Random Graph Theory and Neuropercolation for Modeling Brain Oscillations at Criticality

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Abstract
Mathematical approaches are reviewed to interpret intermittent singular space-time dynamics observed in brain imaging experiments. The following aspects of brain dynamics are considered: nonlinear dynamics (chaos), phase transitions, and criticality. Probabilistic cellular automata and random graph models are described, which develop equations for the probability distributions of macroscopic state variables as an alternative to differential equations. The introduced modular neuropercolation model is motivated by the multilayer structure and dynamical properties of the cortex, and it describes critical brain oscillations, including background activity, narrow-band oscillations in excitatory-inhibitory populations, and broadband oscillations in the cortex. Input-induced and spontaneous transitions between states with large-scale synchrony and without synchrony exhibit brief episodes with long-range spatial correlations as observed in experiments.

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Highlights
Transient brain dynamics as manifestation of a system at the edge of criticality.
Rapid phase transitions between metastable states with cognitive content.
Neuropercolation approach to criticality controlled by inhibition, rewiring, noise.
Collapse of broad-band oscillations to highly synchronous narrow-band dynamics.
Heavy-tail distributions at criticality resembling "Dragon King" extreme events.
Introduction

Experimental results from depth unit electrodes, from surface evoked potential recordings, and from scalp EEGs and MEG/fMRI images indicate the presence of intermittent synchronization-desynchronization transitions across cortical areas. Transitions in temporal and spatial dynamics provide the window for the emergence of meaningful cognitive activity. Gap junctions between interneurons have been shown to promote intermittent synchronization-desynchronization of firing. Transient sequential neural dynamics is not unique to mammals and it has been observed in zebrafish, and in the navigation system of mollusks. We review various theoretical concepts to interpret experimental findings on rapid transitions in brains and cognition, including dynamical systems and chaos, models of criticality, and network science and graph theory. Neuropercolation combines these concepts and provides a powerful tool for efficient model building. Advantages and disadvantages are summarized, and perspectives for future developments are outlined.

Modeling Transient Brain Dynamics

Brains as dynamical systems

Basic models apply Kuramoto’s classical phase oscillator equations to cortical networks. Population models governed by neural mass equations have been used to describe transient synchronization effects in brains. Complex spatio-temporal behaviors have been modeled using nonlinear ordinary and partial differential equations. These approaches view brains as dynamical systems with evolving trajectories over attractor landscapes. With a focus on transient brain dynamics, principles of metastability have been exploited. Chaotic itineracy and Milnor attractors are mathematical models describing cognitive transients. Metastable transients reflect sequential memory, and they have been modeled successfully using stable heteroclinic cycles in competitive networks with excitatory and inhibitory interactions.

Criticality in brain operation

Brains can be modeled as dissipative thermodynamic systems that hold themselves near a critical level of activity that is a non-equilibrium metastable state. The mechanism of maintaining the metastable state can be described as homestasis, or alternatively as homeodynamics and homeochaos, emphasizing the dynamic nature of the resting state. Criticality is arguably a key aspect of brains in their rapid adaptation, reconfiguration, high storage capacity, and sensitive response to external stimuli. During recent years, self-organized criticality (SOC) and neural avalanches became important concepts to describe neural systems. In spite of the successes of SOC for brain dynamics, important questions remain unresolved regarding the generation of experimentally observed rhythms and sequences of transient dynamic patterns. There is empirical evidence of the cortex conforming to self-stabilized, near critical state during extended quasi-stable periods, and existence of rapid transitions exhibiting long-range correlations. For a comprehensive overview of the state-of-art of criticality in neural systems, based on SOC and beyond, see.
Graph theory for brain networks

