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Synchronised firing induced by network dynamics in excitable systems

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Abstract – We study the collective dynamics of an ensemble of coupled identical FitzHugh-Nagumo elements in their excitable regime. We show that collective firing, where all the elements perform their individual firing cycle synchronously, can be induced by random changes in the interaction pattern. Specifically, on a sparse evolving network where, at any time, each element is connected with at most one partner, collective firing occurs for intermediate values of the rewiring frequency. Thus, network dynamics can play the role of noise and connectivity in inducing this kind of self-organised behaviour in highly disconnected systems which, otherwise, would not allow for the spreading of coherent evolution.

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Introduction. – The spontaneous emergence of coherent behaviour in populations of interacting units —be they of physical, chemical, biological, or technological nature— is crucial to their collective function. Synchronisation of several kinds occurs in such disparate systems as mechanical oscillators, biomolecular reactions, neural networks, insect societies, hormonal cycles, coupled lasers, and Josephson junctions. Mathematical models for this variegated class of phenomena have been proposed in terms of ensembles of coupled dynamical systems of different types: linear and nonlinear oscillators, chaotic elements, excitable units, among others [1,2].

It is a well-established fact that, in a population of interacting elements, sufficiently strong, attractive coupling induces self-organised synchronisation. This occurs even in the presence of external noise, or when the individual behaviour of each element is chaotic, or when elements are not identical to each other, with the proviso that the population is well-interconnected in such a way that information about the state of any element can reach any other. While the structure of the interaction network —*i.e.* the connectivity pattern that defines which elements interact with each other— can affect details in the collective dynamics [3], connectedness and strong coupling generally guarantee synchronisation.

It has recently been shown that, both in synchronisation and in contact processes (such as epidemics spreading), instantaneous lack of connectivity can be compensated by dynamical rewiring of the interaction network [4,5]. Specifically, in populations with very sparse, disconnected instantaneous patterns, the respective transitions to full synchronisation and to endemic states are triggered by increasing the rewiring rate. This result is relevant, especially, to biological and social networks, where potential contacts between the members of a population are not continuously realised, but can occasionally be activated.

In this letter, we disclose a novel phenomenon concerning the collective dynamics of populations of excitable units on evolving networks. Interacting excitable elements, which individually perform a “firing” cycle in phase space if perturbed strongly enough from their quiescent state, are known to undergo collective synchronised firing induced by external noise [6,7] and by repulsive interactions [8]. We show here that, even in the absence of noise, an ensemble of coupled FitzHugh-Nagumo excitable elements on an evolving, very sparse, network exhibits collective firing for intermediate values of the rewiring rate. This phenomenon is characterised numerically for different network topologies and semi-quantitatively explained in terms of the perturbations that network reconnections impose on the individual dynamics of each element.

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Excitable elements on an evolving network.

– FitzHugh-Nagumo excitable elements constitute an archetypical model for type-II excitability, which occurs in many natural and artificial systems ranging from epidemic spreading, to neural and cardiac tissues [9,10] to chemical reactions and electronic devices [11]. In type-II excitability, the excitable regime —which, as explained below, is characterised by the existence of a locally stable equilibrium— is reached via an inverse Hopf bifurcation, through the transformation of a limit cycle into a fixed point. The FitzHugh-Nagumo model is defined in terms of an activatory (fast) variable x and an inhibitory (slow) variable y . We consider an ensemble of N sparsely connected FitzHugh-Nagumo elements, whose dynamics is given by

$$\epsilon \dot{x}_j = x_j - \frac{1}{3}x_j^3 + y_j + K_j(t)(x_{j^*} - x_j), \quad (1)$$

$$\dot{y}_j = a - x_j, \quad (2)$$

for $j = 1, \dots, N$. The time-dependent factor $K_j(t)$ weights the interaction between elements j and j^* , as explained below. The small parameter ϵ measures the time-scale ratio between the fast and slow variables x_j and y_j . The positive parameter a characterises the dynamical regime of the non-interacting ($K \equiv 0$) element: for $a < 1$, it performs a periodic oscillation in the (x_j, y_j) -plane, while for $a \geq 1$ its behaviour is excitable. In this latter regime, and in the absence of external perturbations, the non-interacting element asymptotically approaches the sole stable fixed point $(x_{\text{eq}}, y_{\text{eq}}) = (a, a^3/3 - a)$ and remains quiescent there. Under a sizeable perturbation, however, the element may exit the vicinity of the fixed point and return to it after a long excursion in phase space —usually referred to as a firing cycle, or spike.

