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The heavy tail of the human brain

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Fluctuating oscillations are a ubiquitous feature of neurophysiology. Are the amplitude fluctuations of neural oscillations chance excursions drawn randomly from a normal distribution, or do they tell us more? Recent empirical research suggests that the occurrence of 'anomalous' (high amplitude) oscillations imbues their probability distributions with a heavier tail than the standard normal distribution. However, not all heavy tails are the same. We provide canonical examples of different heavy-tailed distributions in cortical oscillations and discuss the corresponding mechanisms that each suggest, ranging from criticality to multistability, memory, bifurcations, and multiplicative noise. Their existence suggests that the brain is a strongly correlated complex system that employs many different functional mechanisms, and that likewise, we as scientists should refrain from methodological monism.

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Introduction

The human brain is a complex dynamical system par excellence, with organizational principles spanning a hierarchy of scales. Oscillations feature at all scales — from high frequency neural bursting through to diurnal neuroendocrine rhythms [1] — and thus may be considered an archetype for understanding and modeling phenomena that span multiple scales. In pursuing this objective, should one pursue detailed neurophysiological models for each scale-specific example of oscillatory activity, or instead seek a single unifying framework? The issue often divides researchers along ideological lines. Proponents of the former ('divide and conquer') approach argue that customized models are required to elucidate specific biophysical mechanisms of oscillations and their functional correlates. Unifying models, by necessity of abstraction, may then be seen as guilty of pursuing tractability at the expense of the very thing they were proposed to explain, namely a particular context-specific phenomenon. Others, however, argue that unnecessarily detailed models overfit conceptual nuances, generalize poorly, and give little additional insight than was already in the details of their construction.

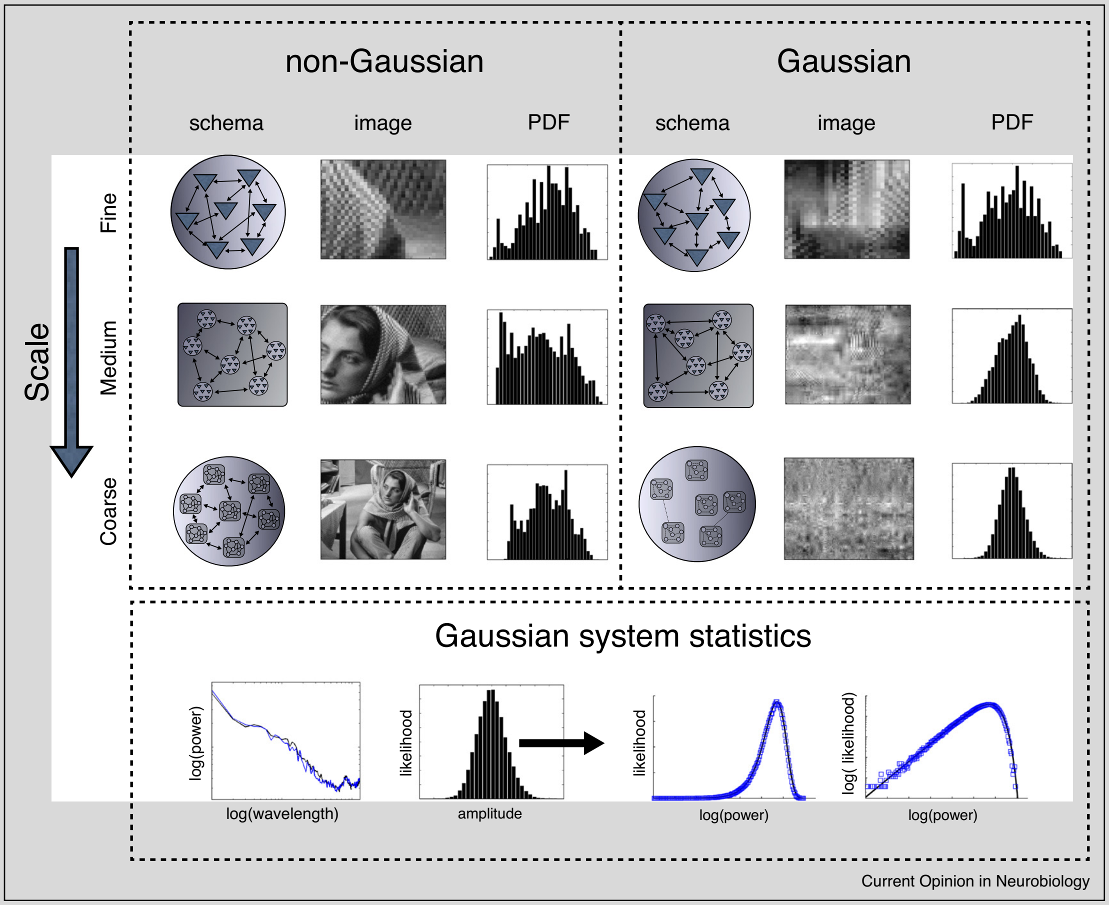
Here we argue for a middle ground: that there indeed exist unifying principles that unite apparently diverse oscillatory phenomena, yet there also exist clear and distinct mechanisms that operate on different occasions even in the same system. Thus there is room for theories that unify phenomena across scales — or even across different physical systems — as well as opportunities to disambiguate competing mechanisms through empirical research.

