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Trends in Neurosciences

Feature Review

How critical is brain criticality?

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Criticality is the singular state of complex systems poised at the brink of a phase transition between order and randomness. Such systems display remarkable information-processing capabilities, evoking the compelling hypothesis that the brain may itself be critical. This foundational idea is now drawing renewed interest thanks to high-density data and converging cross-disciplinary knowledge. Together, these lines of inquiry have shed light on the intimate link between criticality, computation, and cognition. Here, we review these emerging trends in criticality neuroscience, highlighting new data pertaining to the edge of chaos and near-criticality, and making a case for the distance to criticality as a useful metric for probing cognitive states and mental illness. This unfolding progress in the field contributes to establishing criticality theory as a powerful mechanistic framework for studying emergent function and its efficiency in both biological and artificial neural networks.

Highlights

Empirical and theoretical work suggests that the brain operates at the edge of a critical phase transition between order and disorder.

The wider adoption and investigation of criticality theory as a unifying framework in neuroscience has been hindered in part by the potentially daunting complexity of its analytical and theoretical foundation.

Among critical phase transitions, avalanche and edge of chaos criticality are particularly relevant to studying brain function and dysfunction.

The computational features of criticality provide a conceptual link between neuronal dynamics and cognition.

Mounting evidence suggests that near-criticality, more than strict criticality, may be a more plausible mode of operation for the brain.

The distance to criticality presents a promising and underexploited biological parameter for characterizing cognitive differences and mental illness.

Complexity and the critical brain

In probing the deep complexity of the brain, neuroscience is increasingly drawing from the tools and concepts of complexity science. Metrics such as fractal dimension and multifractality [1,2], entropy and Lempel-Ziv complexity (LZC) [3], integration–segregation measures [4–6], and **power laws** (see Glossary) [7], such as the aperiodic '1/*f*' slope of the electrophysiological power spectrum [8,9], each have sought to carve neural complexity at its joints. Each metric reveals a different aspect of brain complexity, yet establishing a coherent picture of how such metrics relate to cognitive processes (or their disruption) has proven challenging.

Criticality, a term increasingly encountered alongside these discussions of brain complexity, may come across as yet another one of these disparate metrics; to be sure, it is not. Far from a metric, criticality is a special kind of collective behavior observed in many-bodied systems. It is one of the ways, perhaps the main way, in which nature produces complexity [10,11]. The concept of criticality was first elaborated to describe materials undergoing a **phase transition**, but it has since found applications in a stunning diversity of complex natural systems, a fact that naturally led to the proposal that the brain, too, may be 'critical'. Specifically, the critical brain hypothesis is the conjecture that the global neuronal dynamics of the healthy brain operate at the boundary of a critical phase transition between an ordered and a disordered phase [1,10,12–27].

Phase transitions are common in nature: liquid water transitions into steam at high temperature, carbon transforms into diamond at high pressures, and iron becomes magnetized under a strong magnetic field. In every case, the large-scale, collective behavior of a system composed of billions of elements is suddenly and qualitatively altered when a certain global parameter, the **control parameter**, crosses a critical point. Put this way, the concept of a phase transition is readily transferable to any large system of very many interacting elements, such as the brain. In this analogy, the many interacting elements are usually the neurons, the control parameter can, for instance, be excitation/inhibition (E/I) balance or a neuromodulator concentration, and the large-scale behavior

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is a dynamical property such as functional integration, neuronal oscillations, or **chaos** in neural dynamics.

Applying this analogy leads to an intriguing observation: for certain interesting phase transitions, such as the one between propagating and fading activity (so-called '**avalanche criticality**') [13,28], or the transition between stable and chaotic activity (the '**edge of chaos**') [11,29], brain dynamics do not 'jump' from one phase to another, as water does when it freezes or boils, but rather, the dynamical state of the brain seems to maintain itself at, or near, the critical boundary between both phases, that is, near criticality. Not all phase transitions allow this behavior. In some, the critical point is too unstable; these are first-order or discontinuous phase transitions, with freezing and boiling water falling into this category. Criticality is maintainable only in second-order or continuous phase transitions, and even then, it requires precise tuning of a control parameter. Distinctively, some systems appear to possess certain mechanisms for 'self-tuning' to the critical point; this phenomenon is called **self-organized criticality (SOC)**. Many diverse natural systems exhibit SOC, such as earthquake fault systems [10], viral evolution and spreading [30], and swarming behavior (e.g., starling murmurations) [31]. In some of these cases, such as earthquakes or sandpiles [32], SOC appears to be a quirk of physics, but when criticality is maintained in living systems, it often suggests some adaptive advantage. Indeed, the critical point boasts some remarkable properties that are highly advantageous for adaptive information-processing systems, including a maximal sensitivity to perturbations, an enriched repertoire of system states, and a high capacity to store and transfer information within the dynamics of the system [18,29,33–36]. Hence the 'strong' formulation of the critical brain hypothesis: evolution may have selected critical brain dynamics for the advantageous information-processing capabilities it confers to the organism. On a more intuitive level, organisms must balance structure (order) and flexibility (disorder) in contending with the predictable and the novel in their changing environment; critical brains may optimize this balance [37].

A now large body of work has found evidence of critical dynamics in the brain, *in vitro* [13,38,39] and *in vivo* in spike recordings [20,23,24,40] and coarser-grained modalities [41–44], including electroencephalography (EEG) [1,45], magnetoencephalography (MEG) [27,46–49], and functional magnetic resonance imaging (fMRI) [50,51]. Critical dynamics are re-established after a disturbance [24,43], attenuated with prolonged sleep deprivation [52], modulated by drugs [13,27,53], and abolished by anesthesia [27,41,54–57]. Behaviorally, brain criticality has been associated with cognitive flexibility [58,59] and fluid intelligence [60], whereas deviations from the critical point have been linked to neurological and psychological disorders such as epilepsy [61,62], schizophrenia [2,63,64], and dementia [65–67].

In spite of the growing appeal of the critical brain hypothesis, it remains somewhat niche even within systems neuroscience, ostensibly due to two main obstacles: first, criticality is complicated. What begins as a clear and simple idea, namely, the middle ground between order and disorder, upon closer study quickly branches out into a labyrinth of subtypes, subtleties, and special cases that impose a steep barrier of entry to the field. Second, there is some disagreement in the literature about whether brain data do indeed support the notion of a fully critical brain, or rather a near-critical brain (see [22] for a review), an intriguing subtlety that may however be misconstrued as a wholesale invalidation of the theory. Together, these obstacles often conspire to dissuade otherwise interested researchers and further progress is stymied as a result.

Recently, the advent of large-scale multineuronal recording techniques has breathed new life into the field [23,26,42,68–71]. The unprecedented scale and coverage of these new datasets are now enabling the application of advanced criticality analyses drawn from **statistical physics**

Glossary

Avalanche criticality: a large class of continuous phase transitions that separate a phase where activity dissipates from a phase where activity is amplified; they are characterized by scale-free avalanches.

