Critical Drift in a Neuro-Inspired Adaptive Network

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It has been postulated that the brain operates in a self-organized critical state that brings multiple benefits, such as optimal sensitivity to input. Thus far, self-organized criticality has typically been depicted as a one-dimensional process, where one parameter is tuned to a critical value. However, the number of adjustable parameters in the brain is vast, and hence critical states can be expected to occupy a high-dimensional manifold inside a high-dimensional parameter space. Here, we show that adaptation rules inspired by homeostatic plasticity drive a neuro-inspired network to drift on a critical manifold, where the system is poised between inactivity and persistent activity. During the drift, global network parameters continue to change while the system remains at criticality.

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Introduction.—The critical brain hypothesis postulates that biological brains operate in a self-organized critical state [1–5]. While there was initially little evidence to support this hypothesis, subsequent advances in neuroscience have made it possible to observe the characteristic power laws and avalanche dynamics associated with critical transitions, first in cell cultures [6–8] and then in live animals and humans [9–13]. Although still controversial [14], the critical brain hypothesis is rapidly gaining support in mainstream neuroscience, fuelled by the growing amount of experimental evidence.

This experimental evidence is complemented by a body of theory that elucidates the mechanisms that allow networks of neurons to self-organize to a critical state. Synapses that connect neurons to each other constantly self-tune their conductance through a variety of processes, collectively known as synaptic plasticity. Building on the early ideas of Bornholdt and Rohlf [15], it has been shown with simulations that commonly observed types of synaptic plasticity, such as homeostatic and spike-time dependent plasticity, are capable of self-organizing neuronal models to a critical state [16–19].

One facet of self-organized criticality that has received surprisingly little attention concerns the dimensionality of the parameter space in which the self-organization occurs. In the vast majority of studies, self-organized criticality is depicted as a one-dimensional process, where one parameter is tuned to a critical point. However, in real-world systems such as the brain, there are several and possibly very many parameters that are controlled dynamically. In such a high-dimensional parameter space, the states of the system that correspond to criticality can be expected to form a larger critical manifold.

It has been conjectured that the same mechanisms that drive the system to criticality will cause a drift along the critical manifold after criticality is reached [20]. While remaining critical, the system can thus continue to explore the parameter space and potentially encounter further instabilities along the way. This opens up the possibility of new phenomena such as high-codimension criticality with multiple order parameters and persistent parametric dynamics in the critical state. Understanding such phenomena may shed light on how the brain can operate in different dynamical states both sequentially and simultaneously.

In this Letter, we use a simple adaptive neuro-inspired network model to show that a self-organizing system can drift on a critical manifold. This model has previously been shown to self-organize to the critical state between neuronal inactivity and persistent activity, called the onset of activity [17]. Here, we show that the system reaches the critical state long before the global network parameters, such as the average connectivity, reach their stable values. We carefully analyze network dynamics after the critical state has been reached, revealing the conjectured drift on the critical manifold where the ongoing plasticity continues to reshape the network structure while the system remains critical. These results provide direct evidence of the critical drift and establish an easily tractable example system where subsequent phenomena can be analyzed.

The model.—We investigate criticality in the model of Droste *et al.* [17] that combines stochastic neuro-inspired dynamics with adaptive network evolution. As the starting point for the adaptation, we consider directed random (Erdős-Rényi, ER) networks of N excitable nodes and M directed links with a mean degree of $\langle k \rangle = M/N$. Each node can take three discrete states: firing (F), refractory

(R), or inactive (I). Nodes in the firing state activate their inactive neighbors stochastically at rate β and then enter a refractory period at rate δ before transitioning back to state I at rate γ. The network topology evolves on a timescale slower than the node dynamics, following rules inspired by homeostatic plasticity that strives to keep the mean firing rate of each neuron constant over the long term (see, e.g., [21]). We use a discrete update rule where firing nodes lose incoming links at rate l, while new links are created between random nodes at rate g. During the network evolution, we allow inactive nodes to fire spontaneously at rate η to counteract activity dying out due to finite-size effects. The network dynamics and topology are evolved using the Gillespie algorithm [22].