Where are the footholds here? Let us suppose that neural spikes hold a privileged position regarding the computational principles of the brain and that detailed models are thus needed to link spike trains, whether they be stochastic or oscillatory, to the specific computations that they subserve. According to this approach, there exists a spatial scale above which 'interesting' computational processes cease to emerge. Signals recorded above this limiting scale, such as fMRI and EEG, merely reflect the aggregate linear superposition of activity at smaller scales. In the limit of sufficiently large scales, the central limit theorem informs us that no matter how interesting the small-scale phenomena may be, the large-scale signal fluctuations arising from their passive summation are drawn randomly from an underlying Gaussian probability distribution (see Box 1) and hence hold no further information than is available in their mean and variance.

The contention between detailed microscopic mechanisms and systems-level processes can thus be re-framed: Do the fluctuations of macroscopic oscillations conform to Gaussian probability distributions? Evidence for fluctuations conforming to non-Gaussian distributions would thus refute this view. The consequences of such a refutation are that correlations amongst neuronal systems

Box 1 Central limit theorem (CLT): The connection between correlations and Gaussian variables can be visualized by examining natural images across a range of scales. The 'schema' columns illustrate the effect of coarse-graining: moving to a coarser scale, direct interactions among units are averaged and replaced by their ensemble average. **Left box:** If that ensemble average interaction is sustained after iterative coarse-graining and down-sampling, the tenets of the CLT will be violated. Natural scenes (middle columns) exhibit power-law spatial spectra and strong interactions that persist between and within all scales (e.g., the woman's high frequency facial features coincide with the low frequency contours of her cheeks). The amplitude histogram is non-Gaussian at all scales. **Right box:** By contrast, if the coarse-grained interactions weaken at larger scales, then the system eventually decorrelates and there exists a scale above which the CLT holds. This is simulated by randomizing the scale-scale relationships of a multiscale wavelet decomposition (middle and right columns; [78]). Apparent detail at the fine scale (top row) is associated with a non-Gaussian amplitude PDF. But at coarser scales, the image decorrelates toward featureless colored noise and the amplitudes sum to a Gaussian. In the absence of inter-scale correlations, the only apparent order is very short-range, even though the spectra remains a power law. **Lower box:** Gaussian statistics. Many interesting systems exhibit power law spectra: Both the original (black) and resampled (blue) natural scenes exhibit a broad linear regime in double logarithmic coordinates. However, by decorrelating the scales, the resampled scene has a Gaussian PDF. This principle applies also to time series, where the variable of interest is often the envelope of the power (amplitude squared). For linear Gaussian fluctuations, this envelope yields a simple exponential PDF, which is thus the null distribution when testing for trivial decorrelated noise in macroscopic variables. Examining the exponential PDF in double logarithmic coordinates (rightmost panel) allows detection of anomalous statistics with heavy right hand tails (Figure B1).

Figure B1



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must survive through to the largest scales of the brain, and that there is hence no privileged scale.

The analysis of anomalous events, and the underlying distributions from which they are drawn, plays a crucial role in the study of many complex systems [2], including exceptional weather events [3], crises in financial markets [4] and forest fires [5]. Whilst anomalous amplitude fluctuations have been anecdotally noted in recordings of neuronal oscillations [1], neuroscientists have only recently sought to draw on this field to understand large-scale cortical oscillations [6]. Although preliminary analyses have been promising [7], a systematic approach has not yet been forthcoming. Here we review the current evidence for non-Gaussian statistics in brain activity, with a focus on cortical oscillations.