Chaos: the property of a process whose trajectory in phase space is sensitive to small differences in initial conditions.

Control parameter: a variable that, when tuned past a critical value, brings about a phase transition in a system, (e.g., temperature in the water–steam transition).

Dynamic range: the range of input rates that are separately encodable within the system dynamics.

Dynamical system: a physical model or mathematical system that evolves in time according to fixed equations, but which often gives rise to complex behavior.

Edge of chaos: a phase transition between a stable phase and a chaotic phase.

Emergence: said of a high-level property that cannot readily be explained in terms of its low-level constituents. This intractability can be variously interpreted. In weak emergence interpretations, the inexplicability is merely a practical one due to the sheer complexity of the computation required to reach an explanation and reductionism still holds in principle. In strong emergence interpretations, the emergent property possesses causal autonomy independently of its constituents, thus challenging the principle of reductionism.

Mutual information: an information-theoretic measure of the amount of information shared between two sources.

Neuronal avalanche: a cascade of neural events (e.g., action potentials) that starts from a single seed event and propagates through a population.

Phase transition: a boundary (hyperplane) in phase space at which a macroscopic property of the system (the order parameter) qualitatively changes (e.g. the water–steam transition, the magnetization of iron, or the onset of chaos in artificial neural networks).

Power law: a mathematical relationship $f(x) \sim x^{\beta}$ where one quantity $f(x)$ varies proportionally to another quantity x raised to a certain power β. Also known as a scaling law.

and **dynamical systems** theory. Their results are at once providing compelling evidence and greater understanding of brain criticality, offering resolutions to past discrepancies in data and suggesting new ways in which criticality and cognition are connected. The time is ripe for neuroscience to give criticality a closer look.

In this review, we provide a concise, didactic overview of the state-of-the-art of criticality neuroscience, covering these latest developments and the new understanding they afford and making a case for the usefulness of criticality models to neuroscientific inquiry. First, we describe two important types of brain criticality, namely, avalanche criticality and the edge of chaos [72], and go over the evidence for their occurrence in the brain. Second, we review the evidence of the hypothesized relationship between criticality and cognition, including conscious states. Third, we discuss potential implications of brain criticality and deviations therefrom for understanding typical and atypical brain function. For complementary overviews of the topic, we refer readers to previous excellent reviews [14,21,25,73,74] and a recent book [75].

Avalanche criticality

Avalanche criticality is the most commonly encountered type of critical phase transition in the neuroscience literature, where it is often called simply 'criticality', or sometimes the 'edge of activity propagation' [21], or 'crackling noise' [28].

The textbook example of avalanche criticality is the magnetization of iron under a magnetic field. The sample of iron is modeled as a lattice of interconnected nodes, each of which occupies one of the two states: spin-up or spin-down (Figure 1A). Iron atoms prefer to align their spin with that of their neighbors; this is the ordering interaction force. Countering this tendency is an intrinsic, random preference of each individual spin to assume an idiosyncratic orientation (due to imperfections in the lattice); this is the intrinsic field, a disordering force. Beginning in the disordered state (i.e., random orientations; Figure 1B, top), an avalanche-critical phase transition can be brought about by exposing the sample to a magnetic field, which progressively coaxes the spins into alignment, amplifying the ordering tendency. Eventually, a point is reached where order just barely overcomes disorder and the iron is on the edge of becoming magnetized (Figure 1B, middle): this is the avalanche-critical point [28,76]. Past this point, the delicate balance is abolished as order reigns over disorder and large regions of the magnet become uniformly aligned (i.e., magnetized; Figure 1B, bottom). In this way, avalanche criticality is the dynamics-rich middle ground between frozen order and disintegrated disorder, a seeming prerequisite for complex behavior.

The model we have just described is the Ising model, the workhorse of statistical physics. How does it map onto the brain? There are many ways in which the model has been applied to neural data [42,50,60,77,78]. Usually, the nodes of the lattice are taken to represent neurons or neuronal ensembles and the binary states of the nodes are high- and low-firing states of neurons/ensembles. Each of the forces acting in magnets then finds counterparts in parameters of brain dynamics: the interaction force between spins models synaptic weights between neurons or excitatory interactions between neuronal ensembles; the intrinsic field of the spins models the variance of neuronal excitabilities; and the external magnetic field can reflect any number of global physiological variables in the brain, such as E/I balance, neuromodulator concentrations, or the strength of sensory input [14,42]. The resulting model of brain dynamics is capable of attaining avalanche criticality with the correct balancing of these physiological parameters. A slightly different critical model, known as the branching model [36,79], is used to model spiking networks, yet the control parameters, large-scale behavior, and computational features are largely the same [14,80].

Scale-free or scale-invariant: said of a shape or process whose statistics remain the same under a change of scale (i.e., spatial, temporal, or energy scale).
Self-organized criticality (SOC): any type of criticality that is autonomously maintained through homeostatic-like feedback loops.
Spin glass: a magnet-like model where the couplings between nodes can be positive or negative (instead of only positive), resulting in so-called frustrated interactions, chaos, and metastable states.
Stability: the property of a system that returns to its initial state within a finite period after a perturbation.
Statistical physics: the branch of physics concerned with explaining the large-scale behavior of systems in terms of the collective action of their constituent elements.
Universality: a property of large classes of dynamical systems whereby their macroscopic properties are independent of many of their microscopic parameters.