Our FitzHugh-Nagumo elements interact through a sparse evolving network such that, at any given time, each element is coupled to *at most* one partner. The coupling constant in eq. (1) is $K_j(t) = k$ when element j interacts with a generic partner j^* (not necessarily the same at all times), and $K_j(t) = 0$ when j is isolated. This rather extreme sparseness determines, in a sense, the most unfavourable situation for the emergence of collective phenomena in an ensemble of interacting units. Based on previous studies on evolving networks [4,5], we expect network dynamics to replace connectivity in triggering collective behaviour.

In our numerical simulations, we study two different schemes for the network dynamics. In the first one, the network consists of exactly $N/2$ undirected links, distributed in such a way that every element is always coupled to exactly one partner. As time elapses, two connected pairs of elements are occasionally chosen at random to mutually exchange their partners. Thus, two links in the network are rewired.

The second scheme for network dynamics is built on top of an underlying (undirected, connected) network G with

a fixed number of links. During the dynamical evolution, however, only a subset of the links is active. The links of the underlying network G thus represent the potential connections in the actual interaction pattern. The initial network is generated by successively selecting elements in a random order. If the chosen element is isolated, the link to *one* of its still isolated neighbours in G gets activated. If no available neighbours exist, the element remains with no active connection. During evolution, an inactive link from G is occasionally chosen at random and gets activated. At the same time, pre-existing links of the newly connected elements become deactivated.

It is not difficult to realise that, if there is no correlation between the degrees of neighbour nodes in the underlying network G , the frequency $\omega_+(z)$ with which an isolated node of degree z becomes connected, exactly equals the frequency $\omega_-(z)$ with which it becomes isolated when it is connected. In turn, the probability P to find the node connected to any partner satisfies

$$\dot{P} = \omega_+(z)(1 - P) - \omega_-(z)P. \quad (3)$$

Therefore, for asymptotically long times, $P = 1/2$ for any z . In other words, in our second reconnection scheme and for long times, there are on the average $N/2$ connected elements —and, consequently, $N/4$ links— at any time. The resulting interaction pattern is thus twice as sparse as in the first scheme.

In both reconnection schemes, we denote by λ the *reconnection rate*, *i.e.*, the probability per time unit that the partner of any given element changes.

Order parameters. – To characterise the collective properties of our system in the framework of the standard theory of synchronised oscillators [12], it is convenient to compute a quantity describing the *phase* of each excitable element along its firing cycle. For the model defined by eqs. (1) and (2), the excursion in phase space occurs around the origin of the (x_j, y_j) -plane. Thus, a suitable definition of the phase is simply

$$\phi_j(t) = \tan^{-1} \left[\frac{y_j(t)}{x_j(t)} \right]. \quad (4)$$

The behaviour of the ensemble, including possible transitions between different collective dynamical regimes, can be statistically characterised by a pair of order parameters defined in terms of the individual phases $\phi_j(t)$ [7,8]. First, we take the average of the location of the particles on the unit circle,

$$\rho(t) \exp[i\Psi(t)] = \frac{1}{N} \sum_{j=1}^N \exp[i\phi_j(t)], \quad (5)$$

and compute the Kuramoto order parameter as $\rho \equiv \langle \rho(t) \rangle$, where $\langle \cdot \rangle$ stands for the time average over a long time interval [12]. This parameter measures the degree of synchronisation attained by the ensemble: with full

synchronisation we have $\rho = 1$, whereas for a state where phases are uniformly distributed over $[0, 2\pi)$ we have $\rho \sim N^{-1/2}$.

In excitable systems, however, the Kuramoto order parameter does not allow to discern between the case where phases are statically synchronised at the fixed point $\phi_{\text{eq}} = \tan^{-1}(y_{\text{eq}}/x_{\text{eq}})$, and the case where they rotate coherently, as expected to occur in the regime of collective firing. To discriminate between static and dynamic synchronisation, we compute the Shinomoto-Kuramoto order parameter [13],

$$\zeta = \langle |\rho(t) \exp[i\Psi(t)] - \langle \rho(t) \exp[i\Psi(t)] \rangle| \rangle, \quad (6)$$

which differs from zero for synchronous firing only.

