Complete Mean-Field Theory for Dynamics of Binary Recurrent Networks

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We develop a unified theory that encompasses the macroscopic dynamics of recurrent interactions of binary units within arbitrary network architectures. Using the martingale theory, our mathematical analysis provides a complete description of nonequilibrium fluctuations in networks with a finite size and finite degree of interactions. Our approach allows the investigation of systems for which a deterministic mean-field theory breaks down. To demonstrate this, we uncover a novel dynamic state in which a recurrent network of binary units with statistically inhomogeneous interactions, along with an asynchronous behavior, also exhibits collective nontrivial stochastic fluctuations in the thermodynamical limit.

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An important means to understand the collective dynamics of high-dimensional spin systems is to use the mean-field theory (MFT) to describe the activity of the system population in terms of associated lower-dimensional dynamics [1]. The classical characterization of the emerging states uses the analysis of the systems' Hamiltonian functions [2]. However, this powerful approach cannot be applied, if the underlying interactions among units are directed and asymmetrically disordered as in various soft materials [3] and, in particular, recurrent neuronal networks [4], in contrast to the bidirectionality of interactions in spin glasses [1]. The formulation of MFTs in these cases typically assumes statistically homogeneous interactions among units in extensively large networks [4,5]. The standard theoretical framework here is to expand the system's master equation (so-called Kramers-Moyal expansion), in which the lowest-order tree-level expansion of these theories yields the mean-field limit and systematic corrections can be obtained by perturbative and renormalization group methods [2]. In the case of statistically homogeneous binary recurrent networks, various methods have been used to obtain finite-size fluctuations [6], and an interesting approach to analyze the mean-field limit of a single instance of asymmetric Ising networks has been investigated [7]. However, no general theory has been developed to treat systems with statistically inhomogeneous and asymmetric interactions. In this Letter, we use a surprisingly elementary method that can be used to remove the need for these assumptions by deriving a novel MFT that captures the dynamic behavior of recurrent networks with binary units, including finite-size effects on population fluctuations. In this framework, we isolate the finite-size fluctuation of the system in the martingale structure of the network's Markovian dynamics and derive the macroscopic behavior of the system given the gain function of individual units. Our mathematical approach readily identifies the conditions on the connectivity structure that are necessary to guarantee the convergence of the average population activity to a deterministic limit. Furthermore, our analysis reveals a novel dynamic state in a network with inhomogeneous coupling, in which the large-amplitude fluctuations of the average population activity survive irrespective of the network size. Such stochastic synchronization could be relevant for the description of collective neocortical network dynamics.

Consider a *model network* that is described by an adjacency binary matrix $\mathbf{J} = (J_{ij})$ of N binary units, whose current states are denoted as $\mathbf{n}(t) \coloneqq (n_1(t), \ldots, n_N(t))$. The vector $\mathbf{n}(t)$ is a time-continuous Markov chain on $\{0,1\}^N$ with a rate matrix, where $Q(\mathbf{n},\mathbf{m}) = 0$ if and only if $||\mathbf{n}-\mathbf{m}|| \geq 2$ and

$$Q(\mathbf{n},\mathbf{m}) = \begin{cases} f_i(\mathbf{n}) & \text{if } \mathbf{m}-\mathbf{n} = \mathbf{e_i} \\ 1-f_i(\mathbf{n}) & \text{if } \mathbf{m}-\mathbf{n} = -\mathbf{e_i}, \end{cases}$$

where $e_j^{(i)} = \delta_{ij}$ denotes the ith unit vector. In order to comply with the centralization property of Q matrices, it follows that $Q(\mathbf{n},\mathbf{n}) = -\sum_{i=1}^N n_i(t)[1-2f_i(\mathbf{n}(t))] + f_i(\mathbf{n}(t))$. The analytical gain function $f_i(\mathbf{n}(t))$ defines the state transition rate of a unit i, given the state of the network $\mathbf{n}(t)$, and it is assumed to take values in the range [0, 1]. Typically, this function is written as $f_i(u_i(t))$, where $u_i(t)$, which represents the input to the unit i with the scaling parameter $0 < \gamma$, is written as