Criticality in static ER networks.—Let us first characterize the transition from inactivity to persistent activity when the adaptation rules are switched off and no spontaneous activity is allowed. This transition separates the phase where any initialized activity dies out exponentially from the phase where exciting a random node leads to sustained activity. The average activity $\langle [F] \rangle$ acts as the order parameter of the transition [see Fig. 1(a)]. In static ER networks, the mean degree $\langle k \rangle$ is the control parameter determining the overall excitability. As the firing dynamics is similar to the SIS model, the transition is expected to belong to the directed percolation universality class [23]. In this universality class, two correlation lengths, $\xi_{\|}$ and $\xi_{\perp}$, diverge at the transition, with the former corresponding to the temporal dimension and the latter to the spatial (network) dimension.

To verify that the system undergoes a continuous phase transition at a critical value $\langle k \rangle^{*}_{\text{static}}$, we initialize several successive cascades of activity in ER networks with different mean degrees $\langle k \rangle$. These avalanches are initialized by activating one random node at a time. We then record the duration and size of the resulting avalanche, where the size indicates the number of firing events (note that one node can fire several times). We set a maximum time limit t_{max} so that avalanches that die out before this limit are considered finite. Their maximum size and duration are then expected to sharply peak at the critical value $\langle k \rangle^{*}_{\text{static}}$ as a result of the diverging correlation lengths.

We observe that, as expected, the system shows the hallmarks of a continuous phase transition at a critical value $\langle k \rangle^{*}_{N,\text{static}}$, with the transition becoming sharper as N increases. At this threshold, the average activity becomes nonzero and the maximum size and duration of finite avalanches diverge (Fig. 1). In line with this, the probability distributions of finite avalanche size and duration appear exponential when $\langle k \rangle$ lies clearly under or above the critical threshold, while close to the critical value the distributions look like power laws with exponents matching the theoretical predictions for critical SIS-like systems derived in [24] (see Supplemental Material (SM) [25], V). The critical mean degree $\langle k \rangle^{*}_{N,\text{static}}$ depends on the transition rates β, δ, and γ, and its value for infinite systems can be approximated with Eq. (7) from [17]. For the parameters used here, Eq. (7) yields $\langle \hat{k} \rangle^{*}_{\text{static}} = 2.21$, which lies slightly below the experimentally extrapolated value $\langle k \rangle^{*}_{N\to\infty,\text{static}}$ (see SM, I [25]).

Evidence for drift on the critical manifold.—Next, we switch on the plasticity rules and observe how the simulated networks evolve in time, using ER networks of different mean degrees in the vicinity of the critical value $\langle \hat{k} \rangle^{*}_{\text{static}} = 2.21$ as the initial condition. We follow the evolution of the networks' key characteristics: leading eigenvalue λ_1 of the adjacency matrix, mean degree $\langle k \rangle$, mean excess degree $\langle q \rangle$, and the Pearson correlation coefficient ρ of the nodes' in- and out-degrees [Figs. 2(a)–2(d)].

We start by analyzing the time evolution of the leading eigenvalue λ_1. This eigenvalue reflects the overall excitability of the network, and the onset of activity is known to