Random graph theory and percolation dynamics are fundamental mathematical approaches to model critical behavior in spatially extended, large-scale networks (36). There has been intensive research in the past decade to develop efficient algorithms evaluating key statistical properties of structural and functional brain networks (37, 38), including hub structures and rich club networks (39, 40), and networks with causal links (41). The relation of fMRI-based slow network dynamics to cognitive processes, their relation to much faster non-stationarities in synchronization patterns measured with EEG and MEG, and their potential significance for clinical studies remain to be explored (42, 43). The presence or absence of scale-free properties is a contentious issue (16, 44, 45). Deviation from scale-free behavior has been demonstrated, for example, in rich club networks (37, 42). There is a dominant view that brains are not random and one should not use the term random graphs and networks for brains. Without going into a metaphysical debate at this point, it can be safely assumed that brains, viewed either as complex deterministic machines or as random objects, can benefit from the use of statistical methods in their characterization (46, 9). The identification of percolation transitions in living neural networks (47) points at the potential relevance of the corresponding mathematical concepts of percolation theory to brains (48). Neuropercolation builds on these advances and establishes a link between structure and function of cortical and cognitive networks by filling in the models with pulsing, dynamic, living content (29, 49).

Summary of neuropercolation approach to brains

Neuropercolation combines three fundamental mathematical concepts: (i) complex dynamics and intermittent chaos; (ii) geometric graphs and percolation theory; and (iii) phase transitions at critical states. Specifically, the neuropercolation model uses geometric random graphs tuned to criticality to produce transient dynamical regimes with intermittent chaos and synchronization-desynchronization transitions. It is based on the premise that the repetitive sudden transitions observed in the cortex are maintained by neural percolation processes in the brain as a large-scale random graph near criticality, which is self-organized in collective neural populations formed by synaptic activity. Neuropercolation addresses complementary aspects of neocortex, manifesting complex information processing in microscopic networks of specialized spatial modules, and developing macroscopic patterns evidencing that brains are holistic organs.

Neuropercolation: A Hierarchy of Probabilistic Cellular Automata

Conceptual outline

The main components of the approach are summarized in Fig. 1 including (a) experiments, (b) model development, (c) model validation, (d) adaptation. Cognitively relevant transient brain dynamics is monitored using high-resolution multichannel experiments. Graph theory reproduces experimentally observed synchronization-desynchronization episodes at alpha-theta rates, leading to the interpretation of the measured transients as critical phenomena and phase transitions in the cortical sheet. Model predictions are tested and validated via various quantitative metrics involving transient desynchronization, input induced narrow-band oscillations, and scale-free PSD functions (49).
Figure 1: Schematics of the critical brain approach with components: (a) experiments, (b) modeling, (c) model validation, (d) adaptation. The 3D plots in (a) and (b) use x-axis for time, y-axis for linear space across the cortical surface, and z-axis as phase synchronization index. Synchrony is marked by blue; brief desynchronization episodes are shown in green, yellow, and red; adopted from (3) and (49). The experimentally observed large-scale synchronization-desynchronization transitions are reproduced by the neuropercolation model. Validation metrics include the slope of the scale-free power spectral density (PSD), input-induced collapse of the broad-band oscillations to a narrow-band carrier wave. By tuning control parameters, various operating modes are simulated.
Probabilistic cellular automata in 2D

When modeling the cortical sheet, the employed graph lives in the geometric space, e.g., over a two dimensional lattice, see Fig. 2. The corresponding mathematical objects are cellular automata, related to Ising spin lattices, Hopfield nets, and cellular neural networks \cite{50,51,52}. In the original bootstrap percolation, lattice sites are initialized as active or inactive, and their activation evolves according to some deterministic rule. Majority voting rule declares that inactive sites become active if the majority of their neighbors are active, while the bootstrap property requires that an active site always remains active. If the iterations ultimately lead to a configuration when almost all sites become active, it is said that there is percolation in the lattice. A crucial result of percolation theory states that on infinite lattices, there exists a critical initialization probability separating percolating and non-percolating conditions \cite{36}.