$$u_i(t) \coloneqq \bar{J} K_i^{-\gamma} \sum_{j=1}^N J_{ij} n_j(t) + K_i^{1-\gamma} \mu_{0,i}, \tag{1}$$

where $\bar{J}$, K_i, and $\mu_{0,i}$ are the coupling strength, the number of recurrent input units ($K_i \coloneqq \sum_j^N J_{ij}$), and the external drive to the ith unit, respectively. For the convenience of the current presentation, we consider here networks with $K_i = K$, $f_i = f$, and $\mu_{0,i} = \mu_0$ for all i. We will provide below [in Eqs. (10) and (11)] conditions on the network structure **J** that imply the convergence of the averaged population activity in the network towards a deterministic limit

$$m(t) \overset{!}{=} \lim_{N\to\infty} \frac{1}{N} \sum_{i=1}^{N} n_i(t). \tag{2}$$

Here, $m(t)$ is known as the mean-field limit and has the following temporal dynamics:

$$\frac{d}{dt} m(t) = -m(t) + F(m(t)) \tag{3}$$

for some *a priori* unknown function F. In order to determine F, we use the following semimartingale decomposition, that specifies the difference between $\bar{n}(t) \coloneqq (1/N)\sum_{i=1}^{N} n_i(t)$ (i.e., the average population activity of a finite-size network) and the mean-field limit $m(t)$ of the system:

$$\begin{aligned} \bar{n}(t) - m(t) = [\bar{n}(0) - m(0)] - \int_0^t ds[\bar{n}(s) - m(s)] \\ + \int_0^t ds \left(\frac{1}{N} \sum_{i=1}^{N} f(u_i(t)) - F(m(s)) \right) \\ + \mathcal{M}(t), \end{aligned} \tag{4}$$

where $\mathcal{M}(t)$ is some square integrable martingale that, according to the general theory of Markov processes [8], satisfies

$$E[\mathcal{M}(t)^2] = \frac{1}{N^2} \int_0^t ds E[-Q(\mathbf{n}(s), \mathbf{n}(s))] \leq \frac{t}{N}, \tag{5}$$

where E is the expectation operator. Note that $E[\mathcal{M}(t)] = 0$ and, in general, $\mathcal{M}(t)$ specify finite-size fluctuations in the average population activity. Provided that $m(t)$ exists [refer to Eqs. (10) and (11) for a justification of this ansatz], we can construct the function F by expanding $(1/N)\sum_{i=1}^{N} f(u_i(t))$ as $N \to \infty$ in Eq. (4) around

$$\mu_1(t) \coloneqq K^{1-\gamma}[\bar{J} m(t) + \mu_0]. \tag{6}$$

Using the lemma that is described in Ref. [9], we obtain the following series expansion:

$$F(m(t)) = f(\mu_1(t)) + \sum_{r=2}^{\infty} \frac{f^{(r)}(\mu_1(t))}{r!} \mu_r(t), \tag{7}$$

where μ_1 represents the average input to a unit in the network at time t. The higher-order coefficients can be computed by expanding $\mu_r \coloneqq \lim_{N\to\infty}(1/N)\sum_{i=1}^{N}[(u_i - \mu_1)^r]$. The second-order coefficient is given by

$$\mu_2(t) = \bar{J}^2 K^{1-2\gamma} m(t)[1 - m(t)], \tag{8}$$

and the subsequent coefficients are given by

$$\mu_r(t) = \bar{J}^r K^{-r\gamma} \sum_{q=0}^{r} a_q m(t)^q \sum_{s=0}^{r-q} b_s m(t)^s, \tag{9}$$