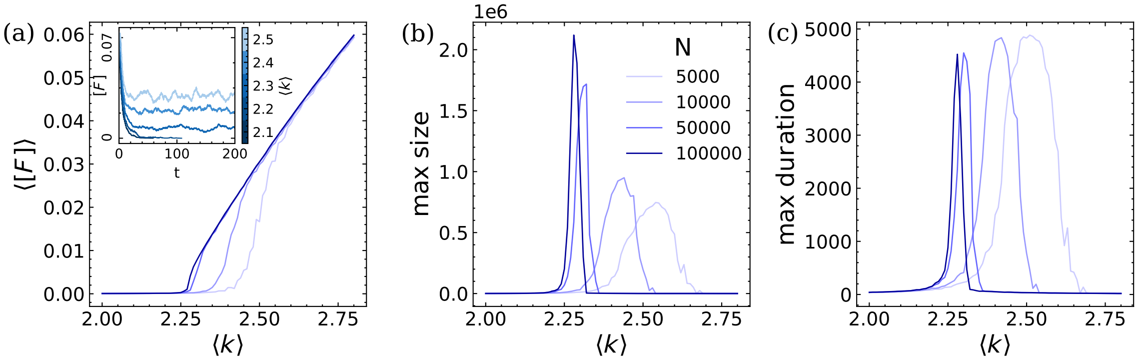

FIG. 1. The onset of activity in static ER networks of different sizes N. (a) The average fraction of firing nodes $\langle [F] \rangle$ (average taken over time) before $t_{\text{max}} = 5000$, with 5% of the nodes initialized as firing. The inset shows the time series of the fraction of firing nodes for networks of size $N = 10^5$ with different mean degrees. (b),(c) The maximum size and duration of finite avalanches (lasting less than t_{max}) in 1000 successive runs. Both quantities display a sharp peak at a critical value $\langle k \rangle^{*}_{N,\text{static}}$, which moves closer to the theoretical estimate as N increases. All results are averaged over 30 network realizations for each mean degree. In these and subsequent figures, we set $\beta = 0.7$, $\delta = 0.95$, and $\gamma = 0.4$.

