25 years of criticality in neuroscience — established results, open controversies, novel concepts

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Twenty-five years ago, Dunkelmann and Radons (1994) showed that neural networks can self-organize to a critical state. In models, the critical state offers a number of computational advantages. Thus this hypothesis, and in particular the experimental work by Beggs and Plenz (2003), has triggered an avalanche of research, with thousands of studies referring to it. Nonetheless, experimental results are still contradictory. How is it possible, that a hypothesis has attracted active research for decades, but nonetheless remains controversial? We discuss the experimental and conceptual controversy, and then present a parsimonious solution that (i) unifies the contradictory experimental results, (ii) avoids disadvantages of a critical state, and (iii) enables rapid, adaptive tuning of network properties to task requirements.

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Introduction

Twenty-five years ago, Dunkelmann and Radons [20] showed that neural networks can self-organize to a critical state. This critical state marks the transition between stable and unstable dynamics (Box 1): On average, the network conserves the number of spikes, thus every spike in one neuron on average causes one spike in all its postsynaptic neurons [54,39,70,56••,73]. At criticality, these networks are characterized by spatio-temporal cascades of activity, called avalanches, that typically are very small, but some span the entire network.

In the past decades, the criticality hypothesis, and in particular the experimental work by John Beggs and Dietmar Plenz (2003), has inspired numerous theoretical and experimental studies. Nonetheless, experimental results are still contradictory. How is it possible, that a hypothesis is at the same time so attractive and fascinating that it has prevailed for more than two decades, but also sparked heated debates and still remains controversial?

The hypothesis that the brain operates at a critical point is attractive for two reasons. On a conceptual level, criticality has been shown to maximize a number of properties that are considered favourable for computation. On an experimental level, there is considerable evidence in support of the criticality hypothesis. However, both of these points are sources of controversy. On the conceptual level, maximization of certain properties is unlikely to explain cortical function, and it is frequently neglected that criticality also maximizes properties that are likely adversarial to cortical function. On the experimental level, assessing criticality is more intricate than first thought, undermining the significance of the accumulated evidence. In the following, we discuss these two points in detail.

Conceptual appeal and controversies

In models of neural networks, criticality maximizes a number of properties considered favourable for computation [5,77]. Tuning models towards critical phase transitions has been shown to maximize the number of metastable states [31], the dynamic range [40,26], information transmission in terms of mutual information [84,78,79], active information storage [9•], and computational power in terms of input-output mappings [48,8,42]. Self-organized critical networks can also efficiently implement non-convex optimization [34]. These functional benefits made criticality an attractive target state for self-organization of cortical networks.

However, criticality also maximizes further aspects, which are likely negative for function. For example, the variability of network responses diverges at the critical point, which comes at the cost of reduced specificity [28] and reliability [91]. Likewise, criticality is accompanied by "critical slowing down" [75], which means that systems might take overly long to finish a computation before being clear for new stimuli.

Instead of *maximizing* particular network properties, *sufficient* performance for a given task is a more likely design principle for network function [9•,69]. This sufficient performance is most likely not achieved by maximizing one particular property alone, but rather by balancing the competing, positive, and negative aspects. This balance may represent, e.g., a balance between sensitivity and