where

$$a_q \coloneqq \binom{r}{q} (-1)^q K^q$$

and

$$b_s \coloneqq \mathcal{S}(r-q, s)(K)_s.$$

Here, $\mathcal{S}$ is a Stirling number of the second kind, and $(\cdot)_s$ denotes the falling factorial. In the binomial expansion of $\mu_r(t)$ given in Eq. (9), the summation over j (note that j is hidden in the definition of u_i) is performed using the ansatz that $m(t)$ exists; thereafter, summation over i in the average operator $\lim_{N\to\infty}(1/N)\sum_{i=1}^{N}[\cdot]$ is applied. In order to provide the sufficient conditions for the existence of a deterministic limit $m(t)$, the summation order must be changed. Therefore, the first condition for $m(t)$ and $\mu_1(t)$ to exist is

$$\lim_{N\to\infty} \frac{1}{N^2} \sum_{j=1}^{N} \left[\sum_{i=1}^{N} \left(J_{ij} - \frac{K}{N} \right) \right]^2 = 0. \tag{10}$$

This condition essentially states that column sum distribution of the connectivity matrix must obey the weak law of large numbers (LLNs), and Eq. (10) implies that the coefficient in front of f' in the series expansion that leads to Eq. (7) vanishes in the thermodynamic limit [9]. The second condition for the pointwise convergence of an averaged population activity to the MFT in Eq. (2) is given by

$$\lim_{N\to\infty} \frac{1}{N^2} \sum_{j_1 \neq j_2}^{N} \left[\sum_{i=1}^{N} \left(J_{ij_1} J_{ij_2} - \frac{K(K-1)}{N(N-1)} \right) \right]^2 = 0. \tag{11}$$

This condition specifies that, as $N \to \infty$, the mean covariance of columns in the connectivity matrix **J** must satisfy the LLNs. The higher-order condition can be similarly determined in order to achieve a pointwise convergence of the averaged population activity to its mean-field limit, as described in Ref. [9]. An important result here is that the condition in Eq. (10) implies that Eq. (11) and all higher-order conditions are satisfied for all fixed-in-degree networks and iid connectivity matrices, and therefore the MFT in Eq. (3) becomes universal for those coupling structures.

In the above calculation, we assume networks with finite input connections per unit (i.e., K). However, it is often of interest to study network dynamics when the number of inputs into units is large (e.g., $K \to \infty$). In order to study this classical case, we must investigate the asymptotic behavior of μ_r in Eq. (9) in the order of K; it can be observed that the odd coefficients are given by

$$\mu_{2k+1} \sim O(K^{1-(2k+1)\gamma})$$

and the even coefficients are given by

$$\mu_{2k} \sim O(K^{1-2k\gamma}) + (2k-1)!!\mu_2^k,$$

for $k \in \mathbb{N}$. Hence, it is apparent that the scaling parameter γ plays a critical role in the large K limit. The scaling parameter γ is generally assumed to take the value 0.5; in this case, $\mu_2 \sim O(1)$ and the mean-field coefficients of Eq. (3) converge as $K \to \infty$, towards the central moments of a Gaussian distribution function, and the network can be asynchronous similar to the nonequilibrium and chaotic dynamics observed in Ref. [4]. As a result, the related power series that is given by Eq. (7) can be reformulated in terms of a simple Gaussian integral; in this special case, Eq. (3) reduces to

$$\frac{d}{dt}m(t) = -m(t) + \int dx f(x)\mathcal{N}(x;\mu_1,\mu_2), \qquad (12)$$

where $\mathcal{N}$ is a Gaussian density. In the above analysis, we first take $N \to \infty$ to arrive at the mean-field of Eq. (3), and then we consider $K \to \infty$ in order to recover Eq. (12). This derivation recovers the result that has been previously known [4,12], while it provides insight on the structure of corrections to Gaussian density for finite K networks. Our analysis here shows that the finite K correction to Eq. (12) is relatively small. Thus, using asymptotic corrections up to the θth order to the Gaussian density, the function F for a finite K is given by

$$F(m(t)) = \int dx f(x)[1+\mathcal{G}_\theta(x)]\mathcal{N}(x;\mu_1,\mu_2), \qquad (13)$$

