Complex self-sustained oscillation patterns in modular excitable networks

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We study the relationship between the modularity of scale-free excitable networks and their ability to support self-sustained oscillation patterns. In the process, we introduce a new method that can be used to analyze the propagation of waves in complex excitable networks at different levels of detail. We find that the probability for a network of given degree distribution exponent to be able to support self-sustained oscillations is strongly affected by its modularity. In addition, both high and low modularity networks are more likely to exhibit long-period oscillatory patterns than those with intermediate modularity, but the levels of complexity of the patterns in these two cases are different. The long period oscillations cannot be explained by the minimum length Winfree loop, but instead arise from the interplay between two or more weakly connected loops.

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I. INTRODUCTION

The propagation of waves in continuous excitable media[1, 2] as well as in discrete lattice structures[3] has been an important research topic for many years[4]. The propagation of spiral and target waves in both of these situations is well understood. In recent years, a number of authors have studied the sustained activity patterns in various complex network models[5–13], including simple small-world networks[14–19] as well as Erdős-Rényi networks[20, 21].

The interest in these network models is driven primarily by neuroscience[22–30]. In particular, it has been shown that wave propagation in complex neuronal networks is involved in many brain functions such as visual perception[28], cognitive processes[23, 29] and sleep-wakefulness[29]. In addition, the presence of high-degree neurons is crucial for the ability of the cortex to perform its information processing functions[31]. Long-period rhythmic synchronous firing has been observed in Barabási-Albert-like scale-free networks[32] and has been hypothesized to be the basis for the memorization of long temporal intervals.

However, all studies published so far are based on simple network models which, with the exception of Ref. 8, do not allow any independent control over important aspects of network topology like clustering, degree-degree correlations or community structure. The latter in particular has been shown to have a significant bearing on a network’s ability to perform its functions as it has generally been observed that subsets of a network whose nodes are more densely connected than in a random “null model” are likely to perform some function together[33–36]. In addition, the role played by the strength of the coupling between the neurons has not yet been systematically studied, even though it has been demonstrated that this parameter can strongly affect the behavior of the network[32]. Finally, no attempts have been made so far to study the statistics of ensembles of networks.

The main obstacle to the establishment of a self-sustained pattern of oscillations on small-world and even Erdős-Rényi networks is the rapid spreading of excitation through the high degree nodes, which places the bulk of the network in a refractory state. Intuitively, it is to be expected that a modular structure will be able to mitigate this effect by limiting the propagation of the excitations, and that it might even lead to situations where wave patterns that are only weakly coupled propagate across separate sets of communities. The results we present for ensembles of networks and for different values of the coupling coefficient confirm and quantify these considerations.

II. METHOD

The concept of community structure arises from the fact that many networks can be naturally divided into subsets of nodes such that the density of connections within these subsets is higher than between them. Networks that exhibit a clear structure of this kind are called modular. The simplest and most straightforward way to quantify the modularity of an undirected unipartite network is by means of the modularity function $Q$ introduced by Newman and Girvan in Refs. 35–37. This function is defined as

$$Q = \sum_{k=1}^{K} \sum_{i,j \in C_k} \left( A_{ij} - \frac{d_i d_j}{2m} \right),$$

(1)

where $A$ is the adjacency matrix of the network, $\{C_k\}$ with $k = 1, K$ is the set of communities, $d_i$ is the degree of node $i$ and $2m = \sum_{i=1}^{N} d_i$. If the community structure of a network is unknown, the maximization of the modularity function provides a way to identify it[38].

We considered ensembles of random scale-free networks with tunable modularity generated using the algorithm...
described in Ref. [38]. These undirected networks have a built-in community structure that is provided on output. The properties of the ensemble are controlled by a number of parameters which include the network size \( N \), the average degree \( \langle d \rangle \), the maximum degree \( d_{\text{max}} \) and the mixing parameter \( \mu \), which represents the average fraction of links running between different modules. The other parameters were kept at their default values, including the exponent of the power-law degree distribution \( \gamma = -2 \). It is important to note that the networks that were not fully connected were rejected.