![Figure 2: Illustration of a 4 \times 4 2D lattice with periodic (toroidal) boundary conditions (a), with vertices labeled from 0 to 15; (b) in simulations, the 2D torus is approximated by a circular arrangement of the vertices.](image)

Neuropercolation as generalized percolation

In neuropercolation, the bootstrap property is relaxed, i.e., a site is allowed to turn from active to inactive. Neuropercolation incorporates the following major generalizations based on the features of the neuropil, the filamentous neural tissue in the cerebral cortex \cite{52}:

- Noisy interactions: Neural populations exhibit dendritic noise and other random effects. Neuropercolation includes a random component (\(\varepsilon > 0\)) in the majority voting rule, demonstrating that microscopic fluctuations are amplified to macroscopic phase transitions near criticality.

- Long axonal effects: In neural populations, most of the connections are short, but there are a relatively few long-range connections mediated by long axons, related to small-world phenomena \cite{53}.

- Inhibition: Interaction between excitatory and inhibitory neural populations contribute to the emergence of sustained narrow-band oscillations.

These parameters can control the system and lead to complex spatio-temporal dynamics. For example, as the noise component approaches a critical value \(\varepsilon_0\), statistical properties such as correlation length diverge and scale as \((\varepsilon - \varepsilon_0)^\beta\), where \(\beta\) is the critical exponent \cite{52}.
Figure 3: Illustration of critical behavior in the neuropercolation model; plots (a), (b), and (c) show examples of time series of average activation \(<a>\) for noise levels near criticality [64]. Case (c) depicts a supercritical (unimodal) regime without phase transitions, while (a) and (b) critical (bimodal) oscillations. Diagram (d) shows the distribution of cluster sizes in the various models; (a) scale-free distribution over a broad range of positive cluster sizes, characteristic of SOC; (b) and (c) deviate from scale-free statistics at the tail of the distribution with high cluster sizes.
Neuropercolation describes the evolution of the cortex at criticality through a sequence of metastable states. The system stays at a metastable state for exponentially long time, and it flips rapidly to another state, in polynomial time \(36, 53\). During the transition, the activity effectively percolates through the system starting from certain well-defined configurations \(\text{percolating sets}\) \(54\). Metastable states may be approximated as self-organized criticality with scale-free behaviors. However, rapid transitions from one metastable pattern to the other are percolation processes, extending beyond SOC dynamics. This important fundamental theoretical result is exploited in neuropercolation models. Fig. 3 illustrates this view using neuropercolation simulations near criticality. The rapid switch from one state to the next is clearly seen in Fig. 3(a-b). Phase transition generate deviations of cluster size distribution from scale-free law at high-size limit, see Fig. 3(d). Such behavior resembles Dragon Kings \(55\), which describe extreme events deviating from SOC scale-free property.

Coupled oscillators with alternating narrow-band and broad-band dynamics

Neuropercolation implements a hierarchical approach to neural populations, illustrated in Fig. 4 employing Freeman K sets \(22\). Two coupled layers of excitatory-inhibitory populations (KII), see Fig. 4(a), exhibit narrow-band, bimodal oscillations for a specific critical range of control parameters, with clear boundaries marking the region of criticality with prominent bimodal oscillations \(52\). Recently the term extended criticality has been used for conditions when criticality exists over an extended range of parameters \(56\). Stretching criticality is yet another related concept introduced for neural systems \(57\). Stretching criticality may contribute to the emergence of hierarchical modular brain networks identified by fMRI brain imaging techniques \(58\). Fig. 4(c) illustrates KIII sets with three coupled oscillators. Fig. 4(d) depicts the ensemble average time series produced by each of the oscillators. As a result of the winnerless competition between the oscillators, complex transient dynamics emerges, see bottom plot in Fig. 4(d). Neuropercolation produces intermittent synchronization effects \(49\) in line with experimental findings.