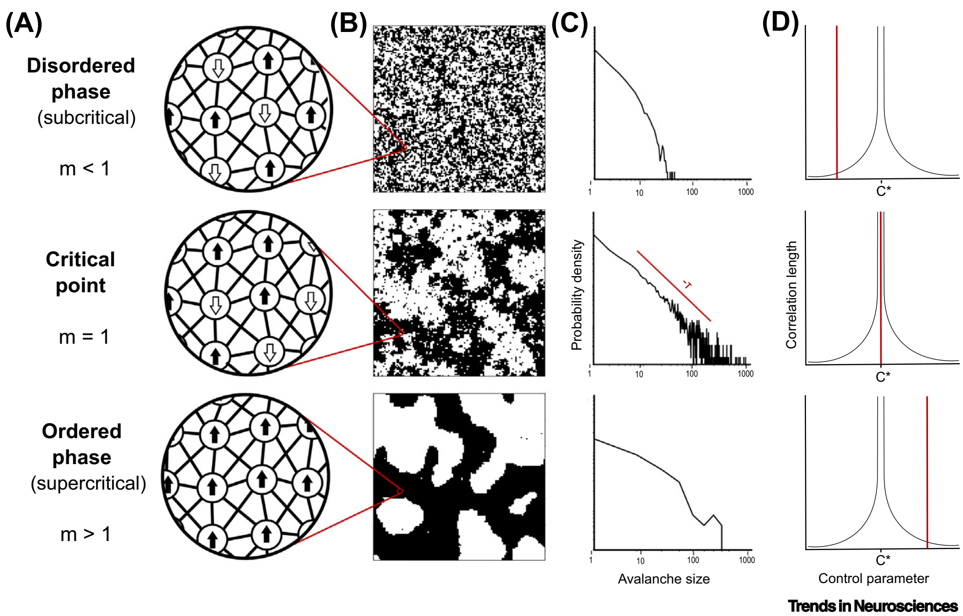

Figure 1. The Ising model captures the essence of avalanche criticality. (A) The model consists of a large lattice of interconnected nodes. Each node can occupy one of the two 'spin' states: spin-up or spin-down. Importantly, neighboring atoms prefer to keep their spins in the same direction, though this tendency to alignment is opposed by a tendency to randomness. Randomness can be supplied by imperfections in the lattice and/or by a temperature parameter; the latter can be a control parameter for the phase transition (as an alternative to the external magnetic field; see main text). (B) The large-scale behavior of an *in silico* Ising model is shown here at three different temperatures. As temperature rises, ambient molecules collide with the spins with increasing speed and frequency, destroying the alignment created by the intermolecular interactions. Starting from an ordered state of broad alignment (bottom panel), rising temperature progressively degrades the inter-spin coherence until the critical point (middle panel), where a flipping spin on average causes only one of its neighbors to flip (i.e., the branching parameter is $m = 1$). This has the effect of producing spin-flip cascades of all sizes, which are visible in this snapshot as fractal patches of aligned spins. A further increase in temperature dissolves these patches into small noise-like fluctuations of a characteristic small size, as any incipient spin correlation is quickly destroyed by ambient heat (top panel). (C) The static picture of the patches is complemented by the dynamic picture obtained by tallying spin-flip cascades, or avalanches. Here, the empirical probability distribution of avalanche sizes is plotted on logarithmic axes. In the disordered phase (top panel), all avalanches are small, reflected in a rapidly slumping curve with increasing size. At the critical point (middle panel), frequency scales evenly with size, yielding a straight line relationship indicative of a power law with exponent τ (tau). In the ordered state (bottom panel), avalanches are typically very large, manifesting as a bimodal distribution with many avalanches spanning across the entire system. The plots shown here were generated using a simulated branching model from [199]. (D) As the control parameter (in this case, the temperature; red line) crosses the critical point C*, a number of interesting properties of the system diverge or reach their peak value, such as the correlation length, both between sites (space) and through time.

The effect of the critical balance of order and disorder on dynamics can be understood through its effect on avalanches, a ubiquitous feature of these dynamics. The term comes from the study of the behavior of critical sandpiles [32], but direct analogs are found in magnets [28], as well as in brain where they are known as **neuronal avalanches** [13]. An avalanche occurs when an activated node in the system (the seed) proceeds to itself activate one or more other nodes through their coupling interactions, creating a 'chain reaction'. Avalanches are not unique to criticality; they can be found in the ordered and disordered phases as well. What is unique to the critical point is the special character of its avalanche distribution. In the disordered phase, the (ordering) coupling is weak compared with the (disordering) intrinsic field and so most avalanches are of a similar small size, not spreading very far (Figure 1C, top). However, when the coupling force instead exceeds the disorder, as in the ordered phase, then avalanches spread easily and many of them take over the entire system (Figure 1C, bottom). The critical middle ground occurs when coupling and disorder are balanced such that every activation event, on average, gives rise to only one other event [13,28]. When this happens, avalanches neither die out too quickly nor do they saturate the system, but instead they come in all sizes equally; they are **scale-free or scale-invariant (**Figure 1C, middle). Scale invariance is the quality of a shape or process that looks similar at every scale and is closely related to fractals [81]. A scale-invariant distribution of avalanche sizes is the cardinal feature that defines avalanche criticality [28,32].

Scale invariance has many surprising effects that are relevant for information processing and computation. The largest avalanches reach across the system with prolonged reverberations, creating long-range correlations in space and time. In space, these divergent correlations effectively nullify the path length between nodes, maximizing information transfer; in time, they endow the system with long memory for its past states, maximizing information capacity [82] and information storage capacity [36]. Another way to understand long memory is to say that a critical system retains maximum information about its own history within its dynamics. The system thus becomes integrated both spatially and temporally. Furthermore, the even spread of correlations across every length scale creates an optimal balance of integration and segregation [5,83,84]. The presence of large avalanches also implies that the system will produce long, drawn-out responses to perturbations, a phenomenon known as critical slowing down [85], which endows the network with a long intrinsic timescale [86–88]. Meanwhile, the small noise-like avalanches provide a rich source of variability, contributing to a large state repertoire and high trial-to-trial variability [18,89]. Last, the one-to-one spreading of activity at criticality maximizes **dynamic range** [18,33,35] and, more generally, makes the system maximally sensitive to perturbations, a phenomenon known as divergent susceptibility [76]. Together, these useful computational features comprise an advantageous operating regime for adaptive information-processing systems such as the brain.

Neural evidence of avalanche criticality

The most salient marker of avalanche-critical dynamics is the occurrence of power laws in many aspects of system dynamics. As the mathematical signature of scale invariance, power laws are ubiquitous in critical systems. The $1/f$ aperiodic scaling of the electrophysiological power spectrum [8,9], is a well-known example of a power law and as such is consistent with critical dynamics [32]. Other neurophysiological observables that are expected to display power laws at criticality are the probability distributions of neuronal avalanche size (Figure 1C) and duration [13,16,45] and long-range temporal correlations (LRTCs) in neural time series [1,90,91].

Indeed, power laws in these neural observables have been observed in a large variety of experimental setups: *in vitro* in local field potentials (LFP) [13,38] and spiking data [16,39] and *in vivo* in humans [17,45,46,56,92] and other species [20,42–44,53,93]; as well as in diverse modalities, including multi-unit recordings [19,20,40], calcium and voltage imaging [41,42,57], EEG and MEG [45,46,48,67,91], and fMRI [17,56]. Importantly, power law distributions appear to be among the outcomes of developmental processes [39] and neural homeostatic regulation [24,43].

An important caveat, however, is that many noncritical processes can also produce power laws (e.g., [9,94–97]). The observation of power laws in neural dynamics does not therefore guarantee that these dynamics are critical. A number of more specific metrics have been developed to more reliably detect avalanche criticality (Box 1).

Taken together, the data garnered from power law analyses and complementary metrics broadly support the hypothesis that brain dynamics are critical, or at least near-critical; the results are somewhat divided as to their precise degree of criticality. While some results suggest dynamics situated exactly at the critical point [13,41,44,45,98], other results, in large part from *in vivo*

Box 1. How is avalanche criticality measured in the brain?

There is no single gold standard measure of criticality. Each metric only probes one part of the proverbial elephant. Only when several of them agree can the case for critical dynamics be made with confidence.