Network dynamics was defined by a variant of the Bär-Eiswirth model[3],

\[
\begin{align*}
    \frac{du_i}{dt} &= \frac{1}{\varepsilon} u_i (1 - u_i) \left( u_i - \frac{v_i + b}{a} \right) + c \sum_{j \in N_i} (u_j - u_i), \\
    \frac{dv_i}{dt} &= f(u_i) - v_i,
\end{align*}
\]

(2)

where \( u_i \) and \( v_i \) are analogous to the concentrations of activator and inhibitor or to the membrane potential and recovery current, \( c \) is the strength of the coupling between neighboring nodes, \( N_i \) is the set of neighbors of node \( i \) and the function \( f(u) \) is defined by

\[
f(u) = \begin{cases} 
0 & \text{for } u < \frac{1}{3} \\
1 - 6.75a(1 - u)^2 & \text{for } \frac{1}{3} \leq u \leq 1 \\
1 & \text{for } u > 1
\end{cases}
\]

(3)

The system of differential equations was integrated using a fourth-order Runge-Kutta routine with integration step \( h = 1/128 \). Following previous work[2, 4, 12, 17, 20, 32], we set \( \varepsilon = 0.04 \), \( a = 0.84 \) and \( b = 0.07 \) but we explored a wide range of values for the coupling constant \( c \) between 0.1 and 0.7.

A number of previous studies have used the dominant phase-advanced driving (DPAD) method[17] to identify the source of the sustained oscillations on the network. This method builds a simplified subnetwork by retaining only the links between each node \( i \) and the neighbor which provides the strongest driving at the moment when \( u_i(t) \) crosses the threshold value \( b/a \) while increasing. Following extensive testing, we identified many situations where this is not the best choice, since it can lead to a false identification of the dominant driving node. Consider the example in Fig. 1 which shows the behavior of a node from a network generated with parameters \( N = 100 \), \( \langle d \rangle = 4 \), \( d_{\text{max}} = 15 \) and \( \mu = 0.3 \) for which the coupling strength was set to \( c = 0.5 \). This is a network with a relatively high modularity \( Q = 0.564930 \). A few nodes exhibit two above-threshold maxima of \( u \) in the course of a period (continuous line), but only one of them represents true firing. The lower maximum occurs while the node is strongly driven by a different set of neighbors, towards the end of its refractory period, but the concentration of inhibitor \( v \) is still too high and \( u \) drops as soon as the driving subsides. A simple way to avoid this problem is to define the dominant phase-advanced node of \( i \) as its strongest driver at the moment when the quantity

FIG. 1. (Color online) Amplitude \( u(t) \) (black continuous) and the factor \( \mu(t) \) (red dashed) for a node where DPAD fails. The horizontal gray line above zero represents the threshold \( b/a \).

FIG. 2. (Color online) Different degrees of simplification of the oscillating core for a network with \( N = 100 \) nodes and \( \langle d \rangle = 4 \): (a) with maximum individual thresholds \( D_{\text{th},i} = D_{i,\text{max}} \) and (b) with maximum collective threshold \( D_{\text{th}} = \min \{ D_{i,\text{max}} \} \).
FIG. 3. Discrete Fourier transforms ((a) and (c)) and plots of \( u_{\text{tot}} \) vs. \( t \) ((b) and (d)) for long-period oscillation patterns of two networks with \( N = 100 \) and \( \langle d \rangle = 4 \) but different modularities.

\[ w_i = (u_i - \frac{w_{i+k}}{a}) \] (dashed line in Fig. 1) crosses 0 while increasing. This provides essentially the same timing as the older version in the case of true firing but avoids the futile firing attempts during the refractory period.

In addition, there are situations when two or more nodes provide roughly equal driving to a common neighbor and, moreover, that neighbor would not be able to fire at the right time to continue the propagation of the wave without all major contributions. Therefore, it is important to be able to generate subnetworks exhibiting a variable degree of simplification. Such a subnetwork would include the links between every node and all its major drivers. One way to achieve this is to build a "driving matrix" whose elements \( D_{ij} \) are the averages of the differences \( (u_j - u_i) \) recorded at times when \( w_i(t) = 0 \) while increasing and then setting all elements below a certain threshold equal to zero. In addition, as a way to focus on the nodes that are essential to the propagation of the self-sustained oscillations, one can recursively remove all the "dead-end" nodes which do not contribute to the driving of any neighbor.

