful mathematical descriptions of biological systems than arrays consisting of identical elements [16,20,21,26–28], little attention has been devoted to the explicit study of effects or possible roles the introduction of heterogeneity can have on the collective dynamics of an array. Besides the enhancement of coherence resonance and with it related possible role to enhance time precision of neuronal firing reported in [21], we found no other theoretical study reporting heterogeneity specific phenomena. Here we describe an interesting and generally applicable mechanism for self-sustained information flow in excitable arrays due to the fluctuating excitability, i.e. heterogeneity, of units that constitute it, thus fuelling speculations as to why nature chose to encompass diversity as an inseparable part of real-life organisms and its building blocks.

2. Mathematical model

To present the results, we make use of the establish FitzHugh–Nagumo model [29,30], which comprised in a one-dimensional diffusively coupled array takes the form

$$\varepsilon \dot{u}_i = u_i(1 - u_i)(u_i - (v_i + b)/a_i) + g(u_{i-1} + u_{i+1} - 2u_i) + f(\tau, p, \chi, d), \quad (1)$$

$$\dot{v}_i = u_i - v_i, \quad (2)$$

where the parameters $\varepsilon = 0.05$, $b = 0.01$, and $a_i = a + \delta a$ determine the excitable dynamics of each unit $i \in [1, n]$, and $f(\tau, p, \chi, d)$ is a localized, i.e. active only if $i = 1$, time-limited periodic pulse train with overall duration τ and oscillation period p , whilst the amplitude and duration of the pulses are given by χ and d , respectively. For $a < 1$ each FitzHugh–Nagumo unit is governed by a single excitable steady state, whereby the threshold for large-amplitude firing increases with decreasing a . The heterogeneity, modelling cellular diversity, is taken into account by letting the excitability fluctuate uniformly around $a = 0.75$, whereby $\delta a_{\max} \in (-0.25, 0.25)$. In Fig. 1, the phase space analysis of units constituting the array is presented, whereby attention is devoted to the response properties at $a = 0.75$ (red trajectory) as well as both limiting cases given by $a = 0.51$ (blue trajectory) and $a = 0.99$ (green trajectory).¹ It is evident that for all

¹ For interpretation of color in Figs. 1 and 3, the reader is referred to the web version of this article.

$a_i \in (0.5, 1.0)$ each unit is governed by a single excitable steady state $u = v = 0$, whereby equally strong perturbations evoke variable excursions of the trajectory in the phase space. In particular, for $a = 0.5$ the excursion is barely visible whilst for $a = 0.99$ the trajectory loops around the whole phase space constituted by the nullclines. In what follows, we will show that the fluctuating excitability, yielding variable responses of the system to an external forcing can lead to symmetry breaking, and thus a preferred direction of speeding of stimuli-induced excitatory events in the array, thereby assuring self-sustained information flow among coupled units.

3. Self-sustained information flow

Let us then analyse the collective dynamics of the array under the action of a short-lasting localized periodic stimuli and fluctuating excitability of coupled units. To this purpose, we set $g = 2.0$, $n = 500$, and impose periodic boundary conditions on the array. At this point, we emphasize that our system setting is different from previous studies reporting noise-induced degradation or enhancement of dynamical stability via a renormalization of system parameters due to the introduction of multiplicative parametric Gaussian noise [31–35] in that we apply uniformly distributed parameter disturbances, and more importantly, the time scale in which δa varies is of the order of magnitude of several oscillation periods of a single array unit. We typically vary all a_i simultaneously about 100 times per simulation to obtain statistical relevancy for each level of excitability fluctuations $|\delta a|$. Although this introduces an additional time scale into the model, we emphasize that qualitatively identical results can be obtained by considering exclusively quenched fluctuations of a_i .