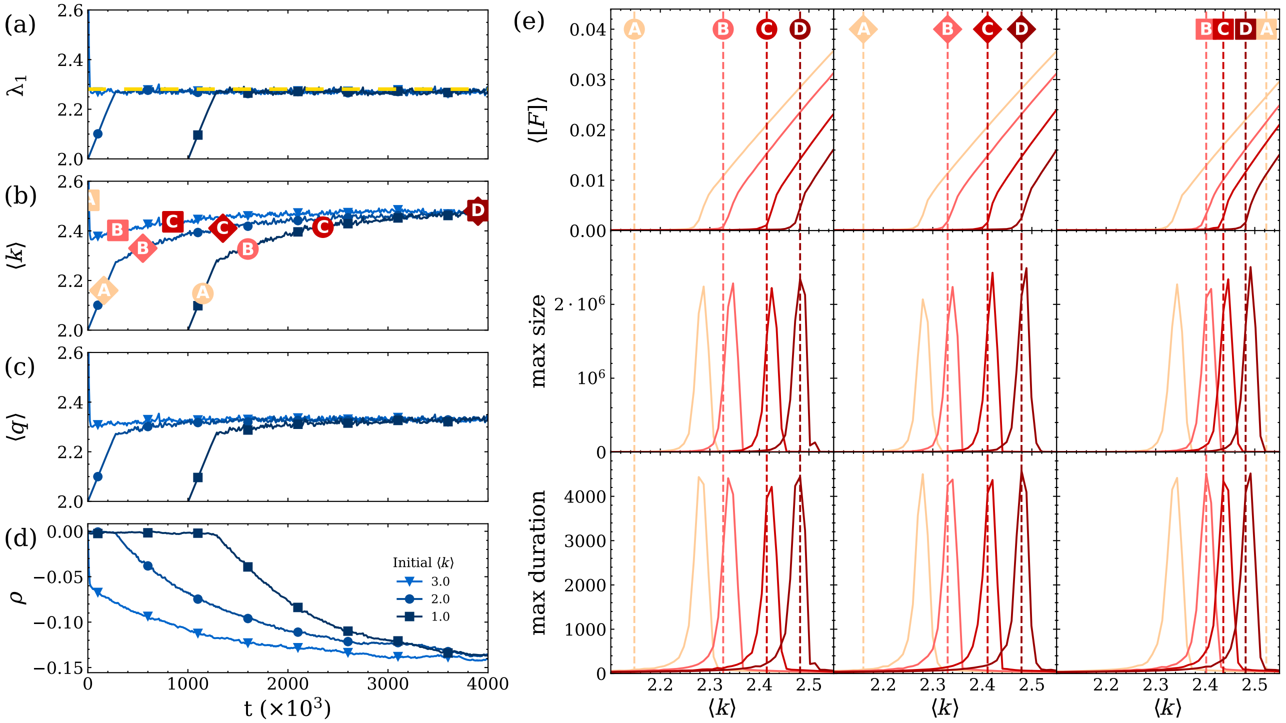

FIG. 2. Critical drift in evolved networks with different initial mean degrees. (a)–(d) Time evolution of the leading eigenvalue λ_1, mean degree $\langle k \rangle$, mean excess degree $\langle q \rangle$, and Pearson correlation coefficient ρ of the nodes' in- and out-degrees. The simulation is initialized with 5% of the nodes in the firing state. The parameter values are $N = 10^5$, $l = 10^{-3}$, $g = 10^{-6}$, and $\eta = 1/(100N)$. For analysis on their effect on the drift, see SM, II and III [25]. The yellow dashed line in (a) shows $\langle k \rangle^*_{N=10^5,\mathrm{static}}$ (determined in SM, I [25]). (e) We freeze the networks at different time points shown in panel (b). These are chosen so that for each network, point A lies before the start of the drift while points B–D correspond to the drift phase. For each time point, the dashed vertical line marks the mean degree in the evolved network at that point, while the curve in the same color shows results for the networks obtained by manipulating the mean degree. The top row shows average activity $\langle [F] \rangle$ before $t_{\max} = 5000$ with 5% of the nodes initialized as firing. The other two rows show the maximum size and duration of finite avalanches in 1000 successive runs. Results are averaged over 30 network realizations for all networks obtained by manipulating $\langle k \rangle$. We observe that during the initial phase (point A), the mean degree lies clearly under or above the onset of activity, while during the drift phase (points B–D), the networks reside at the onset of activity. As the network evolves, the onset of activity happens at higher values of $\langle k \rangle$, which confirms the existence of the manifold. Note that the divergence peaks of avalanche sizes and durations are not exactly at the point where $\langle [F] \rangle$ becomes nonzero (top row); however, these three measures converge to the critical value (or slightly above it due to finite values of g and l) as N is increased (see SM, IV [25]).

occur at a critical value λ_1^* in locally treelike networks. This has been shown previously assuming that the states of neighboring nodes are independent (see, e.g., [29]); here, we derive a more accurate estimate for λ_1^* by relaxing this assumption. Using the so-called pair approximation (see SM, VII [25]), we obtain

$$\hat{\lambda}_1^* = \frac{\delta}{\beta} + \frac{\delta + \gamma/2}{\delta + \gamma}, \tag{1}$$

which is identical to $\langle \hat{k} \rangle^*_{\mathrm{static}}$ derived for static ER networks in Ref. [17]. Note that in general, for static ER networks, $\langle k \rangle$ and λ_1 are approximately equal. If the network structure is less random, $\langle k \rangle$ becomes a poorer approximation for the excitability. The leading eigenvalue, however, remains a more reliable indicator of excitability, unless the network has significant degree correlations [30] or is highly structured [31].

We observe that as the network evolves, the leading eigenvalue λ_1 reaches a stable value after a short transient [Fig. 2(a)]. This value lies close to $\langle k \rangle^*_{N=10^5,\mathrm{static}}$ and moves closer to the theoretical estimate $\hat{\lambda}_1^* = \langle \hat{k} \rangle^*_{\mathrm{static}}$ as N increases (see SM, I [25]), indicating that the system resides at criticality.

To illustrate the drift on the critical manifold, we next analyze the evolution of the mean degree $\langle k \rangle$. We see that $\langle k \rangle$ first changes rapidly, but once λ_1 stabilizes, the average rate of change in $\langle k \rangle$ decreases considerably [Fig. 2(b)]. Subsequently, the mean degree increases gradually and unevenly and finally settles to fluctuate around a constant value that is clearly above $\langle k \rangle^*_{N,\mathrm{static}}$. We interpret these qualitatively different stages as an initial phase where the dynamics approaches criticality, followed by a drift phase, where the system slides along the critical manifold. During the drift, λ_1 stays constant while $\langle k\rangle$ as well as the mean excess degree and the correlation coefficient ρ [Figs. 2(c) and 2(d)] keep changing.

We note that the observation of the final value of $\langle k\rangle$ differing from λ_1 is not novel *per se*; this has already been established for a SIRS-like system evolved with short-term homeostatic plasticity in [32]. Our novel result is the observation of the phase where the system is already critical before the network parameters have reached stable values. It is also crucial to note that while λ_1 stays constant on the manifold in locally treelike networks, its value can change during the critical drift in networks with loops (see SM, VIII [25]).

To confirm that the system remains critical during the drift, we directly assess the distance to criticality at different points in time during the network evolution. For this purpose, we initially evolve the network topology for time t. After this, we switch the plasticity rules off and create several replicas of the system in which we add or remove a small number of links at random. We then analyze the effect of this perturbation of the number of links on the network dynamics by examining the divergence of the size and duration of the largest finite avalanches [Fig. 2(e)]. During the initial phase, a large perturbation is needed to bring the system to criticality [dashed lines marked with A in Fig. 2(e)]. During the drift phase, however, the evolved networks reside at the divergence peak at the onset of activity (dashed lines marked with B-D).