The detailed procedure is as follows:

1. For every node \( i \) and every \( j \in \mathcal{N}_i \), record the values of \( (u_j - u_i) \) at every moment when \( w_i(t) = 0 \) and \( \frac{dw_i}{dt} > 0 \). If the network’s phase space trajectory settles on an attractor, one may wish to consider only values recorded after this has happened.

2. At the end of the simulation, compute the driving coefficients \( D_{ij} = \langle u_j - u_i \rangle \). If \( i \) and \( j \) are not connected set \( D_{ij} = 0 \).

3. For every node \( i \), identify the largest driving coefficient \( D_{i,\text{max}} \).

4. Choose a threshold value \( 0 \leq D_{th} \leq \min\{D_{i,\text{max}}\} \) and if \( D_{ij} < D_{th} \) set \( D_{ij} = 0 \). Alternatively, one can use separate thresholds \( 0 \leq D_{th,i} \leq D_{i,\text{max}} \) for every node.

5. For every node \( i \) that does not contribute to the driving of a neighbor set \( D_{i} = 0 \). Repeat this step until no such nodes are found.

6. Symmetrize the matrix \( D \) by setting \( D_{ij} = \max(D_{ij}, D_{ji}) \) and, if desired, set all non-zero coefficients equal to 1.

7. Treat the rows and columns of matrix \( D \) that contain non-zero elements as the adjacency matrix of the "oscillating core" subnetwork.

Two subnetworks representing different degrees of simplification of the network from which the example in Fig. 1 was taken are shown in Figs. 2 (a) and (b), corresponding to setting individual \( D_{th,i} = D_{i,\text{max}} \) and respectively a global \( D_{th} = \min\{D_{i,\text{max}}\} \). The arrows in these figures show the direction of propagation of the wave,
derived from the coefficients of the “driving matrix” $D_{ij}$ before symmetrization (Step 6). In Refs. [17, 20] the authors describe only situations where the activity on the entire network can be traced to waves propagating along a single Winfree loop [21, 59]. We see from Fig. 2 (a) that this description is incomplete, since multiple loops may be present within a certain wave pattern. Note that the two loops do not have the same length, which means that the network must include a mechanism for their synchronization. Fig. 2 (b) shows a still simple but much more complete picture of the network’s workings. Loop {46, 33, 37, 31, 5, 8} is doubled by another loop exhibiting weaker driving {46, 44/88, 100, 95, 25, 87, 39} with the propagation along the latter (longer) loop being sped up by early activation of node 25 by node 37. At the same time, these loops contribute to the driving of loop {45, 97, 99, 91, 26, 67, 43} through the links {46, 45} and {25, 26}. It is important to note that some of the additional links shown in Fig. 2 (b) are critical for the persistence of the wave pattern on the network. If any one of links {46, 45}, {37, 25} or {39, 46} is removed, no self-sustained pattern can be established on this network. On the other hand, removing only {25, 26} still allows a slightly different self-sustained pattern.

This analysis method was applied systematically, combined with discrete Fourier analysis of the oscillation pattern, to study ensembles of networks with different modularity and different coupling strength parameters $c$. While detailed statistical results are presented in the following section, here we focus on the presence of complex, long-period wave patterns. In Refs. [22, 32], the length of the period on both Erdős-Rényi and some simple models of small-world networks was connected to the length of the minimum Winfree loop on the network. Our results indicate that many complex excitable networks exhibit periodicity that cannot be explained within this framework, but results from the interplay between two or more loops. This is especially true in the case of networks with high modularity. On some of these networks the source of the oscillations can, in fact, be traced to a single short loop, but the response from the rest of the network to the driving produced by this loop involves other loops and spans a large number of its periods. Detailed analysis has frequently shown reversals of the direction of propagation along some of the loops that are part of the “oscillating core”. It is important to note, however, that a given network may exhibit a large number of stable oscillatory patterns with different periods.