Figure 1
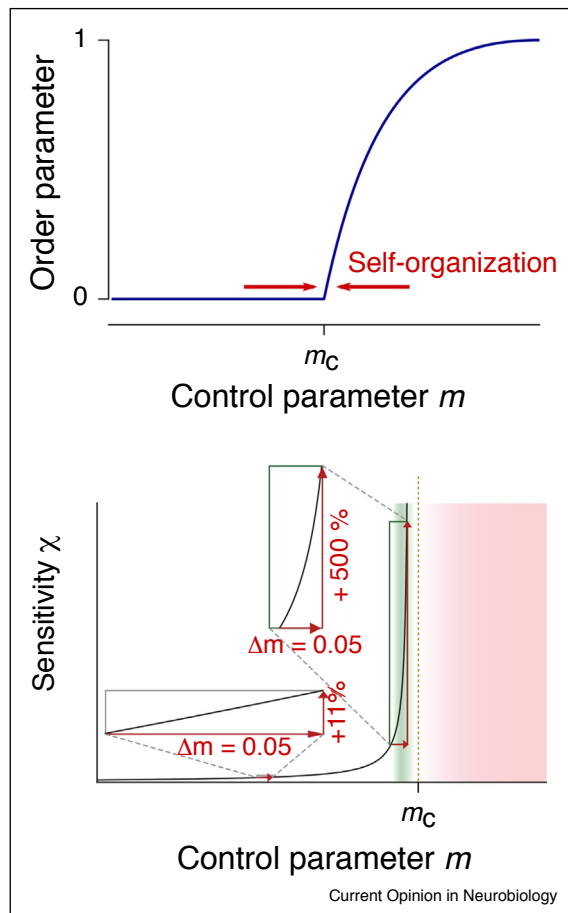
Criticality. (a) In general, if the dynamics of a network can be adjusted by a control parameter m, a critical point m_C marks the transition between distinct dynamical regimes. (Note that in experimental studies, m is often denoted by σ.) One can define an order parameter, which is zero in one regime, but non-zero in the other. For this 2nd order phase transition, the change of the order parameter is continuous, but not smooth at m_C. For avalanche criticality, this order parameter is the probability that an avalanche lasts forever, and thereby marks the transition from stable ($m < m_C$) to unstable ($m > m_C$) dynamics. Other phase transitions occur between ordered and chaotic, oscillatory and non-oscillatory, or asynchronous and synchronized dynamics. If the critical state is an attractor state, i. e. the control parameter is driven back to the critical point (red arrows), this is called self-organized criticality. Certain plasticity rules like homeostatic plasticity or synaptic depletion can implement self-organized criticality (e.g. [45,44●,95●]), but could also promote adaptation to different states [95●]. **(b)** Many network properties, like the sensitivity, variance of responses, correlation length, and autocorrelation time, diverge at the critical point. Therefore, networks poised in a *reverberating regime* (green) can adjust these network properties by very small changes in the control parameter. The same absolute change in the control parameter has hardly any impact for networks poised farther away from criticality (insets).

specificity [28], between quality of representation and integration time [79], or between stimulus detection and discrimination [88,15●] – all under the constraint of

spending as little resources and energy as possible. Importantly, this optimal balance may not be achieved at criticality.

Experimental evidence and challenges

Assessing criticality in experiments traditionally relies on identifying power-law distributions of avalanche sizes. Avalanches are spatio-temporal cascades of activity, whose sizes are expected to follow a power-law distribution [2] if networks are critical (see Box 2). The slope of this distribution depends on the universality class of the underlying dynamics [39,70] and is, e.g., expected to be −3/2 for critical branching processes [32].

Power-law distributions of avalanche sizes were indeed found in many experiments. Following the influential study by Beggs and Plenz [6●●], who identified power-law distributed avalanches in the LFPs of cultured slices, subsequent studies *in vitro* found similar distributions in LFPs and spiking activity of cultured dissociated neurons or cortical slices [51,61,85,25]. In living animals, power-law distributions were found in LFPs of macaque [66], rhesus monkey [62,94], and cat [29,30], in two-photon microscopy in mice [76,7], in light-sheet microscopy of whole-brain GCaMP activity in zebrafish larvae [65], in LFPs from intracranial depth electrodes in humans [68], in MEG and EEG of adult humans [47,78,60] and preterm babies [37], and in human BOLD signals [82].

Surprisingly, avalanche size distribution of *in vivo spiking* activity often differ from power-laws. While most evidence for criticality *in vivo*, in particular the characteristic power-law distributions, has been obtained from *coarse* measures of neural activity (LFP, EEG, BOLD; see [69,63] and references therein), avalanches reconstructed from spiking activity in awake animals typically did not display power-laws [69,71,[66,68,27,69,72,46,92●●],61,29,85]. These deviations from power-laws were attributed to subsampling effects [66], i.e. the limitation that only a small number of neurons can be recorded simultaneously with millisecond precision [66,68,27,69,72,46,92●●]. However, power-laws should retain approximate power-law characteristics under random subsampling [46]. Therefore we argue that these deviations from power-laws actually reflect deviations from critical dynamics, as outlined below.

The extraction of avalanches from neural recordings can be ambiguous. Any two subsequent avalanches are separated by pauses in the activity, i.e. bins without spikes (see Box 2). These empty bins define the end of one avalanche and the start of a new one. However, neural activity does not show a separation of timescales (i.e. clear pauses) that allows for an unambiguous separation of avalanches, because the awake cortex (or a reasonably sized part of the brain, e.g. a cortical column) is certainly never entirely silent for several milliseconds.