There are three main categories of avalanche criticality metrics: avalanche metrics, branching metrics, and time series metrics. The first two categories rely on a signal containing discrete events, either spike recordings, or a thresholded continuous signal. In avalanche metrics, consecutive events are grouped into avalanches based on a selected time bin and avalanche size and duration distributions are plotted for several minutes of signal [13,46]. Critical distributions should show power law scaling in these plots. The slopes of these power laws, known as critical exponents, can assume a range of values dependent on the universality class (e.g., [179]; see Box 4), as well as on other factors such as input properties [42,43,180], the presence of oscillations [44], and subsampling [43,181]. For these reasons, it is difficult to draw conclusions about the distance to criticality on the basis of critical exponent values alone. However, regardless of these factors, critical exponents should obey certain robust interrelations known as scaling relations [16]. Additionally, as fractals, the temporal profile of avalanches of every size should show a same stereotypical shape (i.e., they should respect shape collapse) [16,28,182]. There are different ways to quantify adherence and deviation from each of these metrics [24,129,183], including κ (kappa), which quantifies the deviation of an avalanche distribution from a power law [129] and the deviation from criticality coefficient (DCC), which indexes deviation from certain scaling relations [24].

There are two common branching metrics: the branching ratio, which is the number of events in one time bin divided by the number in the previous time bin [13], and the multistep regression (MR) branching parameter [79], which is more robust to subsampling effects. In both cases, critical systems should have a branching parameter of 1. The MR branching parameter is especially sensitive to deviations from criticality [40].

Time series metrics are applied to continuous time series and include the estimation of long-range temporal correlations (LRTCs) [1,47,90,91] and similar fractal [154] or multifractal scaling measures [2,7]. LRTCs can be straightforwardly estimated on brain signals using detrended fluctuation analysis (DFA) exponents [184], where a larger exponent corresponds to greater proximity to criticality. Oftentimes, LRTCs are estimated on the amplitude envelope of narrowband-filtered brain signal with interesting results (see Box 3) [1,47,55,64,141].

spiking studies, indicate that the brain is not quite critical, but slightly intruding into the disordered, subcritical phase [19,20,24,26,40,92,99–101]. These results further contrast with other reports that instead observe brain dynamics far from the avalanche transition [23,60,71,94,102]. The incompatibility of these results is not always clear. Each set of evidence has its specificities (e.g., experimental conditions) and potential caveats, which are beyond the scope of this review (see [22] for a discussion). For now, the question of the extent of avalanche criticality in the brain is still not settled. This being said, the mounting evidence that normal brains are slightly subcritical has some interesting implications, which we discuss later. Importantly, because the critical region is 'stretched' in systems which, like the brain, are finite, input-driven [26,103,104], nonconservative [103], and hierarchical modular [105], near-criticality retains all the computational properties of criticality, but in a form to a certain degree attenuated in favor of other computational properties associated with the neighboring phase [104,106].

The edge of chaos

The 'edge of chaos' is broadly defined as a transition point between stable and chaotic dynamics. The concept first gained wide currency in the early days of computer science, where it was noted that complex computation spontaneously emerges in artificial systems when their dynamics are just barely chaotic [11,12,107]. The edge of chaos drew further interest with the advent of reservoir computing [108–110], a type of recurrent neural network capable of learning complex tasks and which, it was found, performs optimally at the onset of chaos [29,110–112]. Computational studies further demonstrated that this optimality was supported by a concurrent maximization of the network's information storage and information transfer properties [34], as well as by a maximal signal-to-noise ratio of network inputs [112].

In both artificial and biological neural networks, proximity to the edge of chaos appears to be controllable by the heterogeneity of pairwise coupling interactions between nodes [23,113–115].

Notice that in the avalanche-critical neural model we described (previous section; Figure 1), all couplings were positive. This can be conceived as modeling excitatory neuronal interactions, but what about inhibitory ones? Most often in such models, inhibition is lumped in with excitation in a single control parameter (E/I balance) that results in a single, net positive coupling value for all neuron pairs (as a counterexample, see [116]). But it is also possible to 'unfold' this parameter across the network, such that some neuron pairs are positively coupled and others are negatively coupled, creating a broad, heterogeneous distribution of couplings. In this case, it turns out that the coupling heterogeneity, specifically, the standard deviation of the coupling distribution, becomes a control parameter for a critical phase transition between stable and chaotic dynamics (i.e., the edge of chaos) [23,60,113,115,117–119]. This alternate type of criticality [72] reproduces many of the interesting computational features of avalanche criticality [11,23], while also displaying other remarkable features, including a more generalized sensitivity to perturbations, a rich repertoire of nonlinear transformations on inputs, and an ability to maintain and integrate multiple inputs over diverse timescales (Figure 2, Key figure) [23,29,34,110], all with the added advantage of explicitly accounting for the mix of excitatory and inhibitory interactions found in the brain. Edge of chaos models can be applied equally well to the neuronal level [23], where the positive and negative interactions represent excitatory and inhibitory synapses, or to the higher spatial scale of neuronal ensembles [54,60,71,120], where the interactions may represent effective connectivity between large-scale neuronal populations [121,122].

Interestingly, the shift from positive-only to mixed interactions in neural networks is similar to the transition from the ferromagnetic state to the so-called **spin glass** state in the Ising model [113,123,124]. Many of the tools from the rich literature on spin glasses may thus be applicable within the context of the brain [23,60,115].

It should be noted that avalanche criticality and the edge of chaos are not mutually exclusive [23,36]; (see [36] for a simple example system where both transitions coincide). Furthermore, excitatory–inhibitory coupling heterogeneity does not appear to be a prerequisite for dynamics poised between **stability** and chaos (i.e., neutral dynamics) [36]. That being said, excitatory-only edge of chaos networks do not seem to generically exhibit the rich repertoire of nonlinear transformations and diverse integration timescales that make the mixed-interactions version of the edge of chaos so appealing [23,71,115]. As an emerging topic of interest in neuroscience, much remains to be understood about the edge of chaos, though new insights are accruing at an accelerating pace [23,71,112,115,125–127].

Neural evidence of the edge of chaos

A number of advanced metrics have recently been developed to detect edge of chaos criticality in the brain (Box 2). Thus far, the available evidence consistently supports the conjecture that the waking brain is at, or near, the edge of chaos.

In an early study in macaques [54], the eigenspectrum of the covariance matrix of ongoing electrocorticographic (ECoG) brain activity in awake and anesthetized states was estimated using an autoregressive process. In the waking state, a large number of eigenvalues were found crowding the critical line, suggestive of the edge of chaos. Interestingly, propofol and ketamine anesthesia reduced this number, shifting the bulk of eigenvalues towards zero [54]. In addition, sorting the eigenvalues by their oscillatory frequency (given by their imaginary part) revealed that propofol had the effect of damping eigenmodes across a broad frequency range (5–100 Hz), whereas ketamine only damped high-frequency eigenmodes (>50 Hz) [54]. This difference may reflect the divergent impact of these anesthetics on the level of consciousness.