Results presented in Fig. 2 capture possible scenarios. The upper-most row shows that identical units seize to fire after the stimulus perturbation vanishes. On the other hand, for $\delta a \in (-0.15, 0.15)$ the information flow given by the sustained periodic firing of all coupled units can persist long after τ . As shown in Fig. 2(b), this is not necessarily the case, particularly if several phase slips occurring during τ cancel each other out. Often (exact conditions will be specified below), however, the phase slips induce symmetry breaking in the array and thus yield a preferred spreading direction of excitatory events, which then propagate periodically throughout the whole array, whereby the symmetry break can happen in either direction with equal probability. Notably, if several phase slips occur during τ and do not cancel each other out, the complexity of the firing pattern increases, whereby one can observe duplets or triplets of firing events that propagate with constant speed across the array, as shown in Fig. 2(d) and (e). While the oscillation frequency of excitatory events in duplets and triples t_b is determined by $1/p$, the main oscillation period t_s of the self-sustained information-carrying signal in a single unit is uniquely determined by the array size n and the propagation speed $\sqrt{2\pi g}$ with which locally induced excitations propagate across the array by the evident equation $t_s = n/\sqrt{2\pi g}$. Furthermore, the phase shift t_p between two neighbouring units in the self-sustained oscillatory regime equals $t_p = 1/\sqrt{2\pi g}$. These easily attainable relations indicate that fluctuating excitability in conjunction with a short-lasting local stimulus is able to induce self-sustained and self-organized oscillations in an excitable array, whereby the information can be encoded effectively either by t_b , t_s , or t_p , depending on p , g , and/or n .

It remains of interest to determine optimal conditions for the existence of self-sustained information flow in the array. For this purpose, we introduce a “success” probability $P = S/A$, whereby S is the number of runs for which self-sustained information flow with $t_s = n/\sqrt{2\pi g}$ can be identified in all array units for at least 20 oscillation periods, and $A = 500$ is the number of all test runs. Note that this criterion is sufficient to establish also information flow with $t_p = 1/\sqrt{2\pi g}$ in the array, whilst the existence of information flow encoded by $t_b = 1/p$ was not considered as a necessary condition for positively establishing self-sustained activity. The dependence of P on $|\delta a|$ in conjunction with g , n , and τ is presented in Fig. 3. It is evident that there exists a minimally required dissemination of excitability to obtain $P > 0$ as well as a rather robust optimal $|\delta a| \approx 0.13$ for which P is maximal for given g , n , and τ . For $|\delta a|$ approaching $|\delta a|_{\max} = 0.25 P$ decreases since values of a significantly below 0.6 introduce excitable units with very high excitability threshold (see Fig. 1) that act as insurmountable barriers for the information flow, and thus transduction failure at such conditions is not likely to be avoided. Besides these general conclusions, it is evident that the probability of self-sustained information flow P in the array depends sensitively on g [see Fig. 3(a)]. This is not surprising since low values of g altogether hinder the propagation of locally induced excitations across the array, and thus excitatory fronts cannot even be seeded by the deterministic stimulus. On the other hand, large g make the array act effectively as a single unit, and thus instantaneous synchronization of coupled neurons makes it impossible to induce phase shifts. Notably, for reasonable g the amplitude and duration of stimulus spikes can be adjusted appropriately to still observe the phenomenon. In general, larger g require stronger local perturbations to obtain self-sustained information flow in the array. Moreover, there also exist an optimal array size $n \approx 40$ for which P at an appropriate $|\delta a|$ is maximal. We note that by small arrays ($n < 10$) the heterogeneity of excitable units is not diverse enough to induce phase shifts since the distribution function of $|\delta a|$ cannot reach uniformity. Also, only a small number of units qualify as suitable candidates for