A third relevant order parameter, frequently used in the analysis of stochastic transport [14], is the current, which we compute as

$$J = \left\langle \left| \frac{1}{N} \sum_{j=1}^N \dot{x}_j(t) \right| \right\rangle, \quad (7)$$

i.e., as the time average of the absolute mean velocity along the coordinate x . It gives a measure of the level of (not necessarily synchronised) firing in the ensemble.

Numerical results. – We have performed extensive computer simulations of the model defined by eqs. (1) and (2) for $a = 1.02$ (excitable regime) and $k = 1$, with the corresponding network dynamics. The results presented here are qualitatively representative of a broad parameter range in the same regime. Order parameters were computed after the system reached a stationary state, with no further changes in its dynamical behaviour.

In fig. 1, we show numerical results for the order parameters as functions of the reconnection rate λ , for the first reconnection scheme and various system sizes. Both for small and large values of λ , the Kuramoto order parameter is equal to one, while the Shinomoto-Kuramoto order parameter and the current vanish. This situation corresponds to a state where all the elements of the ensemble are at rest at the same point in phase space, namely, the fixed point $(x_{\text{eq}}, y_{\text{eq}})$.

For intermediate reconnection rates, on the other hand, we find an interval where the Kuramoto order parameter $\rho < 1$, indicating that the elements are distributed over phase space. Within the same interval, both the Shinomoto-Kuramoto order parameter ζ and the current J become positive and attain considerably high maxima. This is an indication of collective firing with a concurrent phase-space flow, and constitutes our main finding: reconnection events at intermediate rates induce self-organised coherent behaviour in an otherwise disconnected ensemble of FitzHugh-Nagumo excitable elements.

Figure 1 also shows that the order parameters become independent of the system size as N grows. This suggests that the regime of collective firing exists even in the thermodynamic limit.

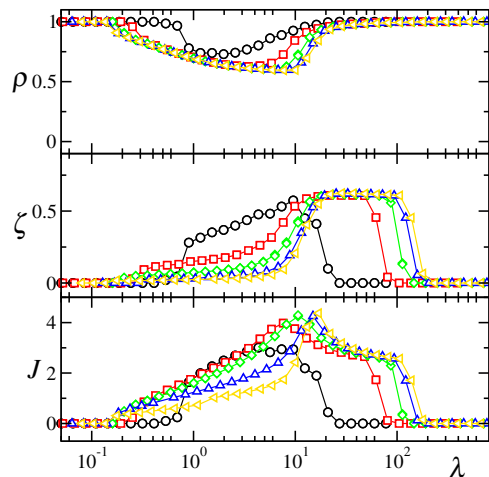


Fig. 1: (Colour on-line) The order parameters as functions of the reconnection rate λ , for the first reconnection scheme, with $k = 1$, $a = 1.02$, and $\epsilon = 10^{-3}$. Upper panel: the Kuramoto order parameter ρ . Central panel: the Shinomoto-Kuramoto order parameter ζ . Lower panel: the current J . Different curves correspond to different system sizes: $N = 10$ (\circ), 50 (\square), 200 (\diamond), 800 (\triangle), and 2000 (\triangleleft). Joining lines are plotted as a guide to the eye.

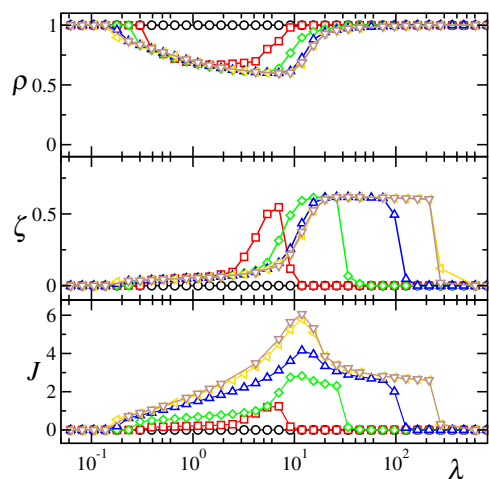


Fig. 2: (Colour on-line) As in fig. 1, for a system of size $N = 400$ and different values of the time-scale ratio: $\epsilon = 1$ (\circ), 10^{-1} (\square), 10^{-2} (\diamond), 10^{-3} (\triangle), 10^{-4} (\triangleleft), and 10^{-5} (∇).