Key figure

Key computational features of individual brains may depend on their position with respect to the avalanche criticality (AC) and edge of chaos (EOC) phase transitions

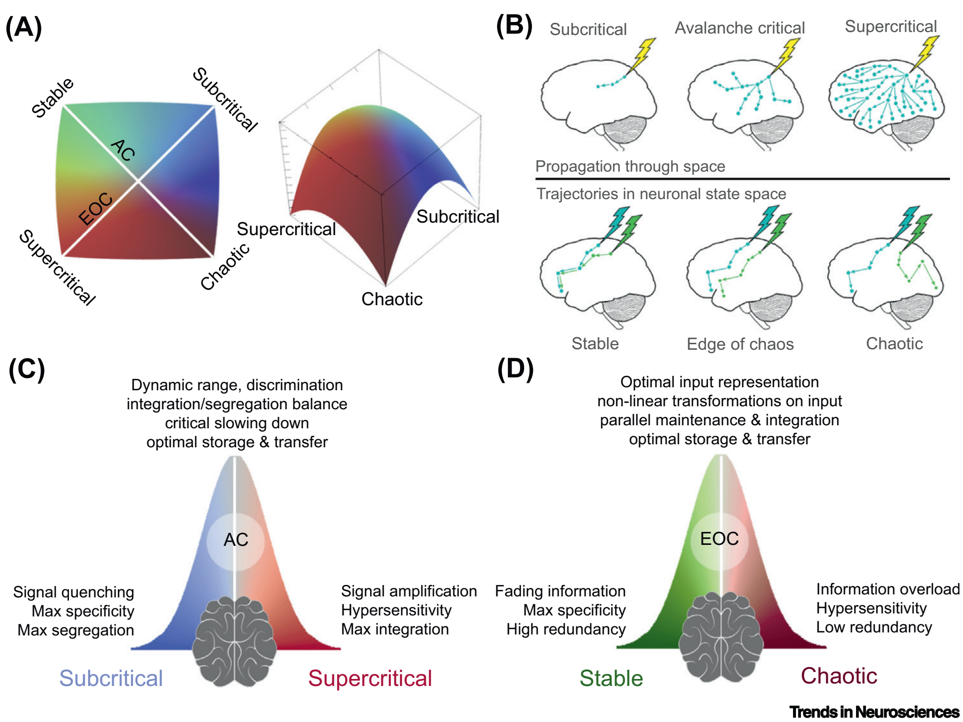

Figure 2. (A) Brain dynamics exist in a high-dimensional space fractured by many phase transitions; here we show the manifold where the AC and EOC transitions intersect (left). The computational features of criticality are maximized as they approach these transitions (right). (B) AC and EOC can be understood as an 'edge of instability' to perturbations; what changes is that which is unstable. In AC (top row), the inactive 'ground state' is stable in the face of perturbations under subcritical dynamics (fading activity) and unstable in supercritical dynamics (exploding activity); criticality teeters at the edge of these two phases. At the EOC (bottom row), a very large number of high-dimensional patterns of activation or modes are similarly on the edge of instability; this introduces an additional form of instability, namely, instability to noise or input differences (i.e., chaos). Taking the differently colored arrows to represent dynamical trajectories in high-dimensional neuronal space, each in response to a slightly different input pattern (e.g., a change in a detail of a visual scene), the nonchaotic stable phase is characterized by converging trajectories and the chaotic phase by exponentially diverging trajectories. Only at the EOC are input differences faithfully represented in the prolonged brain responses. (C) AC and (D) EOC each maximize certain desirable computational features (e.g., optimal input representation); however, these occur at the expense of other desirable features belonging to the surrounding phases (e.g., specificity, or faster dynamics). Each point along these curves interpolates between these feature sets and therefore represents a certain trade-off between critical and noncritical computation. The brain may dynamically adapt this trade-off in response to current computational demands [48,106,133]. Note that many features of AC are carried over to the EOC, albeit in a generalized form (e.g., information storage and transfer). Furthermore, we note that it is not unusual to find computational features assigned to phases slightly differently than presented here; this is often related to the details of how the features are defined (e.g., compare [34] and [133]).

Proximity to the edge of chaos was also estimated in humans using different approaches. In an fMRI study, phase diagram analysis was used to show that waking brain dynamics are slightly on the stable (nonchaotic) side of the edge of chaos [60]. This result is in slight contrast with those of another recent study [27] that measured chaos directly in the MEG and ECoG of humans

Box 2. How is the edge of chaos measured in the brain?

Chaos is difficult to measure in large complex systems such as the brain, since it is not possible to 'reset' the system to its initial state to test for effects of small perturbations. Therefore, measures such as the Lyapunov exponent cannot straightforwardly be applied to neural data and other more sophisticated tests must be used. One such test, the 0–1 chaos test, has recently been adapted for use with human electrophysiological data [27], yielding a measure of the degree of chaos. This same study [27] also proposed that the Lempel-Ziv complexity (LZC) is maximized at the edge of chaos. LZC is an easily deployed and widely used measure that can be applied to any signal to estimate its diversity. The edge of chaos is also associated with maximal information storage, which can be measured with active information storage (AIS) [34]. AIS has been adapted for use in MEG data [144] and is a powerful, model-free measure, though it is computationally demanding.

Proximity to the edge of chaos can also be estimated from the eigenspectrum of the neuronal covariance matrix, though the covariance matrix is vulnerable to subsampling, which is especially problematic in spike recordings [23]. To get around this, a subsampling-invariant method was developed for estimating the largest eigenvalue from the width of the covariance distribution [23]. It is also possible to get a loose estimation of the eigenspectrum from principal component analysis applied to the raw data [23,71]. Eigenspectra have also been estimated from coarse-grained data, which are less affected by subsampling (although it remains to be clarified whether neuron-level edge of chaos criticality can be detected at different coarse-graining scales in the same way as for the more distinctly scale-invariant avalanche criticality). One study obtained edge of chaos-like eigenspectra from ECoG by estimating the covariance matrix from short epochs using an autoregressive process [54]. In another study, the covariance matrix was first estimated from resting-state fMRI and by then sweeping through different tunings of the mean and standard deviation of the matrix, a phase diagram was drawn that allowed the localization of recorded brain dynamics with respect to both avalanche and edge of chaos transitions [60]. This last study drew from the rich literature on spin glasses [113], which are closely linked to the edge of chaos [115,117].

and monkeys and found that normal waking dynamics are slightly within the chaotic phase. Both studies, however, agree that brain dynamics are very close to the edge of chaos [27,60]. In [27], the authors also applied their measure to recordings of anesthetized, epileptic, and psychedelic states in humans. The authors found these three states to be further in the chaotic phase, in the stable phase, and closer to the edge of chaos, respectively [27]. Further, the authors showed that LZC of MEG and ECoG closely tracked proximity to the edge of chaos, providing validation of this simple metric as a signature of criticality [27].