Furthermore, we observe that the onset of activity occurs at higher values of the mean degree as the network evolves (see SM, VI [25], for further illustration). In other words, $\langle k\rangle^*$ drifts toward higher values as the network evolves. At the same time, the network remains at criticality, as also seen in the PDFs of the sizes and durations of finite avalanches that remain unchanged during the drift and agree well with the theoretical predictions for critical SIS-like systems derived in [24] (SM, V [25]).

To understand why the mean degree $\langle k\rangle$ increases during the drift, we turn to analyze the characteristics of the links that the plasticity mechanism removes. As the mechanism removes links from firing nodes, links that often forward activation are likely to be erased. Intuitively, removing such links tends to reduce the overall excitability more than adding random links increases it on average. Consequently, more links need to be added than removed to keep the excitability at a constant level. This imbalance leads to $\langle k\rangle$ increasing until the most active links have been removed and the average effect of a random addition and a targeted removal even out.

This intuition can be expressed in more formal terms using the leading eigenvalue λ_1 and the corresponding left principal eigenvector. In SIS-like models [23], a node's eigenvector centrality (given by the left principal eigenvector) correlates with its probability of being in the firing state, and this relation is particularly strong if the system is close to criticality (see SM, IX [25]). Consequently, the plasticity mechanism tends to reduce the in-degrees of nodes with high centrality. As these links contribute to the magnitude of λ_1 more than a randomly chosen link on average, the removals needs to be compensated by adding links to the network to keep λ_1 close to the critical value. As time passes, the effects of link addition and removal gradually even out (see SM, X [25]). Consequently, $\langle k\rangle$ increases more and more slowly and eventually levels off. This drift can be observed for a wide range of values of β, δ, and γ, as long as the critical value of λ_1 is low enough (see SM, XI [25]).

The leading eigenvalue depends on many topological characteristics, such as the mean excess degree $\langle q\rangle$ and the cyclic patterns in the network. In directed networks, $\langle q\rangle$ is defined as the average out-degree of nodes reached by following a link, $\langle q\rangle = (1/|\{s_{ij}\}|)\sum_{\{s_{ij}\}} k_{\mathrm{out},j}$, where $\{s_{ij}\}$ denotes the set of all links and $k_{\mathrm{out},j}$ denotes the out-degree of node j. It is relevant in the context of activity spreading as it equals the expected number of new nodes that an arriving avalanche can excite. In the considered sparse ER networks, $\langle q\rangle$ increases only slightly during the drift [Fig. 2(c)], which indicates that the plasticity mechanism controls excitation mainly through restricting its growth. This is because firing nodes are likely to have predecessors with higher-than-average in-degrees, and hence the plasticity mechanism effectively reduces the out-degrees of nodes with many incoming links. This trend is reflected in the decreasing Pearson correlation coefficient ρ of nodes' in- and out-degrees [Fig. 2(d)] and aligns with the results in [32], where a negative correlation between incoming and outgoing synaptic weights was found to explain the deviation of the self-organized stable value of the branching ratio (equivalent to $\langle k\rangle$ in our model) from the mean-field prediction.

While the mean excess degree increases only slightly during the drift, it increases nonetheless. This implies that, similarly to $\langle k\rangle$, its critical value depends on other network parameters, such as the number and configuration of cycles. Consequently, the magnitude of the increase depends largely on the original network topology.

In this Letter, we have shown that rules resembling homeostatic plasticity drive simple neuro-inspired networks to drift along a critical manifold. During this drift, the network stays at the onset of activity while global network parameters continue to change. Our findings underscore that criticality should not be understood as a one-dimensional point but rather as a high-dimensional manifold embedded in a vast parameter space, as hypothesized in [17]. As a consequence, residing at the onset of activity does not set strict constraints to any specific network parameter, as the change in one parameter can be compensated by adjusting some other variable accordingly.