Figure 2
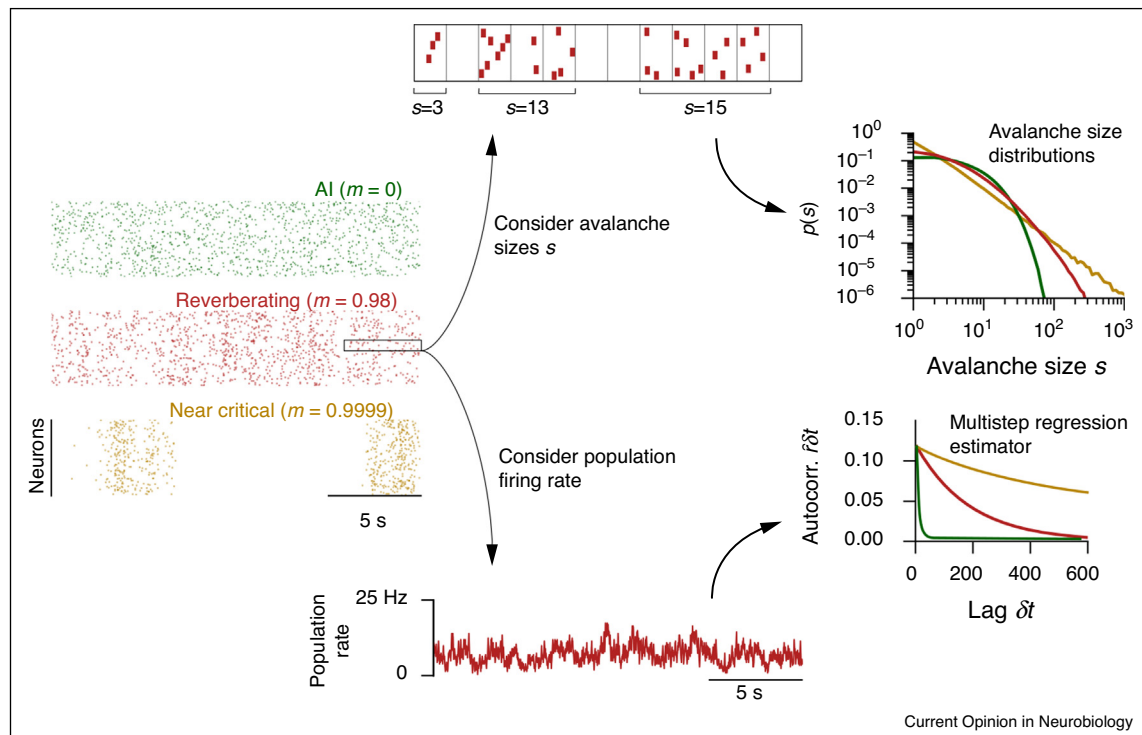
Assessing criticality in experiments. **Left.** Raster plots of the population activity for three different dynamics, asynchronous and irregular (AI), reverberating, and near critical. **Upper part.** A subset of all neurons is recorded experimentally, and avalanches are extracted using temporal binning. Empty bins (pauses) separate subsequent avalanches. The avalanche size s is the total number of spikes in a sequence of non-empty bins. In critical systems, the avalanche size distribution $p(s)$ follows an (approximate) power-law if the system is critical, even if only a random subset of neurons was sampled [46], whereas for Poisson activity it is approximately exponential [67]. **Lower part.** The ongoing activity considers the total number of spikes in each bin, without isolating avalanches. From this ongoing activity, the multistep regression estimator [92**] allows one to infer the distance to criticality based on the autocorrelation of the ongoing population activity.

Instead, avalanches are continuously initialized, merge and split up, presenting a melange that cannot be separated into the individual cascades from spike recordings alone [69]. Hence, for analysis purpose, empty bins are only found if (i) the bin size tends towards zero, (ii) the system is heavily subsampled, or (iii) thresholding is applied to the activity [18,64,69]. This dependence on the experimental setting and analysis parameters renders the definition of avalanches ambiguous. The analysis ambiguity is inherent, because causal avalanches cannot be tracked, and thus is not solved by more dense recordings that are recently developed [80,81]. As a consequence, the resulting avalanche distribution depends on the choice of the bin size, threshold, and the number of analyzed neurons or channels.

Power-law distributions may also arise in the absence of criticality. Priesemann and Shriki [67] showed that time-varying network input can give rise to power-law distributed avalanches even though the underlying network did not self-organize to criticality. Furthermore, power-law distributions may arise simply because of logarithmic

representations or thresholding [89]. Hence, power-law statistics alone are not necessarily indicative of self-organized criticality.