Figure 2 displays the order parameters for different values of the time-scale ratio ϵ in a system of size $N = 400$. These results show that, when there is no difference in the time scales associated to the variables x and y ($\epsilon = 1$), collective firing is absent and all the elements remain quiescent at the fixed point. As ϵ decreases, however, the phenomenon takes place for intermediate values of λ and seems to approach a well-defined limit for $\epsilon \rightarrow 0$. We provide a semi-quantitative analysis of this limit in the next section.

To relax the condition that every element has a partner at any time, we have used our second reconnection scheme with two kinds of topologies for the

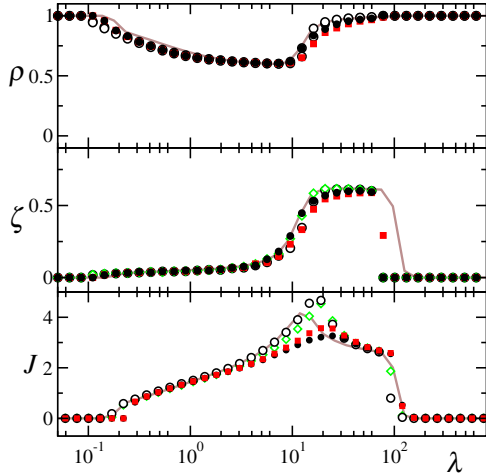


Fig. 3: (Colour on-line) As in fig. 1 for the second reconnection scheme, with $\epsilon = 10^{-3}$ and $N = 400$. Open symbols: scale-free underlying network generated by preferential attachment with $m = 3$ (\diamond) and 10 (\square). Full symbols: small-world underlying networks generated by rewiring with $p = 0.01$ (\bullet) and 0.1 (\blacksquare). The solid line corresponds to the results for the first reconnection scheme.

underlying network G . We recall that, with this scheme, the resulting instantaneous interaction pattern is —as was shown above— more sparse than in the previous case. Firstly, we have considered a scale-free underlying network generated by the preferential attachment rule [15], where each added node is connected to m pre-existing nodes. Secondly, we have taken a small-world network built up from the rewiring, with probability p , of the links of a two-dimensional network with Moore neighbourhood, following the Watts-Strogatz prescription [16]. We have numerically verified that, as advanced above, the average number of connected elements at long times fluctuates around $N/2$. For the scale-free networks, this number is slightly, but systematically, larger, which can be attributed to spurious degree-degree correlations in the highly heterogeneous degree distribution generated by preferential attachment in our finite-size system.

Figure 3 shows the order parameters for a system of size $N = 400$, underlain by scale-free networks with two values of m and small-world networks with two values of p . Solid curves stand for the corresponding results for the first reconnection scheme. Overall, the results are largely independent of both the reconnection scheme and the topology of the underlying network and, consequently, of the number of connected elements.

Interpretation. — Whereas a full analytical description of synchronised firing in dynamical networks of FitzHugh-Nagumo excitable elements seems to be out of reach, it is possible to sketch a semi-quantitative picture that plausibly explains the occurrence of this collective phenomenon for intermediate values of the network reconnection rate. The following arguments focus on our

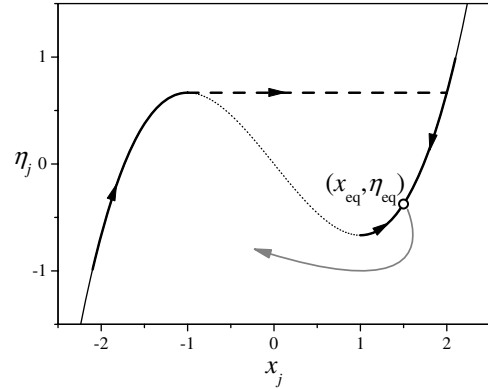


Fig. 4: Phase-space dynamics of a single non-interacting FitzHugh-Nagumo excitable element j on the (x_j, η_j) plane. The narrow line represents eq. (8). Arrowed bold lines are possible trajectories of the element. The fixed point $(x_{\text{eq}}, \eta_{\text{eq}})$ is represented as an empty circle. The grey arrow schematises the effect of a perturbation from the fixed point toward negative values of η_j .

first reconnection scheme, but can be straightforwardly extended to the second.