This flexibility allows for considerable variation in network topology while at criticality. We emphasize that the core message of our work lies in establishing that a self-organizing system can drift along or close to a critical manifold; whether the system is exactly critical or slightly sub- [33,34] or supercritical [35] likely depends on the self-organizing mechanism in question. While the model studied in this work is inspired by neuronal networks, it is very far from being biologically realistic; investigating more detailed and realistic models is best left for future work that builds on the foundations established here.

In the sparse random networks considered in this Letter, the values of the tracked parameters eventually stabilized. In real systems, however, external stimuli and a number of different driving processes continue to perturb the system. Introducing additional driving processes—-such as another type of plasticity rule [36]—could cause the network to continue to drift along the manifold or possibly even induce periodic parameter dynamics. If the changes in network configuration entail changes in the dynamical behavior, the system can explore different dynamical regimes while remaining critical at all times. An interesting question concerns whether critical manifolds associated with different phase transitions intersect. For example, can a system drift to the onset of synchrony while still remaining at the onset of activity? Exploring the structure, dynamical regimes, and intersections of these critical manifolds is an exciting avenue for future research.

The implementation of the model is available on GitHub [37].

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[1] D. Chialvo, Emergent complex neural dynamics, Nat. Phys. **6**, 744 (2010).

[2] A. Herz and H. J, Earthquake Cycles and Neural Reverberations: Collective Oscillations in Systems with Pulse-Coupled Threshold Elements, Phys. Rev. Lett. **76**, 1222 (1994).

[3] B. A. Pearlmutter and C. J. Houghton, A new hypothesis for sleep: Tuning for criticality, Neural Comput. **21**, 1622 (2009).

[4] N. M. Timme, N. J. Marshall, N. Bennett, M. Ripp, E. Lautzenhiser, and J. M. Beggs, Criticality maximizes complexity in neural tissue, Front. Oral Physiol. **7**, 425 (2016).

[5] J. Hesse and T. Gross, Self-organized criticality as a fundamental property of neural systems, Front. Syst. Neurosci. **8**, 166 (2014).

[6] J. M. Beggs and D. Plenz, Neuronal avalanches in neocortical circuits, J. Neurosci. **23**, 11167 (2003).

[7] M. Yaghoubi, T. de Graaf, J. G. Orlandi, F. Girotto, M. A. Colicos, and J. Davidsen, Neuronal avalanche dynamics indicates different universality classes in neuronal cultures, Sci. Rep. **8**, 3417 (2018).

[8] E. D. Gireesh and D. Plenz, Neuronal avalanches organize as nested theta- and beta/gamma-oscillations during development of cortical layer 2/3, Proc. Natl. Acad. Sci. U.S.A. **105**, 7576 (2008).

[9] M. Kitzbichler, M. Smith, S. Christensen, and E. Bullmore, Broadband criticality of human brain network synchronization, PLoS Comput. Biol. **5**, e1000314 (2009).

[10] C. Meisel, A. Storch, S. Hallmeyer-Elgner, E. Bullmore, and T. Gross, Failure of adaptive self-organized criticality during epileptic seizure attacks, PLoS Comput. Biol. **8**, e1002312 (2012).

[11] K. Linkenkaer-Hansen, V. V. Nikouline, J. M. Palva, and R. J. Ilmoniemi, Long-range temporal correlations and scaling behavior in human brain oscillations, J. Neurosci. **21**, 1370 (2001).

[12] A. J. Fontenele, N. A. P. de Vasconcelos, T. Feliciano, L. A. A. Aguiar, C. Soares-Cunha, B. Coimbra, L. Dalla Porta, S. Ribeiro, A. J. Rodrigues, N. Sousa, P. V. Carelli, and M. Copelli, Criticality Between Cortical States, Phys. Rev. Lett. **122**, 208101 (2019).

[13] E. Tagliazucchi, P. Balenzuela, D. Fraiman, and D. Chialvo, Criticality in large-scale brain fMRI dynamics unveiled by a novel point process analysis, Front. Oral Physiol. **3**, 15 (2012).

[14] J. Wilting and V. Priesemann, 25 years of criticality in neuroscience–established results, open controversies, novel concepts, Curr. Opin. Neurobiol. **58**, 105 (2014).

[15] S. Bornholdt and T. Rohlf, Topological Evolution of Dynamical Networks: Global Criticality from Local Dynamics, Phys. Rev. Lett. **84**, 6114 (2000).