Intriguingly, results reminiscent of the edge of chaos were found fortuitously in a recent, massively parallel two-photon calcium imaging study of behaving mice [69]. In this study, the eigenspectra of neural responses to natural image presentations were found to obey a power law, suggestive of criticality. The authors showed that the exponent of this power law was perfectly tuned to balance generalization and coding efficiency in learning and recognizing stimuli. If the decay of the eigenspectrum was any slower, the system would place too much importance on small differences to the detriment of perceiving generalities [69]. The connection between these data and the edge of chaos was recently supported by a computational study [125], which found that the breakdown of the smoothness of the coding manifold in reservoir computing networks trained to classify natural images occurs exactly at the edge of chaos. Considering that human brain dynamics may be slightly in the chaotic phase [27,112], it is interesting to consider what effect varying degrees of chaos, and of criticality more generally, has on cognition.

Criticality links neuronal dynamics to cognition

What makes brain criticality especially interesting for neuroscience is its strong link to cognition, which presents an appealing theoretical framework for thinking about brain function and dysfunction. This link is made by way of the **emergent** [128] computational features that are intrinsic to criticality. If brain dynamics are indeed critical, then each of these features may well provide a direct, formal connection between neurons and cognition (Figure 2C,D). For example, the long memory of the critical point can act as a purely dynamical short-term memory, without any change in synaptic strengths [106]; and the high variability of critical dynamics may explain the slow fluctuations of cognitive and psychophysical variables [7,47,59]. In experiments, each of these cognitive processes would be expected to show an inverted U-shaped relationship with canonical signatures of criticality such as scale-free avalanches or LRTCs, with computational efficiency dropping off in tandem with critical signatures. In the following, we review evidence for the computational features of criticality at work within cognitive processes.

A first place to look for these computational features is directly in neural activity. A series of studies by the same group took this approach examining dynamic range and **mutual information** with inputs, both forms of divergent susceptibility [53,82,93,129]. The authors found that scale-free neuronal avalanches co-occurred with the maximization of the dynamic range of cortical responses, both in cell cultures responding to electrical stimulation [82,129] and in the anesthetized rat cortex in response to whisker stimulation [53]. Importantly, pharmacological modulation of E/I balance simultaneously disrupted criticality and reduced the dynamic range. Similar results were found for the mutual information between inputs and neural activations [82,93], as well as for the Shannon entropy of activation states, which measures state diversity [82]. These same measures were also applied to mice awaking from anesthesia [57]. Here, the mutual information was calculated between recording sites as an estimate of information transfer. Again, the maximization of both information transfer and state diversity coincided with the emergence of scale-free avalanches in the awake state, as measured by power law avalanche distributions [57]. Additionally, in a recent human study, fluctuations in cortical excitability were measured by stimulating the median nerve of the hand and then detecting evoked responses in somatosensory cortex [90]. It was found that the highly variable response fluctuations showed strong LRTCs, consistent with the long memory of critical dynamics.

The second place to look for the computational features predicted at criticality is in behavior. Divergent susceptibility is expected to manifest as high sensitivity to stimulus differences, such as in a visual oddball task. Indeed, in a human EEG study using such a task, greater performance in terms of shorter response time (RT) was associated with stronger LRTCs of EEG oscillations, a sign of criticality [130] (Box 3). Furthermore, in similar task-based studies, LRTCs in RT fluctuations showed a tight relationship with LRTCs of MEG and EEG oscillations [47] and high RT LRTCs were associated with greater cognitive flexibility [59], another expected consequence of divergent susceptibility.

Another intriguing result comes out of behavioral studies as well: focused attention on a task [48,130] or in meditation [131] is associated with a slight shift from avalanche criticality into the disordered, subcritical phase. This may reflect a task-specific shift in the trade-off between sensitivity and response reliability [89], wherein generalized sensitivity to the environment is traded off for consistent, controlled, 'local' response to specific stimuli. This is aligned with the attractive notion, recurrent in the literature, that the 'unfocused' brain shifts towards the critical point in order to maximize exploration, both in terms of receptiveness to external stimuli (divergent susceptibility) and also in terms of a broad sampling of internal states (large state repertoire); whereas in the focused task state, the brain shifts its dynamics to the disordered (disintegrated) phase so as to promote exploitation, narrowing the set of possible responses in order to favor response stability and minimize distractions [20,42,48,130]. The critical resting state may then be understood as optimizing a generic prior expectation of task demands [106,132]. These ideas underscore the relevance of the distance to criticality for cognition: this distance may be dynamically varied at a moment-to-moment timescale in order to flexibly adapt to task requirements [48,106,133]. Indeed, many studies show that in the resting state, brain dynamics do not stay fixed at or near the critical point, but wander within a broad near-critical region [17,20,53].

Box 3. How is criticality related to brain rhythms?

Much of the evidence for critical dynamics in EEG and MEG has taken the form of LRTCs not in the raw signal itself, but in the phase and amplitude dynamics of narrowband neuronal oscillations [185], especially in the alpha (8–12 Hz) and beta (20–30 Hz) ranges [1,47,49,63,64,131,141,158]. At first blush, the characteristic temporal scale of neuronal oscillations may seem at odds with criticality, which is scale-invariant. How can these be reconciled?

A first possibility is that (large-scale) brain rhythms are an emergent consequence of critical dynamics at the (small) scale of spiking neurons. For instance, it has been shown that neural networks with heterogeneous couplings exhibit transient oscillatory modes at multiple timescales [23,118]. In addition, a well-studied neural network model with local connectivity [166,186], under balanced E/I balance conditions, was shown to produce both scale-free avalanches and an emergent alpha oscillation that exhibits strong LRTCs [166] and long-range amplitude coupling [35].

A second possibility, not necessarily exclusive of the first, is that oscillations are themselves critical independently of small-scale neuronal spiking. This is consistent with the notion that neuronal oscillations, rather than being entirely driven by underlying spiking activity, also reciprocally entrain and couple this neuronal activity in a bidirectional interplay [121,168,187–189]. In this case, the specific phase transition at work may be the 'edge of synchrony' [51,155,158,167,170,190,191], of which the Kuramoto model [192] is the paradigmatic example. The model involves a network of coupled oscillators that undergoes a transition between desynchronized and uniformly synchronized oscillations at a critical value of the coupling. At the edge of network-wide synchronization (the critical point), the oscillators show maximal variability in phase-coupling configurations, a phenomenon often referred to as 'metastability' and which is hypothesized to enable flexible switching between a wide variety of cognitive/behavioral states [7,84,121,168].