Consider eqs. (1) and (2) for $\epsilon \rightarrow 0$. In this limit, and in the absence of interactions ($k = 0$), the fast variable $x_j(t)$ follows adiabatically the slow variable $y_j(t)$ along the nullcline $\dot{x}_j = 0$. Let us introduce the auxiliary variable

$$\eta_j(x_j) = \frac{1}{3}x_j^3 - x_j \quad (8)$$

which, along the nullcline, satisfies $\eta_j = y_j + k(x_{j^*} - x_j)$. For $k = 0$, we have $y_j \equiv \eta_j$. Differentiating with respect to time and taking into account eq. (2) yields

$$\dot{\eta}_j = a - x_j(\eta_j) + k\xi_j, \quad (9)$$

with $\xi = \dot{x}_{j^*} - \dot{x}_j$ and $x_j(\eta_j)$ given by the inverse of the function in eq. (8). Note that $x_j(\eta_j)$ is defined piecewise, depending on how x_j compares with ± 1 .

The arrowed bold lines in fig. 4 represent the phase-space trajectories of a non-interacting element. In the limit $\epsilon \rightarrow 0$, it is always found on the stable branches (either $x_j < -1$ or $x_j > 1$) of the nullcline, and asymptotically approaches the fixed point at $(x_{\text{eq}}, \eta_{\text{eq}}) = (a, a^3/3 - a)$, plotted in the figure as an empty dot. If, as illustrated by the grey arrow, the element is perturbed from the fixed point toward negative values of η_j and beyond the minimum $\eta_j(x_j = 1) = -2/3$, it immediately reaches the leftmost stable branch and begins its excursion upwards. When it reaches $\eta_j(x_j = -1) = 2/3$, it jumps to the rightmost branch and, from then on, it moves toward the fixed point. The firing cycle is thus completed. Integration of eq. (9) with $k = 0$ and $a \gtrsim 1$ shows that, if the leftmost branch is reached at $\eta_j \approx -2/3$, the time spent on that branch is $\tau_{\text{left}} = 1/2 + \mathcal{O}[a - 1]$. In turn, the typical time for relaxation toward the fixed point on the rightmost branch is $\tau_{\text{right}} = a^2 - 1$.

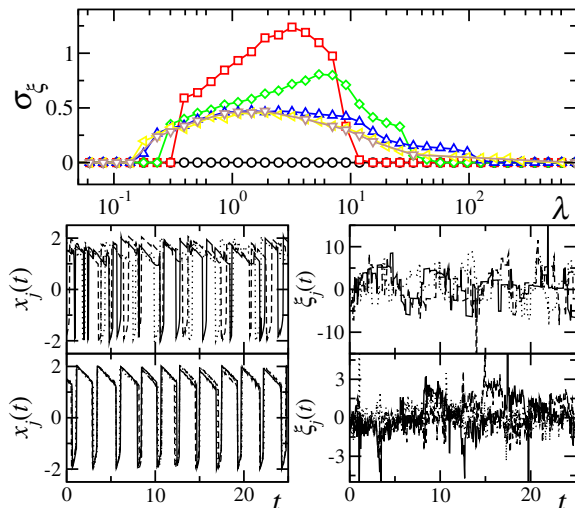


Fig. 5: (Colour on-line) Upper panel: standard deviation σ_ξ of the “noise” $\xi_j(t)$ as a function of the reconnection rate λ , for $k=1$, $a=1.02$, $N=400$, and different values of the time-scale ratio: $\epsilon=1$ (\circ), 10^{-1} (\square), 10^{-2} (\diamond), 10^{-3} (\triangle), 10^{-4} (\triangleleft), and 10^{-5} (∇). Lower panels: time evolution of the coordinate x_j and the “noise” ξ_j of three randomly selected elements, for $\epsilon=10^{-3}$, with $\lambda=0.32$ (upper row) and $\lambda=3.2$ (lower row).