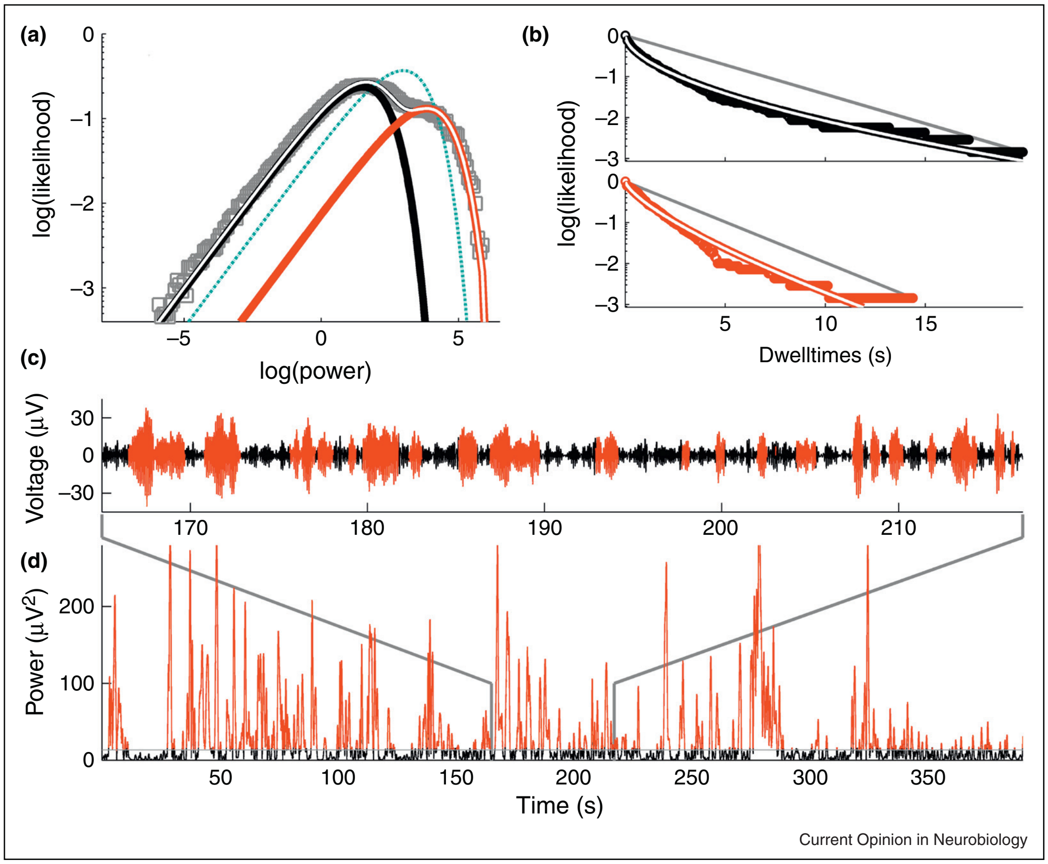
Bistability and scale invariance in the alpha rhythm

Alpha oscillations dominate electrical recordings at the largest scale of the brain, namely intracranial ECoG and scalp EEG. The traditional view of the alpha rhythm — that its 'waxing and waning' are featureless random fluctuations — is thus a clear test case of the discussion at hand. In fact, recent analyses have revealed that the scalp EEG alpha rhythm jumps erratically between low-power and high-power modes [8]. These two modes appear as distinct peaks in the distribution of instantaneous power, violating the traditional view that alpha wanders back and forth around a unimodal distribution (Figure 1). Important information is also carried in the switching times — namely in the distributions of times that the system dwells in each mode. A stochastic process without memory (i.e., an uncorrelated process) would exhibit exponential distributions. On the contrary, the switching times here exhibit trapping (Figure 1b), following heavy-tailed stretched-exponential distributions [8,9]. This means that the alpha rhythm dwells in each mode for longer than would be expected for Gaussian fluctuations in a two-state bistable system. The trapping (the system is less likely to jump the longer it has been in either mode) implies that the alpha rhythm has memory.