where $\mathcal{G}_\theta(x) \coloneqq \sum_{k=3}^{\theta}[(-1)^k\mu_k/k!\mu_2^{k/2}]H_k(x-\mu_1/\sqrt{\mu_2})$; here, H_k is a Hermite polynomial of kth order. This representation is the usual form of the Gram-Charlier expansion (the so-called type A series) is an expansion of a probability density function about a Gaussian distribution with common μ_1 and μ_2 [13]. This expansion has been used in Eq. (C2) of Dahmen, Bos, and Helias [12] to include finite-size corrections due to pairwise correlations in the MFT. The structure of centralized moments in Eq. (9) allows for an arbitrary precise calculation of the mean-field limit. It is noteworthy that Eq. (13) is the steady-state mean-field limit for all possible fixed-in-degree networks.

The semimartingale decomposition that is given in Eq. (4) provides information on the *finite-size* scaling of the system. Using Eq. (5), we can determine the fluctuation magnitude of the average population activity in finite networks in the mean-square sense as

$$E[\mathcal{M}(t)^2] = \frac{1}{N^2}\int ds E\left(\sum_{i=1}^{N} n_i(s)[1-2f(u_i(s))] + f(u_i(s))\right),$$

and, by expanding $(1/N)\sum_{i=1}^{N} f(u_i(t))$ at $\mu_1(t)$, we arrive at

$$E[\mathcal{M}(t)^2] = \frac{1}{N}\int_0^t ds(m(s)\{1-2[g(\mu_1)+\mathcal{R}]\}+g(\mu_1)+\mathcal{R}), \qquad (14)$$

where $g(\mu_1) \coloneqq f(\mu_1(t)) + f''(\mu_1)\mu_2/2$ and $\mathcal{R} \coloneqq \sum_{r=3}^{\infty}[f^{(r)}(\mu_1)/r!]\mu_r$ denotes the remainder terms of the expansion. The average population activity dynamics of a finite-size network can be described approximately in terms of the following Ornstein-Uhlenbeck process:

$$d\bar{n}(t) \approx [-m(t) + F(m(t))]dt + \frac{\sigma(t)}{\sqrt{N}}d\mathcal{B}_t, \qquad (15)$$

where $\sigma^2(t) \coloneqq m(t)[1-2g(\mu_1(t)) + g(\mu_1(t))]$ and $\mathcal{B}_.$ is Brownian motion. In the approximation of Eq. (15), we ignore the contribution of remainder terms (e.g., $\mathcal{R}$) to $\sigma(t)$. Our result recovers previously known scaling of the finite-size fluctuations [14] using the semimartingale method.

In order to *demonstrate the applicability* of our approach, we consider two scenarios that are relevant to the theoretical analysis of neural systems. The first scenario is that units receive a constant external input $\mu_0 > 0$. When $\bar{J} < 0$ and $\gamma = 0.5$, this system exhibits a nonequilibrium and chaotic state for which the external input is canceled by internal recurrent dynamics [4]. We choose a widely used gain function in the neural networks theory which is given by

$$f(x) \coloneqq \frac{1+\mathrm{Erf}(\alpha x)}{2}. \qquad (16)$$

The parameter α describes the intrinsic noise intensity of the individual units and therefore must be positive. When $\alpha \to \infty$, this transfer function approximates to the well-studied Heaviside step function [4,12]. Using the transfer function given by Eq. (16) (with $\alpha = 5$) and a directed fixed-in-degree Erdős-Rényi network (with $K = 10$), we compute the complete steady-state mean-field limit using Eq. (13) by including up to the fifth-order corrections (Fig. 1, red line). We compare the complete MFT (Fig. 1, red line) with the mean-field prediction that assumes only Gaussian statistics (i.e., $K \to \infty$) in Eq. (12) (Fig. 1, dashed gray line). The difference between the predictions becomes apparent as $|\bar{J}|$ increases. Numerical simulations of a finite-size network ($N = 1000$) are used to estimate the steady-state population activity by averaging 20 independent trials (Fig. 1, black dots). The equilibrium population average activity of simulated networks (Fig. 1, black dots) exhibits excellent agreement with both the complete (Fig. 1, red line) and the Gaussian approximation (Fig. 1, dashed gray line) of the mean-field limit in the case of weak coupling. However, in cases where the coupling is strong, the average population equilibrium activity deviates from the Gaussian