Pros and Cons

Criticality in brains is extensively studied in the literature, with SOC being a highly popular model of criticality reproducing various experimentally observed properties. Its cons are that it cannot produce the sequence of transient patterns observed in cognitive experiments. Neuropercolation reproduces important experimental observations, including deviation from strict scale-free SOC behavior, resembling Dragon King effects \(55\). Neuropercolation has demonstrated biologically feasible adaptation using Hebbian learning with reinforcement, when Hebbian cell assemblies respond to stimuli by destabilizing broad-band chaotic dynamics via narrow-band oscillation at gamma frequencies \(49\).

Differential equations require some degree of smoothness in the described process, which poses difficulties when describing sudden changes and phase transitions in neurodynamics. The advantage of neuropercolation is that it can produce rapid spatio-temporal transitions with possible singular space-time dynamics. Models based on stable heteroclinic cycles can produce the required switching effects as well \[24-25\], and they may be viewed as a high-level formulation of the symbolic dynamics, which may emerge from the population dynamics of neuropercolation approach.
Figure 4: Hierarchy of the neuropercolation models; (a) coupled excitatory-inhibitory layers (KII); (b) impulse response of KII: average density \(<a>\) of inhibitory population follows excitatory population with a quarter-cycle delay; (c) three coupled oscillators (KIII), \(O_0, O_1,\) and \(O_2\), each with a pair of excitatory-inhibitory layers; (d) top 3 diagrams: examples of time series of three isolated oscillators; (d) bottom panel: broad-band chaotic time series produced by interconnected six-layer oscillators; adopted from [49].

A potential shortcoming of neuropercolation is that it requires massive computational resources to achieve the needed spatial and temporal resolution with proper accuracy. This shortcoming can be mitigated by dedicated computational resources, as cellular automata allow massively parallel implementations. In addition, analog platforms can be explored, which benefit from the intrinsic noise and memristive dynamics in such systems [59]. Neuropercolation uses the constructive role of noise to tune the system to criticality, much like
the temperature can serve as a macroscopic control parameter in non-equilibrium thermodynamic systems [60].

Conclusions

There are several fundamental theoretical paradigms used in modeling experimentally observed transient brain dynamics and rhythms, including nonlinear dynamics with metastable states, phase transitions, and criticality. The field is rapidly developing with frequent new discoveries in all of these areas. Neuropepercolation is a natural mathematical domain for modeling collective properties of networks, when the behavior of the system changes abruptly with the variation of some control parameters. It provides a convenient framework to describe phase transitions and critical phenomena in spatially distributed large-scale networks, in particular in brain networks with transient dynamics.

Acknowledgments

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References


[3] W.J. Freeman, R. Quirán-Quiroga, Imaging brain function with EEG: advanced temporal and spatial analysis of electroencephalographic signals, Springer, 2013. This volume provides a state-of-art overview of EEG monitoring techniques, including single trial experiments, high-density arrays, and space-time spectral analysis. Instantaneous phase differences are evaluated based on Hilbert transform, indicating the presence of metastable states with large-scale synchrony (small phase dispersion), interrupted by brief periods of desynchronization (high phase dispersion) at alpha-theta frequencies. This work addresses the apparent contradiction between distributed cortical representations and concept cells.


A systematic study describing the significance of multiple temporal and spatial scales in brain dynamics and cognitive processing, based on MEG/EEG experiments using source reconstruction techniques. Long–range temporal correlations (LRTCs) over time scales of several seconds or longer are compared with neuronal avalanche dynamics spanning over time scales of orders of magnitude shorter, in the ms range. Power–law scaling is observed over both short and long scales, with power exponents correlated with behavior, such as resting state and audio–visual cognitive tasks. Short latency of 10–20 ms has been detected between posterior, temporal, and post–central cortical areas, which is consistent with the concept of rapid propagation of phase gradients as part of the cognitive cycle; see Ref. (3).


[23] E. Tognoli, J. A. S. Kelso, The metastable brain, Neuron 81(1) (2014) 35–48. Metastability has been identified in coordination dynamics as the result of competing tendencies leading to intermittent oscillations in brains. Metastability is described as a dynamic balance between processes of local segregation and global integration. Intermittent emergence of synchronous neural ensembles observed in EEG data illustrate neurophysiological correlates of metastability.