Another important feature of the bimodal distribution is that the mode width scales with the mean — the high power mode exhibits an order of magnitude increase in mean power *and* an order of magnitude increase in standard deviation. The relative width (i.e., coefficient of variation) is thus scale invariant (as apparent in double logarithmic coordinates, Figure 1a). Scale invariance is a ubiquitous feature of human perception: disparate 'laws' of human behavior posit scale-invariance in uncertainty, such as the Weber-Fechner law governing uncertainty in perceptual discrimination [10] and Fitts' law governing uncertainty in movement precision [11].

A biophysical mechanism for these features of switching dynamics was proposed using a corticothalamic neural field model with multiplicative noise and bistability near

Figure 1



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Non-Gaussian fluctuations in the human alpha rhythm. **(a)** PDFs derived from long recordings of EEG time series exhibit a low (black) and a high (red) amplitude mode. The overall PDF is well described by their bimodal sum (white), and not by a unimodal fit (blue). Logarithms are base *e*. **(b)** The corresponding dwell times of each mode are well described by stretched exponentials (white), and not by the simple exponential (gray). **(c)** Time series of filtered (8–12 Hz) EEG with low (black) and high (red) amplitude modes highlighted. **(d)** Corresponding power fluctuations of 10 Hz oscillations. Figure adapted from Ref. [12•].

a sub-critical nonlinear instability [9]. This is in fact an example of a more general switching mechanism of wide applicability in natural systems [12•,13].

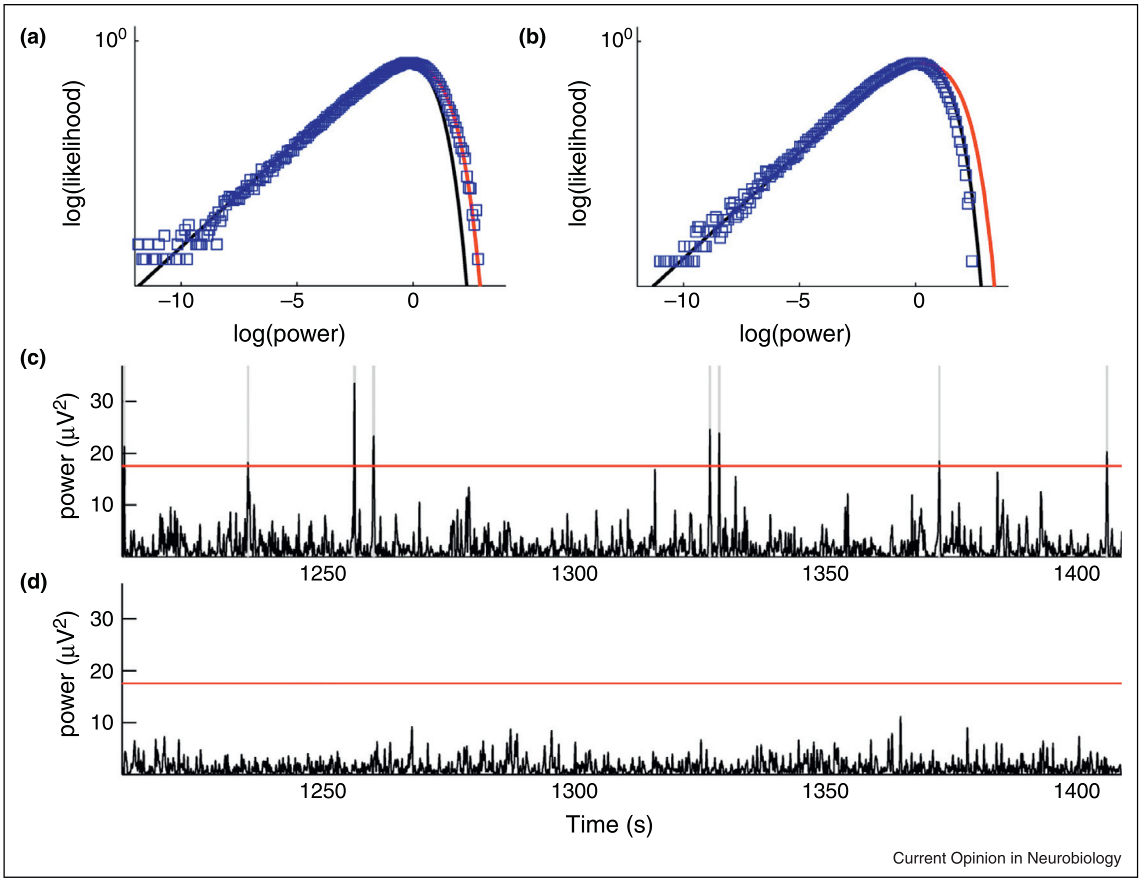
Thus the characteristic bistable dynamics of the dominant oscillation at the brain's largest scale cannot be reduced to the collective sum of uncorrelated spiking units, but instead reflects behavior emergent at the macroscopic scale. Contrary to the principle of linear superposition, this finding suggests that large-scale alpha oscillations 'enslave' activity at smaller scales (including individual spikes [14]), analogous to the enslavement of electron spins in coherent laser phenomena [15]. We return to this issue below.