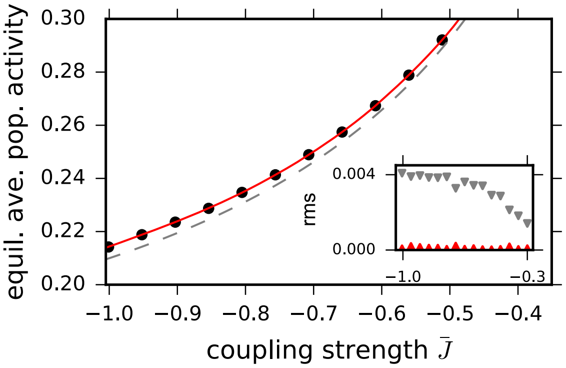

FIG. 1. Convergence of the average population activity to the steady-state MFT predictions. The red line indicates the predictions of the complete MFT up to fifth-order correction. The dashed gray line is the predictions of mean-field equation (12), assuming only Gaussian fluctuations. The black dots represent network simulations averaged over 20 independent trails (error bars are smaller than the symbol size). The inset is the root mean square of error (rms) between simulations and the complete theory (upward red triangles) and the Gaussian approximate theory (downward gray triangles). The simulations were performed using a Gillespie algorithm for $T = 5 \times 10^5$ steps with the gain function given by Eq. (16). The averaged activity was estimated in the last 5×10^3 steps across all trials. Parameters: $N = 1000$, $\gamma = 0.5$, $\alpha = 5$, $K = 10$, and $\mu_0 = 0.1$.

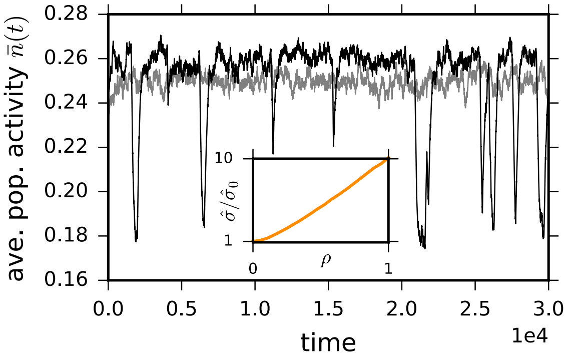

FIG. 2. Emergence of stochastic MFT. The black line shows the temporal evolution of a simulated network; this network does not have a deterministic MFT, since the condition in Eq. (10) is not satisfied. The out degree of a single unit in the network was set to be N [i.e., $\rho = 1$ in Eq. (17)]. For comparison, the gray line shows the average population activity of a similar network for which $\rho = K/N$. The inset indicates the normalized empirical standard deviation of population activity temporal dynamics ($\hat{\sigma}/\hat{\sigma}_0$) as a function of ρ (averaged over 20 independent trials with an expected number of 650 updates per unit). Simulations for the inset were performed using the stochastic update scheme described in Ref. [4]. Parameters: $N = 5000$ and $\bar{J} = -0.7$, and all other parameters are as in Fig. 1.

approximation (Fig. 1, dashed gray line) and, instead, follows the predictions of the complete mean-field limit (Fig. 1, red line). Therefore, the Gaussian approximation that is given in Eq. (12) is reasonable only for weak coupling and a relatively large value of K. The error between steady-state population activity from the simulations (Fig. 1, black dots) and the Gaussian approximation (Fig. 1, dashed gray line) increases as $|\bar{J}|$ becomes larger (Fig. 1, downward gray triangles in the inset), in contrast to the complete MFT staying constant (Fig. 1, upward red triangles in the inset).