Consider now the effect of interaction ($k \neq 0$) on the individual dynamics of element j . If the reconnection rate λ is sufficiently small, so that $\lambda^{-1} \gg \tau_{\text{left}}, \tau_{\text{right}}$, element j remains connected to the same partner j^* over times which are long as compared with the typical time scales needed to reach the vicinity of $(x_{\text{eq}}, \eta_{\text{eq}})$. Irrespectively of the value of k , the two coupled elements approach the fixed point well before their mutual link breaks and they are reconnected to different partners. When reconnection finally happens, however, all elements will be found near the fixed point and the change of partner will have essentially no effect on the subsequent dynamics of j . Therefore, the whole ensemble converges to $(x_{\text{eq}}, \eta_{\text{eq}})$ over times of order $\tau_{\text{left}} + \tau_{\text{right}}$ and remains there indefinitely. For sufficiently small λ , hence, sustained collective firing is absent.

As λ grows and reconnection becomes more frequent, the term $k\xi_j$ in the right-hand side of eq. (9) acquires the character of a fluctuating force, analogous to additive noise. Since $\xi_j(t) = \dot{x}_{j^*}(t) - \dot{x}_j(t)$, its time dependence consists of a relatively smooth variation along the periods where element j ’s partner j^* does not change, punctuated by sharp delta-like “kicks” when reconnection occurs. Even if j has already reached the vicinity of $(x_{\text{eq}}, \eta_{\text{eq}})$, a kick due to reconnection with an element which is transiting the leftmost branch region may force j to move away from the fixed point and reinitiate its firing cycle. This event is schematised by the grey arrow in fig. 4. At appropriate values of the reconnection rate, with most of the ensemble near $(x_{\text{eq}}, \eta_{\text{eq}})$, just a few “outliers” along the firing cycle are able to induce a cascade of transitions from the fixed point to the cycle, and collective firing is

thus triggered. Our numerical results show that, precisely, collective firing occurs for $\lambda \gtrsim 1 \sim (\tau_{\text{left}} + \tau_{\text{right}})^{-1}$.

If reconnection grows even more frequent, within the time scales relevant to the dynamics of a single element, the “noise” term $k\xi_j$ averages out to its mean value over the whole ensemble. Therefore, each element is effectively subject to the action of the average state of the ensemble. In this situation, the interaction between elements is equivalent to global (all-to-all) coupling [4,5]. Since all the elements are identical, global coupling leads the ensemble to collapse to the fixed point [2], and collective firing is thus suppressed.

The upper panel of fig. 5 shows the standard deviation σ_ξ of the “noise” $\xi_j(t)$, averaged over the ensemble and over time, as a function of the reconnection rate λ and for various values of the time-scale ratio ϵ . The lower panels show the coordinate $x_j(t)$ and the “noise” $\xi_j(t)$ as functions of time for a few selected elements, and two values of the reconnection rate: $\lambda=0.32$ (upper row), which corresponds to the threshold of global firing, and $\lambda=3.2$ (lower row), where global firing is well developed. For the latter, the synchronous pulsing of the coordinate $x_j(t)$ is apparent.

Conclusion. – Synchronised collective firing in ensembles of coupled excitable elements was known to be triggered by external noise [6,7] and by disorder in the interaction pattern [8] —in this latter case, due to the simultaneous presence of attractive and repulsive interactions. In both situations, the emergence of this form of collective behaviour requires the intensity of noise or the degree of disorder to be neither too small nor too high: it is at an intermediate level of fluctuations that the system has the appropriate dynamical flexibility as to self-organise into coherent evolution.

In this letter, we have shown that, in the absence of external noise, the fluctuations associated with network dynamics —when the interaction pattern is rewired with a certain frequency— are as well able to induce collective firing of coupled excitable elements. As in the previous instances, coherent evolution is observed for intermediate values of the rewiring frequency. In the present situation, network dynamics has the crucial additional role of replacing the connectivity necessary to warrant the spreading of information about the individual states of the excitable elements all over the ensemble. In fact, by construction, the instantaneous interaction pattern is highly diluted, with at most one neighbour connected to each element at any time. This effect of network dynamics had already been pointed out in chaotic synchronisation and in contact processes [4,5]. Our results suggest that the phenomenon of collective firing is remarkably independent of the underlying structure of interactions and has a well-defined behaviour in the thermodynamic limit of infinitely large ensembles.

The present analysis pertains to the study of the ample variety of systems where interaction patterns are not

static, but change with time either driven by external influences or in response to the state of the system itself, or as a combination of both effects. While this important dynamical aspect of complex systems has often been disregarded, our results —among other recent work— highlight its role in the emergence of self-organised collective evolution.

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