Of note, the Kuramoto model maps closely onto the Ising model of avalanche criticality, where binary nodes are replaced by oscillators and ordered spin orientations are replaced by ordered phase synchrony [123,193]. Similarly, it has been conjectured that critical 'glassy' oscillator systems [i.e., with disordered (positive and negative) couplings] map closely onto spin glasses at the edge of chaos [194,195]. In both cases, many of the computational features of the non-oscillatory phase transition, such as divergent susceptibility and critical slowing down, are carried over to the oscillatory kind [193] and may be expected to have similar impacts on cognition.

Criticality in brain rhythms is signaled by LRTCs in their amplitude envelope or instantaneous phase dynamics, measurable by DFA [184]. Other metrics of edge of synchrony criticality include the phase synchronization [196], the global lability of synchronization [51], and the pair correlation function [138,190,193].

While relatively small shifts in the distance to criticality are expected to stay within the near-critical region and manifest as changes in the efficiency of cognitive processes, larger shifts may escape this region and lead to more drastic changes, such as transitions between states of consciousness, as some data indeed suggest. Anesthetic-induced unconsciousness has been associated with shifts in both avalanche [41,55,56,134] and edge of chaos criticality [54]. Sleep is also associated with shifts in avalanche criticality [92]. The association of criticality with consciousness is consistent with the intuitive notion that a conscious brain should maintain a high diversity of states, while also comprising an integrated whole [135,136]; the scale-free correlations of criticality guarantee this balance [83]. Indeed, integrated information [135], a hypothesized marker of consciousness, was found to be maximized at the critical point in a computational model [137] and in human EEG [138].

Together, these studies demonstrate how both neural mechanisms and behavior can be tidily explained within the framework of criticality and its intrinsic computational features. The foregoing discussion also introduces the distance to criticality as a potentially relevant biological/psychological variable.

How critical? The distance to criticality

The hypothesis that the brain exploits a critical phase transition for its adaptive computational properties has a corollary, namely, that a loss or attenuation of criticality in brain dynamics should result in a degradation of these same computational properties. This highlights the potential of the distance to the critical point as a biological parameter of interest in understanding cognitive differences, not only within individuals with regard to brain states [27,48,54], as we have just discussed, but also between individuals with regard to psychological traits [139] and mental illness [2,140–142]. A growing body of literature has indeed observed deviations from neurotypical neural dynamics in atypical brains [2,63,64,141,143–149] (see [150] and [151] for recent reviews).

Critically, recent findings suggest that the healthy brain is not quite critical, but close to critical [19,20,24,26,27,40,60,92,99–101,152,153]. For example, avalanche size distributions are often found to fall away from a power law relationship for the largest avalanches [19,20,92,99,100] and precise estimation of the branching parameter [79] (Box 1) yields values just shy of criticality [24,40]. The elicited notion that the healthy resting brain is not quite critical adds a new dimension to the relationship between criticality and cognition: not only a loss, but also an enhancement of criticality may underlie certain cognitive-behavioral alterations from normal or healthy functioning. Notably, this point is reinforced by the aforementioned finding, in a few recent studies, that the psychedelic state may be closer to the critical point than normal brain function [27,101,154,155].

How can near-criticality be explained from a normative perspective? Why wouldn't the brain exploit the (exactly) critical point if it is computationally optimal? One possible explanation is that slight subcriticality provides a buffer with the supercritical phase, which has been suggested to correspond to epileptic seizure [19]. While some findings of critical deviations in epileptic patients seem to support this notion [61,62,156], a recent study where single-unit spike recordings from epilepsy patients were analyzed using advanced metrics [79] did not bear out such a link [157] and recent work points instead to a discontinuous phase transition underlying epilepsy [158].

A second, related explanation is theoretical: strictly speaking, exact criticality can only occur in equilibrium systems (i.e., systems with no inputs or outputs). By contrast, the brain is a driven system (i.e., with inputs from the senses, internal organs, etc.). Therefore, to maintain a critical-like balance and prevent a build-up of activity from incoming inputs that would tip global dynamics into the supercritical phase, the brain must absorb excess activity by assuming a slightly subcritical, or 'quasi-critical', operating point [26,40]. Importantly, this operating point shares the same computational features as the critical point, only less pronounced.

A third intriguing potential explanation of near-criticality may relate to an oft-overlooked nuance of the critical brain hypothesis: while criticality confers efficiency advantages for many computational tasks [18], not all computational tasks are optimized at criticality [89,106,107]. For example, the high sensitivity to detail of the critical point may be distracting for tasks that demand focused attention on only a few parameters [48,130]; and the high variance of critical dynamics, which is useful for generating a large repertoire of available states, also produces high trial-to-trial variability that erodes response reliability [89,106]. Ultimately, no computational property is universally optimal [159], so that it may be more appropriate to speak in terms of computational trade-offs associated with the proximity to criticality. Different tunings along these trade-offs may correspond to different cognitive profiles [139,160]. We have discussed some of these trade-offs earlier, namely, between sensitivity and response reliability [89,130] and between generalization and efficient coding of stimuli [69,125]. The latter trade-off seems to align with theories that conceptualize some of the manifestations of autism as alterations in sensory generalization [161] and findings that brain dynamics in autism show reduced active information storage [144] and LZC [148], suggesting more chaotic, less critical, and less 'generalizing' dynamics. Other computational trade-offs related to criticality include detection versus discrimination [93] and network refresh rate versus information integration [106].

Through these computational properties and their trade-offs that are intrinsic to shifts in criticality, the distance to criticality may constitute a well-placed biological variable for understanding both healthy and pathological changes in cognition and behavior, one that forms a direct mechanistic link between neurons and neuronal ensembles at the micro scale and computation at the macro scale.

Universality guarantees the robustness of critical models

Taking a step back, the skeptical reader might think this is all indeed a nice analogy between brains and magnet-like systems, but how can such a simple, tidy model at the neuronal level ever hope to retain any explanatory power when applied to a system as large and complex as the brain, with its countless hidden variables and moving parts? The answer is **universality**, and herein lies a great strength of critical models. Universality is an intrinsic feature of all critical systems. What it means, in a nutshell, is that at criticality, large classes of systems that can be tremendously varied in their detailed small-scale design, with different structural properties, substrates, modulating variables, etc., all indistinguishably converge onto a single dynamical behavior at the large scale (Box 4).

A case in point is a recent study where stable, chaotic, or critical dynamics were simulated on different intrinsic networks of an *in silico* brain built from connectomic maps [162]. The authors then tested the ability of these networks to perform computations in a reservoir-computing paradigm. Strikingly, they found that despite a varied range of structural properties (clustering, betweenness centrality, modularity, etc.), and despite the fact that some networks performed better in the stable phase and others better in the chaotic phase, all intrinsic networks performed best, and

Box 4. What is the origin of universality?