In the second scenario, we show that an inherently stochastic mean-field limit with nontrivial fluctuations can emerge in a network with statistically inhomogeneous out degrees. The condition in Eq. (10) guarantees the convergence of the average population activity to the prediction of MFT. Indeed Eq. (10) indicates that, as $N \to \infty$, the average column sum of the connectivity matrix $\mathbf{J}$ should be K. It is straightforward to construct networks that do not obey this rule; such networks lose their pointwise convergence to a deterministic MFT in Eq. (3). An extreme example of a network of this kind is a network that has a single unit, n_{j_*}, that connects into ρN units in the circuits, where $0 < \rho \leq 1$ is the fraction of units in the network that are postsynaptic for n_{j_*}. Numerical simulations of such a network ($N = 5000$ and $\rho = 1$) show large-amplitude population activity fluctuations (Fig. 2, black line), in contrast to the smaller fluctuations of a homogeneous network (Fig. 2, gray line). Our approach allows the construction of stochastic correction terms to the mean-field limit by isolating the unit n_{j_*} from the network and then taking the limit $N \to \infty$. Therefore, a first-order correction to the function F of Eq. (7) can be derived as

$$F_s(m(t)) \approx F(m(t)) + \rho \bar{J} K^{-\gamma} f'(\mu_1(t)) n_{j_*}(t). \tag{17}$$

F_s is a stochastic function, since n_{j_*} is a binomial random variable for which the probability of being at state one is $m(t)$; the mean-field equation is thus transformed into an ordinary stochastic differential equation. The correction term in Eq. (17) indicates that the observed large fluctuations (Fig. 2, green line) are indeed a finite K phenomenon. Therefore, in large networks that have a finite number of connections between units (e.g., finite K networks), it suffices that only one unit breaks the condition (i.e., $\rho > 0$) and, as a result, the deterministic MFT collapses (Fig. 2, inset). The emergence of large-amplitude population events in Fig. 2 has been observed previously as the indication of the "synfire chain" in cortical network simulations [15]. It is noteworthy that there is compelling evidence that a few neurons can form an extensive number of postsynaptic connections in cortical microcircuits [16]. In Eq. (17), we observe that a unit with a high out degree can influence the macroscopic dynamics of the system. Therefore, recent experimental results that indicate the diverse couplings between single-cell activity and population averages in cortical networks [17] can be the result of inhomogeneity of out degrees.

In this Letter, we studied a simplified model that captures the essential nonequilibrium aspects of a cortical asynchronous state [4], and it allowed us to demonstrate the calculation of a complete statistics of fluctuations in fixed-in-degree networks. Our results show that the MFT for binary units can be fundamentally constructed from the LLNs and the emergence of intrinsic fluctuations does not require the application of the central limit theorem. It is noteworthy that considering other heterogeneities in the system requires extra averaging operations and performing self-consistent calculations of temporal and spatial fluctuations. For instance, in a network in which unit i has K_i incoming connections, it can be shown that the power of m in Eq. (9) must be replaced by moments of the rate distribution, $E(m^r)$, which can be self-consistently determined.

The semimartingale decomposition captures the finite-size effect [Eq. (15)] in the orthogonal direction to the average correlations between units. These correlations have been investigated previously [6]. Here, the finite-size scaling of fluctuations can be derived directly from rate matrix Q. In a recent study by Dahmen, Bos, and Helias [12], the MFT of binary units is extended by a cumulant expansion that allows the systematic calculation of finite-size corrections to cumulants of arbitrary order. In contrast, in our analysis all remaining correlations are implicitly encapsulated in the martingale part. Importantly, the application of the martingale theory and the expansion of the averaging operator allows a tractable alternative to the perturbative expansion of the system's state-space evolution to formulate an exact theory for network collective dynamics.