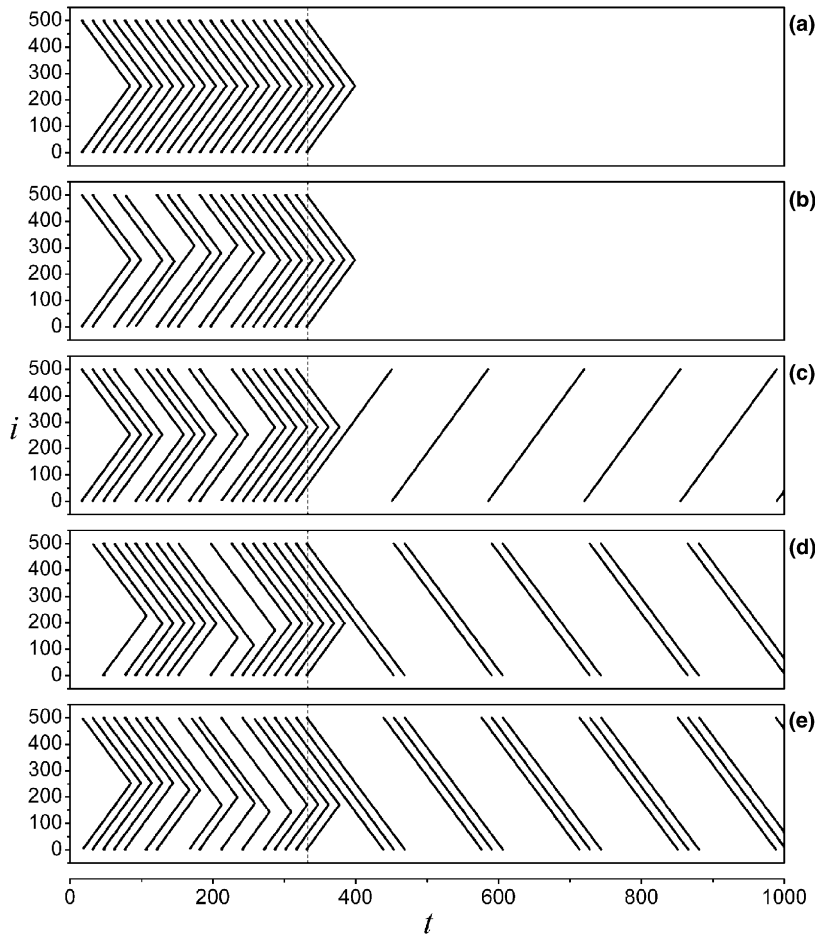


Fig. 2. Self-sustained information flow failure (a,b) and success (c,d,e) after a localized periodic stimulus $f(\tau,p,\chi,d)$ with $\tau = 330$ (vertical dashed lines), $p = 15$, $\chi = 0.7$, and $d = 0.5$ was applied to the first ($i = 1$) unit of the array. In (a) all $a_i = 0.75$, whilst in (b,c,d,e) $\delta a \in (-0.15, 0.15)$. Black dots indicate firing units.

inducing a phase shift. Contrary, since the coupling is diffusive, large n constitute a challenge for the locally induced excitations in that it is not likely that they can propagate through the whole array without being extinguished, although this effect is not decisive [see Fig. 3(b)]. Finally, the duration of the local deterministic stimulus is also somewhat important [see Fig. 3(c)], since longer τ obviously provide more time for phase shifts to occur. However, the effect is of saturating nature [see Fig. 3(d)] since larger τ also provide more opportunity for phase shifts to cancel each other out, as exemplified in Fig. 2(b). In summary, we show that in order to minimize the probability of self-sustained information flow failure parameters determining the strength of the localized deterministic stimulus have to be adjusted in accordance with g , whilst for diffusively coupled arrays medium n provide an optimal compromise between a large probability to obtain phase shifts and a small probability to experience information flow failure due to extensive distances a locally induced excitation has to surmount. Also, it is favourable to let the local stimuli act on the system for at least a few oscillation periods p .