Universality in critical systems is deeply related to scale invariance, as demonstrated by the renormalization group interpretation of criticality [197]. The renormalization group is essentially a family of mathematical techniques for coarse-graining the dynamics of physical systems while making appropriate corrections. The coarse-graining process involves zooming out and formulating an effective description of the system in terms of larger composite particles. With each successive 'blurring' of a system's dynamics, the new dynamics corresponds to those of a system with a different set of parameters and these parameters can be represented as a new set of coordinates in a high-dimensional parameter space. Over many coarse-graining transformations, the system traces a flow in parameter space. The key finding of the renormalization group is that when systems are at criticality, their coarse-graining flows converge on fixed points in parameter space [28,197]. What this means is that after a finite number of coarse-graining operations, the dynamical state, as quantified by its coordinates in parameter space, starts to map onto itself. This is a very strong form of scale invariance, whereby the system can grow to any size without any change in its macro-scale dynamics.

The deeper significance of this comes from considering the wider parameter space. The existence of a coarse-graining fixed point implies that there is a broad region of the parameter space (a surface or manifold) that flows into this point and therefore that a multitude of microscopic systems, with a wide variety of parameters and corresponding small-scale dynamics, all exhibit the same dynamics when observed at the macroscopic level. This is the essence of universality.

Universality confers a special kind of robustness to physical systems. It implies that only a small number of microscopic parameters, the relevant operators, exert influence on a system's large-scale behavior and that all other irrelevant operators are ultimately 'blurred out' and can change with no large-scale effect [163,198]. For instance, the small-scale details of iron at the ferromagnetic transition and those of water at its critical boiling point are quite different (e.g., they have entirely different molecular structures, different types of order, and different intermolecular forces); nonetheless the large-scale dynamics are the same [76]. The reason for the robustness of critical systems is that the correlation length becomes much longer than the range of small-scale interactions, so that the large-scale behavior can act independently from the smaller subsystems and may even control them [163,168,187].

equally well, at the critical point [162]. This demonstrates a weak dependence of computational function on structure in brain-like networks when the dynamics are critical.

The robustness inherent to universality thus makes criticality particularly attractive for modeling immensely complex systems such as the brain: it implies that one need not account for every detail, nor even for most details, of the microscopic interactions of a system in order to make some predictions about its macroscopic behavior [72,163].

Interestingly, linking back to brain disorders, the robustness of critical dynamics to structural alterations of the underlying network may potentially be protective against neurological damage and in this way may underlie concepts of cognitive reserve in dementia [164,165]. Some work indeed reports attenuations of criticality associated with dementia [65–67].

Concluding remarks and future perspectives

How critical, then, is brain criticality? This titular question is intended as a pun and can be understood in two ways. First, how close to the critical point is the resting human brain? And second, how important is the framework of criticality theory for understanding brain function? While unequivocal answers to these questions remain out of reach, with this review we hope to motivate further inroads into this potentially fruitful area of inquiry, placing emphasis on promising avenues for future work, namely, the continued exploration of criticality beyond the avalanche type (i.e., the edge of chaos and the edge of synchrony; Box 3), the expanded framework of the near-critical brain [26,40,106], and the utility of the distance from the critical point as a biological variable in neuroscience, particularly with regard to cognition and psychopathology. Going forward, we propose that both these questions may be convincingly addressed through studies connecting criticality and cognition.

As it is, the field is still rife with questions and opportunities. The application of advanced criticality metrics (Boxes 1 and 2) to neuroimaging data in clinical populations and in altered behavioral states will be especially informative as to the relevance of criticality to cognition and behavior. More experimental work using high-resolution datasets and advanced analyses where possible [23,27,60,68,69,71] will be needed to settle inconsistencies in the literature and more confidently situate brain dynamics with respect to the avalanche and edge of chaos transitions. The edge of synchrony, a critical transition that we did not cover in depth for length considerations (though see Box 3), may also play an important role in the brain, particularly with regard to neuronal oscillations [35,51,155,158,166–170]. Relatedly, many of the interesting features present at criticality (e.g., susceptibility or state diversity) also occur in other nonlinear dynamical models of whole-brain dynamics involving E/I balance and 'metastability' [84,168,171,172]. Careful theoretical work will be needed to compare, contrast, and possibly even merge these perspectives. Last, the advancement of our understanding of brain criticality will benefit greatly by continuing to borrow from historical and ongoing work in physics, such as the rich theory of spin glasses [113,123,124].

From the current vantage, criticality holds great promise for neuroscience [75]. A firm understanding of the dynamical phase transitions at work in the brain would set a trusswork upon which to build our models of brain function. The computational aspects intrinsic to criticality promise a mechanistically grounded understanding of cognition and its alterations, which may help light the way to better-targeted treatments for mental illnesses, as well as a clearer appreciation of the trade-offs inherent to neurodiversity. The insights gained from studying criticality in the brain may also find applications in artificial intelligence [125,162,173–176], where the study of phase transitions, self-organization, and scaling laws is an emerging topic [177,178] and in turn may help guide the use of artificial neural networks in modeling information processing in the brain.

Outstanding questions

How can the distance to criticality be leveraged to better understand neurological and neurodevelopmental conditions such as autism, schizophrenia and depression? Are some of these conditions characterized by a dynamical operating point that is further from (or closer to) the critical point?

Implicit in brain criticality models is the existence of control parameters which tune the distance to criticality, such as the input rate (avalanche criticality), the strength of excitation and inhibition (edge of chaos), and input synchronization (edge of synchrony). Could these control parameters be harnessed in targeted therapeutic interventions or in the development of coping strategies for clinical conditions involving an altered distance to criticality?

How does each type of criticality change throughout the sleep–wake cycle and how might these dynamics contribute to learning and memory?

How does the distance to different types of criticality change across the lifespan in health and disease? Is cognitive reserve in neurodegenerative diseases associated with increased brain criticality?

How is brain criticality related to current theories of consciousness? Which properties of critical dynamics are shared with consciousness models? Can criticality neuroscience contribute a common model or framework in which to evaluate, arbitrate, or perhaps even integrate current theories of consciousness?

The distance to criticality in information-processing systems is bound to certain computational trade-offs, such as sensitivity versus response reliability and generalization versus efficient coding. What other computational trade-offs are inherent to avalanche and edge of chaos criticality and how are these reflected in cognitive processes, traits, and pathologies?

How can criticality theory contribute to the bidirectional dialogue between neuroscience and artificial intelligence? Could brain criticality models help

Overall, the perspective of criticality neuroscience, combining knowledge from statistical physics and dynamical systems, offers a rare window into the brain's complexity, allowing inferences about its large-scale behavior to be made from simple yet parametrically robust models of its complex neuronal interactions. With many beckoning questions yet to be answered and much terrain still unexplored (see Outstanding questions), the field of criticality neuroscience is rich with opportunities for significant advancements in our understanding of the brain, its functions, its ailments, and its differences.

solve problems of robustness and generalization in artificial neural networks?

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Declaration of interests

The authors declare no competing interests in relation to this work.

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