Our approach in this Letter goes beyond the classical asymptotic analysis of random connectivities, which requires statistical conditions for connectivity matrices, $\mathbf{J}$, to ensure pointwise convergence to a deterministic MFT, irrespective of any fine or major motifs in the connectivity matrix, and suggests a universality class of MFT for all fixed-in-degree and iid networks. Furthermore, we demonstrated a computationally interesting phenomenon for the emergence of a stochastic MFT by breaking the first condition [Eq. (10)]. Our framework can be readily exploited to determine the mean-field equilibrium of symmetrically disordered systems, in the presence of microstructures in their interactions such as spin glasses and associative neural networks [18], similarly. Once the connectivity matrix is given, it is straightforward to determine if the system's mean population activity converges to the MFT in an annealed dynamics with independent initial conditions. In the quenched dynamics, the analysis of metastability requires a further investigation of the invariance measures of the state space. Taken all together, we believe this approach paves the way for investigating the MFT of various network collective phenomena.

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[1] M. Mézard, G. Parisi, and M. Virasoro, *Spin Glass Theory and Beyond: An Introduction to the Replica Method and Its Applications*, Lect. Notes Phys. Vol. 9 (World Scientific, Singapore, 1986).

[2] E. Ising, Z. Phys. **31**, 253 (1925); P. C. Hohenberg and B. I. Halperin, Rev. Mod. Phys. **49**, 435 (1977).

[3] I. W. Hamley, *Introduction to Soft Matter: Synthetic and Biological Self-Assembling Materials* (Wiley, New York, 2013).

[4] C. van Vreeswijk and H. Sompolinsky, Neural Comput. **10**, 1321 (1998).

[5] R. J. Glauber, J. Math. Phys. (N.Y.) **4**, 294 (1963).

[6] I. Ginzburg and H. Sompolinsky, Phys. Rev. E **50**, 3171 (1994); M. A. Buice, J. D. Cowan, and C. C. Chow, Neural Comput. **22**, 377 (2010); A. Renart, J. d. l. Rocha, P. Bartho, L. Hollender, N. Parga, A. Reyes, and K. D. Harris, Science **327**, 587 (2010).

[7] M. Mézard and J. Sakellariou, J. Stat. Mech. (2011) L07001.

[8] D. W. Stroock, *An Introduction to Markov Processes*, 2005 ed. (Springer, Berlin; New York, 2008).

[9] See Supplemental Material at http://link.aps.org/supplemental/10.1103/PhysRevLett.119.208301 for a detailed calculation of sufficient conditions for the existence of MFT, fluctuations centralized moments and numerical simulation method, which includes Refs. [10,11].

[10] D. T. Gillespie, J. Comput. Phys. **22**, 403 (1976).

[11] J. L. Doob, Trans. Am. Math. Soc. **52**, 37 (1942).

[12] D. Dahmen, H. Bos, and M. Helias, Phys. Rev. X **6**, 031024 (2016).

[13] A. Stuard and J. K. Ord, *Distribution Theory*, Kendall's Advanced Theory of Statistics Vol. 1 (Halsted Press, New York, 1994).

[14] N. Brunel and V. Hakim, Neural Comput. **11**, 1621 (1999); M. Mattia and P. D. Giudice, in *Artificial Neural Networks—ICANN 2002*, Lect. Notes Comput. Sci. Vol. 2415, edited by J. R. Dorronsoro (Springer, Berlin, 2002), pp. 111–116; D. Grytskyy, T. Tetzlaff, M. Diesmann, and M. Helias, Front. Comput. Neurosci. **7**, 131 (2013).

[15] Y. Aviel, C. Mehring, M. Abeles, and D. Horn, Neural Comput. **15**, 1321 (2003).

[16] W.-C. A. Lee, V. Bonin, M. Reed, B. J. Graham, G. Hood, K. Glattfelder, and R. C. Reid, Nature (London) **532**, 370 (2016).

[17] M. Okun, N. A. Steinmetz, L. Cossell, M. F. Iacaruso, H. Ko, P. Barthó, T. Moore, S. B. Hofer, T. D. Mrsic-Flogel, M. Carandini, and K. D. Harris, Nature (London) **521**, 511 (2015).

[18] E. Agliari, A. Barra, A. Galluzzi, F. Guerra, and F. Moauro, Phys. Rev. Lett. **109**, 268101 (2012); P. Sollich, D. Tantari, A. Annibale, and A. Barra, Phys. Rev. Lett. **113**, 238106 (2014).