Heavy-tailed beta rhythms

Applying the above analysis to beta rhythms reveals that while the power envelopes of beta activity are unimodal, they nonetheless depart from the exponential distribution (Figure 2) [8]. The right tail is 'fatter' than an exponential, closely following a Fisher-Tippett (double-exponential) distribution. This means that large-amplitude events occur by chance more often than expected for an exponential distribution because they are drawn from a heavier right hand tail. Although the deviation of the beta rhythm from a unimodal exponential PDF is less spectacular than alpha, the functional significance of beta oscillations to human motor output in health [16,17] and disease [18] underlines the importance of identifying generative mechanisms. Fisher-Tippett heavy tailed distributions are typical of highly-correlated complex systems, where the core assumptions of independence for Gaussian fluctuations are violated [19]. Heavy-tailed Fisher-Tippett distributions describe extreme events in financial [4] and climate [20] systems. Generative mechanisms for their appearance in human beta oscillations are yet to be established, although stochastic perturbations at the point of a Hopf bifurcation in a cortical neural mass model is a possible scenario [21].

Non-Gaussian statistics are seen in other measures derived from EEG amplitude envelopes. Band-pass filtering EEG leads to low-frequency 'beats' that modulate the amplitude stochastically [6]. Transient drops to

Figure 2



Non-Gaussian fluctuations in the human beta rhythm. **(a)** Distribution of instantaneous beta power (blue) with fits to exponential (black) and Fisher-Tippett (red) distributions. Logarithms are base *e*. **(b)** Distribution of instantaneous beta power in phase-randomized surrogate data. **(c)** Bursts in instantaneous beta power. **(d)** Instantaneous beta power in phase-randomized surrogate data. Figure adapted from Ref. [8].

near-zero amplitude are spaced in time with intervals distributed according to the heavy-tailed Rayleigh or Rice distributions for most frequency ranges. It has been suggested that the brain may exploit this general feature of band-passed signals: a population of neurons sensitive to inputs over a limited frequency band would have reduced background noise, increasing the likelihood of a response to a well-timed stimulus [7].