A necessary condition for the reported self-sustained information flow, which until now has not been awarded any attention, is also the periodic boundary condition. Although at first sight unlikely to be fulfilled in real-life situations, we argue that small-world networks [36,37] might provide an appropriate environment for the above-reported phenomenon. In particular, we argue that a diffusively coupled array with periodic boundary conditions can be seen as a special example, or a part, of a bi-directionally coupled small-world-like network with only one shortcut link, which is of course the one connecting the first and the last array unit. By accepting this hypothesis, small-world networks can be considered as sources of variable eigen-frequencies (given by $1/t_s$ or $1/t_p$ and variable sizes n of diffusively coupled clusters that are linked via shortcuts) that can be exploited for self-sustained and self-organized information flow. To

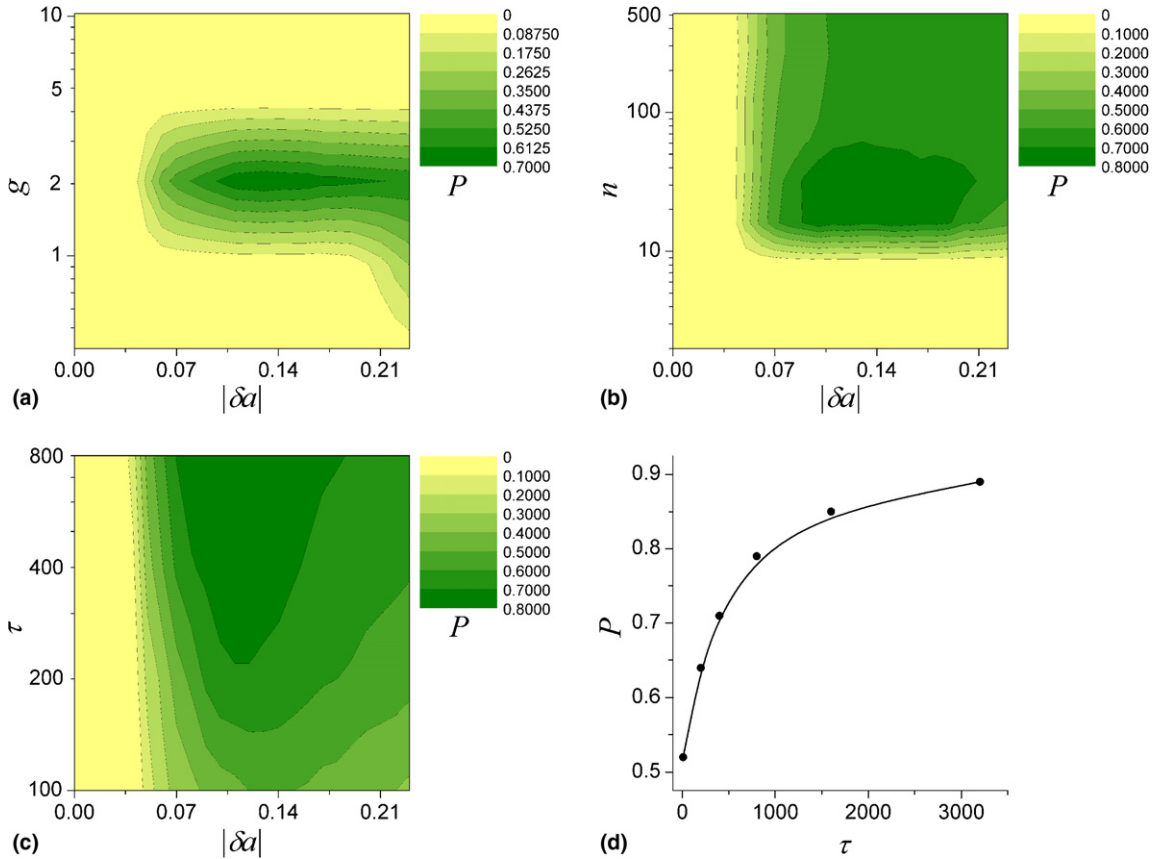


Fig. 3. (colour online) Conditions for self-sustained information flow in the array in dependence on various system parameters. In all calculations, we set $p = 10$, $\chi = 0.7$ and $d = 0.5$, whilst specific to (a) $\tau = 200$ and $n = 50$; (b) $\tau = 200$ and $g = 2.0$; (c, d) $n = 50$, $g = 2.0$ [the line in (d) is intended solely to guide the eye].