Qualitatively different types of long-period behavior have been observed in the case of low- and high-modularity networks. Representative results are shown in Fig. 3. The Fourier transform of $u_{tot} = \sum_{i=1}^{N} u_i$ and a plot of $u_{tot}$ vs. time are shown in Figs. 3 (a) and respectively (b) for a scale-free network of $N = 100$ nodes,
average degree \(\langle d \rangle = 4\) and relatively low modularity, \(Q = 0.404074\). The coupling parameter in this case is \(c = 0.30\). The oscillatory pattern consists of a series of nonidentical bursts of synchronous firing interrupted by longer periods of low activity, with a period \(P_L = 64.8\). This pattern is qualitatively typical for the low modularity networks that exhibit long periodicity. Note that the same network also supports an oscillatory pattern with a much shorter period, \(P_S = 7.42\), slightly different from the 7.2 period of the prominent ninth harmonic of the long period variant. The picture is quite different in the case of high modularity networks. Results for one such network, also with \(N = 100\) and \(\langle d \rangle = 4\) but a much higher modularity \(Q = 0.765741\), are shown in Figs. 3 (c) and (d). A lower value of the coupling parameter \(c = 0.15\) was used in this case. The oscillatory pattern now consists of three distinct, less synchronous, bursts, each confined to a different part of the network. This shows that a modular structure may indeed prevent global synchronous firing, instead causing the excitation to cycle through the set of communities. The resulting period in this case is \(P_L = 82.6\). The same network also exhibits two periodic oscillation patterns of periods 32.7 and 34.3, as well as sustained non-periodic oscillations.

III. RESULTS FOR STATISTICAL ENSEMBLES

In this section we present results concerning the relationship between modularity and the likelihood for a network to exhibit self-sustained oscillation patterns, as well as between modularity and the period of the wave pattern. The statistical ensemble for each set of parameters \(N, \langle d \rangle, d_{\text{max}}\) and \(\mu\) consisted of 100 networks. Each network was started 1000 times with random initial conditions, the sets \(\{u_i\}\) and \(\{v_i\}\) being independently and uniformly distributed between 0 and 1.

Fig. 4 shows the fraction \(f_{\text{sust}}\) of networks of size \(N = 100, \langle d \rangle = 4\) and \(d_{\text{max}} = 15\) that exhibit self-sustained oscillation patterns as a function of the mixing parameter \(\mu\) for different values of the coupling parameter ranging from \(c = 0.1\) to \(c = 0.7\). Note that a high value of \(\mu\) means a low average modularity of the network ensemble, with \(\langle Q \rangle\) decreasing from about 0.8 to about 0.4 from left to right. These results prove that modularity plays a critical role in a network’s ability to support self-sustained oscillation patterns. The fraction \(f_{\text{sust}}\) exhibits a rapid overall increase with \(c\) between 0.1 and 0.15. Above \(c = 0.2\), \(f_{\text{sust}}\) begins to decrease with increasing \(c\) in the case of low modularity networks due to the fact that the hubs can now be excited by the simultaneous firing of a smaller number of neighbors, leading to “epileptic” firing. However, a highly modular structure is able to mitigate this effect and \(f_{\text{sust}}\) remains high for such networks until it finally starts to decrease above \(c = 0.7\).

The dependence on \(c\) and \(\mu\) is similar but much more pronounced if one looks at the average number of successful phase space realizations \(\langle n \rangle\) (out of 1000), displayed in Figs. 5 and 6. This count is averaged over the 100 realizations of the network ensemble. The error bars in these figures represent the error on the mean. The results in Fig. 5 are for \(N = 100, \langle d \rangle = 4\) and \(d_{\text{max}} = 15\) while those in Fig. 6 are for \(N = 300, \langle d \rangle = 5\) and \(d_{\text{max}} = 20\). Thus, the ratio \(d_{\text{max}}/\langle d \rangle\) is essentially the same but the ratio \(N/\langle d \rangle\) is significantly larger in the second case. The larger but sparser networks exhibit a new feature, namely an optimum for values of the mixing parameter around \(\mu = 0.2\) but \(\langle n \rangle\) still decreases rapidly with decreasing modularity beyond that. We also counted the number of distinct oscillation pattern variants, which is typically much less than the number of successful phase space realizations, but the results for that quantity are similar to those for \(\langle n \rangle\).