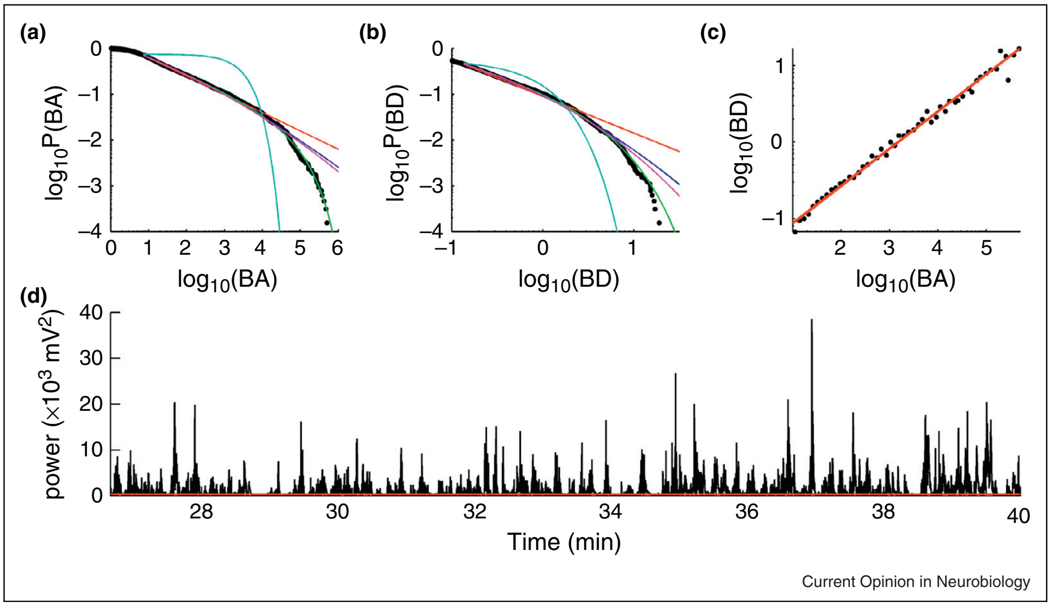
Scale-free dynamics

One of the most striking departures from Gaussian statistics is the power-law distribution [22], a hallmark of scale-free dynamics. Scale-free distributions have garnered significant attention across the physical and biological sciences as a signature of criticality — a state in many-bodied systems poised between order and disorder. In the brain, criticality is seen as a powerful paradigm for explaining optimal information transfer [23–25], storage capacity [24–26], and flexibility [26,27] (for recent reviews, see [28,29,30••,31,32]).

Scale-free critical dynamics arise in space and/or in time. Spatial scale-free activity, termed neuronal avalanches, is well-studied in slice preparations [23,33••], *in vivo* local-field potentials [27,34–37], fMRI [38,39], and magnetoencephalographic recordings [40]. Here 'avalanches' are events spanning multiple electrodes/channels across space, with event size quantified by the number of channels active. Calculated in this way, event sizes exhibit power-law distributions indicative of scale-free dynamics and long-tailed non-Gaussian statistics. The essential feature of these dynamics is that events have no characteristic scale — although small events are the most common, events up to two orders of magnitude larger (spanning up to the entire sensor array) are much more likely than would be expected with Gaussian statistics. Theoretically, the variance of a scale-free process is infinite (assuming the power law has exponent <2), although in practice the finite size of the system inevitably imposes an upper bound.

The brain also exhibits scale-free *temporal* dynamics — indeed the durations of some of the aforementioned spatial avalanches are power-law distributed (e.g., [33••]). But scale-free dynamics can even be observed in single-channel data [41], as exemplified by Barkhausen noise in magnets [42,43]. This is because even though the microscopic dynamics may be inaccessible (e.g., single neurons in humans *in vivo*, or magnetic domains in ferromagnetic samples), near the critical point their bulk activity yields macroscopic signals that can be detected with EEG (or in the case of Barkhausen noise, a pickup coil). Recently it was shown that human neonatal EEG following hypoxia at birth exhibits bursty activity with lengthy power laws spanning several orders of magnitude (Figure 3a) [44•]. In this context, size is not a spatial property but rather a measure of the energy released in an event. The scale-free properties extend also to distributions of burst durations

Figure 3



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Scale-free dynamics in post-hypoxic neonatal EEG. **(a)** Upper CDF of burst area (BA) with fits to candidate distributions: power law (red), exponentially-truncated power law (green; exponent 1.36), lognormal (blue), stretched exponential (magenta), and exponential (light blue). **(b)** Upper CDF of burst duration (BD) with fits (truncated power law, green, has exponent 1.56). **(c)** Relationship between BD and BA with least-squares fit (red; slope 0.51). **(d)** Example burst suppression instantaneous power with threshold overlaid (red). Figure adapted from Ref. [44•].

(Figure 3b) and to the relationship between burst size and duration (Figure 3c). The various exponents obey scaling relations in line with the theory of crackling noise [42] and experimental results in spatial neuronal avalanches [33••].

We have focused on the scale-free distributions of directly-observable system fluctuations in the temporal domain. Power-law scaling regimes are also frequently observed in Fourier spectra [45–47], although the relationship to scale-free activity in the underlying system is not straightforward [48]. Neural field models successfully explain the '1/f spectra' typical of various arousal states as arising from linearly filtered white noise without needing to impose any non-Gaussian statistics onto the noise input [49]. In general, a linear scaling of the power spectra with frequency in double logarithmic coordinates is only indicative of scale-free activity when the slope is shallow (e.g., <1.5) and the scaling regime covers several orders of magnitude. Otherwise, particularly for slopes >2, the fluctuations can be well described by uncorrelated Poisson-like spiking [46,48]. Detrended fluctuation analysis (DFA) has also been used to highlight scale-free statistics in myriad neurophysiological recordings [50] including the amplitude envelope of macroscopic cortical rhythms [51,52,53•] and measures of system correlations [54]. DFA exponents indicate the presence or absence of correlations in time series, and are linearly related to slopes of power spectra. However, DFA essentially offers no additional information beyond that already in the power spectrum [55], so the caveats highlighted above still apply.