[25] M. I. Rabinovich, Y. Sokolov, R. Kozma, Robust sequential working memory recall in heterogeneous cognitive networks, Frontiers in Systems Neuroscience 8 (2014) 220. This is a recent addition to the mathematical theory and interpretation of stable heteroclinic channels (SHC) describing transient dynamics in brains and in cognitive functions. The introduced model describes attentional switching in coupled Lotka–Volterra equations manifesting the winnerless competition principle. Coexisting SHC and chaotic attractors are interpreted as manifestations of heteroclinic chimeras in the attractor space of attentional dynamics under healthy and pathological conditions.


This work describes a hierarchical neural network called Freeman KIII model, motivated by the multi-layer structure of the cortex. KIII encodes input data in chaotic spatio-temporal oscillations (AM patterns), in the style of brains. The original KIII uses a system of nonlinear ordinary differential equations (ODEs), which is replaced here by a six-layer neuropercolation model. The multi-layer neuropercolation model exhibits phase transitions between fixed point, limit cycle, and broad-band chaotic regimes, as well as intermittent synchronization–desynchronization transitions.


This is a systematic study of second order phase transitions in cortical networks, involving scales from microscopic to macroscopic levels. The role of self-generated, endogenous fluctuations (noise) is emphasized in brains as non-equilibrium thermodynamic systems, as opposed to noise introduced ad hoc to fit measurement data.


This edited book provides a comprehensive overview of criticality in neural systems from leading experts in the field. It includes detailed description of experimental evidences of criticality in neural tissues and brains, as well as theoretical interpretation of the observations. Large part of this volume expands on self-organized criticality, scaling laws, long-range correlations, and avalanche dynamics. It also contains important contribution to brain theories in the context of statistical physics of universality classes and non-equilibrium thermodynamics of brains with intermittent transitions.
This handbook describes advances in large scale networks, including mathematical foundations of random graph theory, modeling and computational aspects, topics in physics, biology, neuroscience, sociology and engineering. Chapter 7 includes a unique description of scale-free cortical planar graphs. The described evolution rules differ from preferential attachment and they are relevant to brain networks with pioneering neurons, related to "rich club" nets described later in the literature Ref. (39).


This work describes the resting state network (RSN) using a simple model with a connectivity matrix derived from fMRI studies. The state of each unit is either excited, quiescent, or refractory, and the states evolve in time using a threshold-based probabilistic update rule. The model gives evidence of brains tuned to criticality by exhibiting important hallmarks of criticality, such as divergent correlation length, anomalous scaling, and the existence of large-scale resting networks.


G. Werner, Consciousness viewed in the framework of brain phase space dynamics, criticality, and the renormalization group, Chaos, Solitons, and Fractals 55 (2013) 3–12. This work presents an inspiring vista of the paradigm of criticality applied to higher cognition and consciousness. In this posthumously appeared swan song by an iconic researcher of the field, plausible arguments are introduced for employing renormalization group theory to model the nested hierarchy of brain operating levels, progressing through
phase transitions from one level to the other in the intentional brain–body–environment cycle.


This work introduces the newest developments in multi-layer neuropercolation models with Hebbian learning. The broad-band (chaotic) basal state of coupled oscillators can be destabilized by learnt input, and the system briefly collapses (condenses) to a highly coherent narrow-band oscillatory state. The condensed state is transient and it gives rise to a new basal state that correspond to the experienced input in the context of past experiences.


A theory of extreme events is developed in conjunction with the experimentally-observed deviation from power law behavior in a number of natural systems, including solar flares, earthquake, and stock market crashes. The phenomenon is named ”Dragon King” (DK) and it is described by mechanisms distinct from self-similarity and the corresponding ”Black Swans” (BS). It is argued that DKs are predictable, which is a clear difference from the unpredictable nature of BSs. Our essay puts forward the hypothesis that cognitive phase transitions are manifestations of DKs.