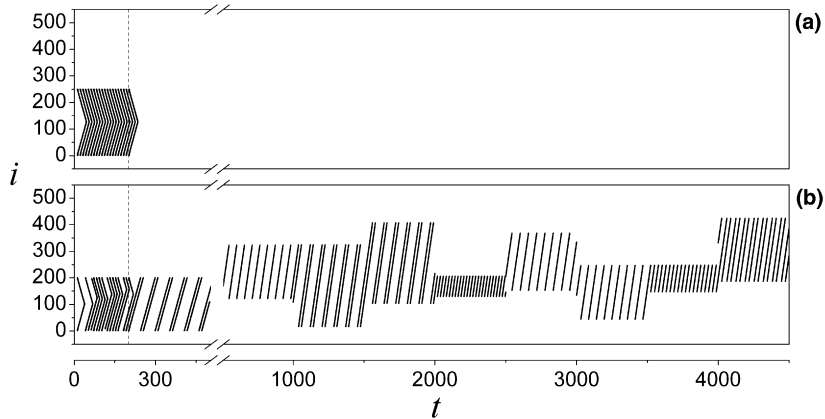


Fig. 4. Self-sustained information flow failure (a) and success (b) after a localized periodic stimulus $f(t, p, \chi, d)$ with $\tau = 200$ (vertical dashed lines), $p = 10$, $\chi = 0.7$, and $d = 0.5$ was applied to the first ($i = 1$) unit of the array, whereby n varied randomly every $\Delta t = 500$. In (a) all $a_i = 0.75$, whilst in (b) $\delta a \in (-0.15, 0.15)$. Black dots indicate firing units. Note that the x-axis has a break at $t = 500$ to enable optimal viewing possibilities of events induced by $f(t, p, \chi, d)$.

concretise this conjecture, we introduce variable n in time and repeat calculations as in Fig. 2, thereby modelling the propagation of a short-lasting localized stimulus across diffusively coupled clusters that are connected via shortcut links to other clusters to form an overall small-world-like network. Evidently (see Fig. 4), similarly as by constant n , variable cluster sizes connected via shortcut links also provide a suitable environment for self-sustained and self-organized information flow in the array induced solely by fluctuating excitability of constituting units, whereby a nearly continuous repertoire of information-carrying frequencies given by t_b , t_s , or t_p can be exploited. Importantly, note how the system self-organizes its oscillation frequency in accordance with the size of individual diffusively coupled clusters [see Fig. 4(b)]. Thus, by accepting the fact that diffusively coupled arrays with periodic boundary conditions can be treated as small-world-like networks with a single shortcut link, the model used to obtain results presented in Figs. 2 and 3 can be seen as the minimal model in which heterogeneity of excitability of coupled units can assure self-sustained information flow in an excitable array.

4. Summary

In conclusion, we present an interesting and generally applicable mechanism for self-sustained and organized information flow in diffusively coupled excitable arrays due to the fluctuating excitability of units that constitute it. Feasible oscillation frequencies for the information transmission are expressed analytically, and optimal conditions for the reported phenomenon with respect to the coupling constant, system size, and duration of the localized deterministic stimulus are derived. Also, we demonstrate that an upgraded approach encompassing also small-world connectivity of diffusively coupled clusters can lead to a virtually continuous repertoire of available frequencies that can be exploited for self-sustained transmission of information throughout the nervous system.

Interestingly, our findings suggest that the inherent cellular diversity present throughout the nervous apparatus [22–25] might constitute our ability to retain information to which we are exposed only temporarily. Thus, even in the absence of immediate external stimuli, the activity in the brain can be sustained due to the inherent cellular diversity, thus yielding a continuous processing of perceived data, which could possibly facilitate brain evolution and effectiveness of involved mechanisms for information processing, retrieval, and storage.

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