The last set of results concerns the relationship between modularity and the average period \(\langle P \rangle\) of the wave pattern on the network. The period was calculated from the lowest frequency peak (not necessarily the highest) in the discrete Fourier transform of \(u_{\text{tot}} = \sum_{i=1}^{N} u_i\) using the last 4096 recorded sets of values. To better correlate the average period with modularity, we considered the union of all network ensembles with given \(N, \langle d \rangle\) and \(d_{\text{max}}\) but different values of \(\mu\) and the resulting range for \(Q\) was divided into 10 bins. The period was averaged over all “successful” phase space realizations of all networks with modularity within a given bin.

Results for networks of size \(N = 100\) are shown in Fig. 7 where the horizontal bars represent the extent of each modularity bin and the vertical bars represent the error on the mean. While the dependence of the average period on modularity changes in complex ways when the coupling coefficient is varied, there is a clear trend of overall decrease with increasing \(c\), again as a result of the network hubs’ increased susceptibility. The curves for \(c > 0.4\) are statistically indistinguishable from that
FIG. 7. (Color online) The average period $\langle P \rangle$ for different modularity ranges and different values of the coupling coefficient $c$ for networks of size $N = 100$ and average degree $\langle d \rangle = 4$. The vertical bars represent the error on the mean while the horizontal bars show the extent of each modularity bin.

It is important to mention that, while the average period varies as shown in Fig. 7, the actual values of the periods in each $Q$ range are distributed over wide intervals, from less than 10 up to hundreds in some bins. The question that arises is whether there is a correlation between period and some other quantity characterizing either the topology of the network or the oscillation pattern. Tests failed to reveal any correlation between period and the average degree of the network within a given modularity range or for a given value of the mixing parameter $\mu$. Likewise, there is no correlation between period and the size of the smallest oscillating core defined using individual link thresholds $D_{th,i} = D_{i,max}$ or the size of the larger core defined using a global $D_{th} = \min\{D_{i,max}\}$. However, we found a positive correlation between period

for $c = 0.4$. The most important feature is the presence of a minimum of the average period around $Q = 0.6$, which suggests different mechanisms for the generation of long period oscillations at the two ends of the modularity range. The results for $N = 300$ are qualitatively similar but the modularity values are higher and the minimum is around $Q = 0.75$.
and the fraction $f_{\text{mod}}$ of modules that have at least one node in the larger core component, as shown in Figs. 5 (a) and (b), where the average period is plotted against $f_{\text{mod}}$. Interestingly enough, the correlation with the fraction of modules represented in the smaller core is much weaker. These results seem to hold regardless of network size, the value of the coupling parameter, or, more importantly, the value of the modularity and show that long periods are associated with propagation patterns where most of the modules are involved in at least one loop, not necessarily the ones that are the primary source of the oscillation.

IV. CONCLUSIONS

We introduced a new method for analyzing the self-sustained oscillation patterns on complex excitable networks, which can be used to analyze the propagation pattern at different levels of detail. We studied the relationship between modularity and the oscillatory patterns for networks of different sizes and found that high modularity networks are much more likely to be able to support self-sustained oscillation patterns compared to low modularity networks of the same size and average degree. In addition, the measure of the subset of points in phase space from which a self-sustained oscillation pattern can be initiated increases quickly with increasing modularity. The same is true about the number of distinct oscillation pattern variants.

We found that both low- and high-modularity networks can support long-period oscillations, but these oscillations are qualitatively different, with series of synchronized network-wide bursts in the case of low-modularity networks and series of complex, localized bursts in the case of networks with high modularity. Regardless of modularity, such long period oscillations cannot be explained by the length of any simple loop on the network, but by interactions between excitations driven along different loops. This proves that the memorization of complex, long duration patterns does not necessarily require long minimum Winfree loops, as it has been shown to be the case with Erdős–Rényi and certain simple small-world networks.