[16] C. Meisel and T. Gross, Adaptive self-organization in a realistic neural network model, Phys. Rev. E **80**, 061917 (2009).

[17] F. Droste, A. Do, and T. Gross, Analytical investigation of self-organized criticality in neural networks, J. R. Soc. Interface **10**, 20120558 (2013).

[18] A. Levina, J. Herrmann, and T. Geisel, Dynamical synapses causing self-organized criticality in neural networks, Nat. Phys. **3**, 857 (2007).

[19] F. Y. K. Kossio, S. Goedeke, B. van den Akker, B. Ibarz, and R.-M. Memmesheimer, Growing Critical: Self-Organized Criticality in a Developing Neural System, Phys. Rev. Lett. **121**, 058301 (2018).

[20] T. Gross, Not one, but many critical states: A dynamical systems perspective, Front. Neural Circuits **15**, 614268 (2021).

[21] G. Turrigiano, Homeostatic synaptic plasticity: Local and global mechanisms for stabilizing neuronal function, Cold Spring Harbor Perspect. Biol. **4**, a005736 (2011).

[22] D. T. Gillespie, Exact stochastic simulation of coupled chemical reactions, J. Phys. Chem. **81**, 2340 (1977).

[23] H. Hinrichsen, Nonequilibrium critical phenomena and phase transitions into absorbing states, Adv. Phys. **49**, 815 (2000).

[24] D. Larremore, M. Carpenter, E. Ott, and J. Restrepo, Statistical properties of avalanches in networks, Phys. Rev. E **85**, 066131 (2012).

[25] See Supplemental Material at http://link.aps.org/supplemental/10.1103/PhysRevLett.130.188401 for analysis of the effect of parameters on the drift as well as for

further evidence for the critical drift. The Supplemental Material includes Refs. [27–29].

[26] P. Bak, C. Tang, and K. Wiesenfeld, Self-Organized Criticality: An Explanation of 1/f Noise, Phys. Rev. Lett. **59**, 381 (1987).

[27] A. Goltsev, S. Dorogovtsev, J. Oliveira, and J. F. Mendes, Localization and Spreading of Diseases in Complex Networks, Phys. Rev. Lett. **109**, 128702 (2012).

[28] A. Mata and S. Ferreira, Pair quenched mean-field theory for the susceptible-infected-susceptible model on complex networks, Europhys. Lett. **103**, 48003 (2013).

[29] B. Prakash, D. Chakrabarti, M. Faloutsos, N. Valler, and C. Faloutsos, Threshold conditions for arbitrary cascade models on arbitrary networks, Knowl. Inf. Syst. **33**, 549 (2012).

[30] Z. Chen, Characterising spatial dependence on epidemic thresholds in networks, Int. J. Secur. Networks **15**, 1 (2020).

[31] O. Givan, N. Schwartz, A. Cygelberg, and L. Stone, Predicting epidemic thresholds on complex networks: Limitations of mean-field approaches, J. Theor. Biol. **288**, 21 (2011).

[32] J. Campos, A. Costa, M. Copelli, and O. Kinouchi, Correlations induced by depressing synapses in critically self-organized networks with quenched dynamics, Phys. Rev. E **95**, 042303 (2017).

[33] V. Priesemann, M. Wibral, M. Valderrama, R. Pröpper, M. Le Van Quyen, T. Geisel, J. Triesch, D. Nikolić, and M. Munk, Spike avalanches *in vivo* suggest a driven, slightly subcritical brain state, Front. Syst. Neurosci. **8**, 108 (2014).

[34] J. Wilting and V. Priesemann, Between perfectly critical and fully irregular: A reverberating model captures and predicts cortical spike propagation, Cereb. Cortex **29**, 2759 (2019).

[35] L. De Arcangelis, Are dragon-king neuronal avalanches dungeons for self-organized brain activity?, Eur. Phys. J. Spec. Top. **205**, 243 (2012).

[36] M. Girardi-Schappo, L. Brochini, A. Costa, T. T. Andrade de Carvalho, and O. Kinouchi, Synaptic balance due to homeostatically self-organized quasicritical dynamics, Phys. Rev. Res. **2**, 012042(R) (2020).

[37] Code for the IFRI model, https://github.com/sasormunen/critical_drift.git.