Recent advances in the study of subsampled systems overcome many of the ambiguities of avalanche size analysis. A novel estimator that relies on ongoing neural activity can precisely quantify the distance from criticality on a continuous spectrum [92**], and is easy to apply to data (Box 2): It requires only a few tens of multi-unit spike recordings, is subsampling-invariant, and does not require a separation of timescales, or spike sorting. It can reliably infer the distance from criticality, and thus is a valuable tool to investigate cortical network dynamics, and the changes thereof.

Reverberating dynamics

This novel estimator suggests that cortical dynamics is not critical, but reverberating. We applied the estimator to *in vivo* spike recordings and identified a reverberating regime $(0.94 < m < 0.998)$, consistently across brain areas, species, and tasks [92**,93]. This reverberating

regime has also been found by a complementary approach by Dahmen et al. [16], who inferred it from the distributions of spike covariances.

This reverberating regime may resolve many of the conceptual controversies [91,93]. First, instead of solely maximizing singular properties, the reverberating regime can balance competing requirements, e.g. sensitivity vs. specificity [28], quality of representation vs. integration time [79], or stimulus detection vs. discrimination [88,15•]. Second, the reverberating regime allows flexible adaptation to task requirements, because small parameter changes can induce rapid, strong changes of computational properties, which we called dynamic adaptive computation [91] (see Box 1). Third, it allows amplification of small stimuli, while keeping a safety margin from supercriticality, which has been associated with instability [69]. Fourth, the reverberating regime offers the substrate to tune short-term memory, as information about the input is maintained for well-defined time-spans ranging from a few hundred milliseconds to a few seconds, which has been exploited in echo state networks [48,38,9•]. Last, the reverberating regime offers a loop hole from the platonic idea of criticality. In contrast to the view of "as close to critical as possible", which still holds criticality as the ideal target [90,50], cortical networks might self-organize to different points in the reverberating regime, and thereby gain flexibility and the ability to balance competing requirements.

The reverberating regime may also resolve experimental controversies. Considering experiments in humans or awake animals, most power-law distributions, evidencing criticality, have been found in coarse measures like population spikes, LFP, EEG or MEG signals. For all these signals, the electrodes may sample from overlapping populations. This enhances the *observed* correlations between electrodes, and can lead to power-laws, even if the underlying population is not critical but in a reverberating regime [63]. In contrast, in spike recordings *in vivo* power-laws were typically not observed [69,71,4,17]. A parsimonious explanation is that *in vivo*, cortical dynamics is not critical, but resembles a reverberating regime. This does not contradict the evidence for criticality — including spiking activity — in *in vitro* setups. The emergence of very different states, a reverberating state *in vivo* and a critical state *in vitro*, can be explained by differences in topology [41], or the lack of external input characterizing isolated *in vitro* networks [95•].

Open topics
It is unclear how different concepts of criticality relate to each other. The term criticality is not strictly defined, and it is used for multiple concepts in neuroscience [56••]. Besides the avalanche criticality discussed in this review, which is a transition between stability and instability, similar phenomena arise at different dynamical critical

transitions, e.g. between ordered and chaotic, called the edge of chaos [8,9•], or between non-oscillating and oscillating, called the edge of synchrony [12,49,59,10]. Although these three concepts share some features like avalanche size distributions [19] and critical slowing down [75], a definite justification for their interchangable use in the literature remains desirable. Apart from dynamical criticality, neural networks might exhibit statistical criticality, identified by diverging specific heat in maximum entropy models [55,86,87,36,74•,58]. How statistical and dynamical criticality precisely relate to each other in neural networks is yet another topic of open research.

Dynamic adaptive computation allows experimental predictions to be tested in the future. A hierarchy of distances to criticality and the corresponding network timescales has been observed across visual and sensory pathways [57] and may represent a specialization to network function [33,35,14,13•]. The concept of dynamic adaptive computation predicts that a modulation of this hierarchical backbone can be observed in various contexts, and can depend on vigilance state and task. Indeed, there is evidence that the power-law nature of avalanche size distributions changes with cognitive states, for example across the sleep-wake cycle [71,68,53,52] or under changes of consciousness [83,7,23,21,24,43]. Markers of criticality have been shown to transiently change depending on the behavioral state [30], attention [22,88], and stimuli [1,94,11]. These studies provided evidence that the brain may not be self-organized critical, but is capable of self-organization to different states. Precisely linking the changes in the reverberating regime to the specific task at hand remains a challenge for future work.

Conflict of interests
The authors declare that there was no conflict of interests.

Acknowledgments

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- •• of outstanding interest

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