[1] R. Kapral, Physica D 86, 149 (1995).
[2] E. Meron, Physics Reports 218, 1 (1992).
[3] J. Chen, L. Peng, Y. Zhao, S. You, N. Wu, and H. Ying, Commun. Nonlin. Sci. Numer. Simulat. 19, 60 (2014).
[4] M. Bär and M. Eiswirth, Phys. Rev. E 48, R1635 (1993).
[5] O. Steinbock, J. Schütze, and S. C. Müller, Phys. Rev. Lett. 68, 248 (1992).
[6] I. Aranson, L. Kramer, and A. Weber, Phys. Rev. Lett. 72, 2316 (1994).
[7] Y. Qian and Z. Zhang, PLoS ONE 11, e0149842 (2016).
[8] M. C. Cross and P. C. Hohenberg, Rev. Mod. Phys. 65, 851 (1993).
[9] M. Müller-Linow, C. C. Hilgetag, and M.-T. Hütt, PLoS Comput. Biol. 4, e1000190 (2008).
[10] O. I. Kanakov and G. V. Osipov, Chaos 17, 015111 (2007).
[11] J. Ma, X. Song, J. Tang, and C. Wang, Neurocomputing 167, 378 (2015).
[12] X. Liao, Q. Xia, Y. Qian, L. Zhang, G. Hu, and Y. Mi, Phys. Rev. E 83, 056204 (2011).
[13] F. M. M. Akmeni, E. M. Inack, and E. M. Yamakou, Phys. Rev. E 89, 052919 (2014).
[14] H. Riecke, A. Roxin, S. Madruga, and S. A. Solla, Chaos 17, 026110 (2007).
[15] Y. Qian, Commun Nonlinear Sci Numer Simulat 27, 12 (2015).
[16] S. Sinha, J. Saramäki, and K. Kaski, Phys. Rev. E 76, 015101(R) (2007).
[17] Y. Qian, X. Huang, G. Hu, and X. Liao, Phys. Rev. E 81, 036101 (2010).
[18] Y. Kobayashi, H. Kitahata, and M. Nagayama, Phys. Rev. E 96, 022213 (2017).
[19] A. Roxin, H. Riecke, and S. A. Solla, Phys. Rev. Lett. 92, 198101 (2004).
[20] Y. Qian, Phys. Rev. E 90, 032807 (2014).
[21] Y. Qian and Z. Zhang, Commun Nonlinear Sci Numer Simulat 47, 127 (2017).
[22] Y. Qian, X. Cui, and Z. Zheng, Scientific Reports 7, 5746 (2017).
[23] A. Avena-Koenigsberger, B. Misic, and O. Sporns, Nature Reviews Neuroscience 19, 17 (2018).
[24] Z. Zheng and Y. Qian, Chin. Phys. B 27, 015101 (2010).
[25] M. Bazhenov, I. Timofeev, M. Steriade, and T. J. Sejnowski, Nat. Neurosci. 2, 168 (1999).
[26] N. F. Rulkov, I. Timofeev, and M. Bazhenov, J. Comput. Neurosci. 17, 203 (2004).
[27] G. Buzsáki and A. Draguhn, Science 304, 1926 (2004).
[28] W. M. Usrey and R. C. Reid, Annu. Rev. Physiol. 61, 435 (1999).
[29] L. M. Ward, Trends Cognit. Sci. 7, 553 (2003).
[30] M. Steriade, D. A. McCormick, and T. J. Sejnowski, Science 262, 679 (1993).
[31] N. M. Timme, S. Ito, M. Myroshnychenko, S. Nigam, M. Shimono, F.-C. Yeh, P. Hottowy, A. M. Litke, and J. M. Beggs, PLoS Comput Biol 12, e1004858 (2016).
[32] Y. Mi, X. Liao, X. Huang, L. Zhang, W. Gu, G. Hu, and S. Wu, PNAS, E4931 (2013).
[33] S. Fortunato, Physics Reports 486, 75 (2010).
[34] M. E. J. Newman and M. Girvan, Phys. Rev. E 69, 026113 (2004).
[35] M. E. J. Newman, Phys. Rev. E 74, 036104 (2006).
[36] M. E. J. Newman, Proc. Natl. Acad. Sci. USA 103, 8577 (2006).
[37] M. E. J. Newman, Phys. Rev. E 69, 066133 (2004).
[38] A. Lancichinetti, S. Fortunato, and F. Radicchi, Phys. Rev. E 78, 046110 (2008).
[39] W. Jahnke and A. T. Winfree, Int. J. Bifurcation Chaos Appl. Sci. Eng. 1, 445 (1991).