Finally, we reconcile the apparent paradox regarding oscillations — which by definition have a characteristic time scale — and their possible scale-free statistics. The key point is that their amplitude fluctuations can still exhibit scale-free statistics. In neural field models, critical amplitude fluctuations arise from the real part of the model's eigenspectrum, specifically when the system is close to an instability [56–58]. The oscillatory content arises from the imaginary component of the eigenspectrum.

Log normal

The near-ubiquity of Gaussian statistics derives from the central limit theorem: independent processes added together, whatever their distributions, asymptotically yield Gaussian statistics. Similarly, log–normal distributions are ubiquitous from *multiplicative* processes. Because $\Sigma_i \log(x_i) = \log(\Pi_i\ x_i)$, summing logarithms of independent variables x_i yields Gaussian statistics, implying that the product of independent variables $\Pi_i\ x_i$ exhibits log–normal statistics. Log–normal distributions occur in many neurophysiology data — including spiking neurons in rat [59] and human [60] cortex — and in human behavior — such as durations of active periods [61] and the velocity of fixational eye movements [62]. Although we are not aware of log–normal statistics in rhythmic activity in very large-scale recordings, we include them in our inventory because they complete the list of candidate heavy-tailed probability distributions of relevance to empirical neuroscience. We direct the reader to Ref. [63••] for a very recent detailed review.

Discussion

In summary, several striking examples of non-Gaussian PDFs have been found in neurophysiological oscillations since attention recently turned in this novel direction. Stretched exponential, power law, Rayleigh, double exponential and lognormal PDFs each arise through specific underlying dynamical mechanisms, including state-dependent and multiplicative noise; criticality and multistability; trapping and memory [12•,64,65]. Such insights place important constraints on the analytic form of generative models, including (1) the balance of excitation and inhibition [24,44•,66,67•]; (2) the analytic form of stochastic influences [9,12•]; (3) the coupling of fast neuronal and slow metabolic variables [68,69]; (4) the proximity of the system to a critical instability [58,65,67•]; and (5) the nature of that instability [9,12•]. Crucially, different examples of these processes can occur in the same system (as in the preceding examples of alpha and beta cortical oscillations). Likewise, when these same core processes occur in different physical systems, they become united by the behavior they exhibit — regardless of the physical substrate in which they arise — a phenomenon known as universality. For example, stretched exponential dwell times characterize the human alpha rhythm, wave-interactions in semi-conductors [70], and activity patterns of behavior in humans [61] and fruit flies [71]. Oscillations are a hallmark of neurophysiological recordings, few of which have been studied using the preceding principles. It may be that anomalous statistics are the norm and not the exception, and that methodological pluralism should therefore reign in this field.

An important implication of anomalous statistics in large-scale neurophysiological recordings is the violation of the principle of independence. This argues against the notion that any scale might yield a privileged description of the brain, in favor of a framework of pervasive causal correlations across scales [72]. It further implies that activity at small scales can be enslaved to mean field oscillations arising at larger scales [14,15,73]. This is a stronger ontological position than that of 'joining the dots' [74], which remains wedded to the salience of the component pieces. In highly correlated systems, macroscopic effects exert a pervasive influence on the behavior and interactions of local elements. These effects (which to some extent define the nature of those units) can fundamentally re-organize following a phase transition [75]. Another possible viewpoint is of correlated microscopic units observed 'from afar', such that the macroscopic signal exhibits non-Gaussian statistics without any feedback from the large scales to the small. Indeed while it is unlikely that the scalp potential itself directly influences the neurons, the mean-field activity of the neurons (which the scalp potential reflects) likely does feed back onto the individual spike times [14]. The process that achieves this may be a simple as a random sparse sampling of the mean field by each neuron through its extensive dendritic arbors. In this way, a substantial subset of neurons in any region receive a coherent, if weak, common input sufficient to partially enslave their activity. This is a purely dynamic process, akin to recasting the Kuramoto model in terms of a population (Fokker Planck) description [76], and hence does not require recourse to any additional physical mechanism such as ephaptic coupling. More broadly, linking spiking-neuron models to mean-field models remains an active area of research [77]. As the neuroscience community moves deeper into the era of very large international projects, the presence of heavy-tailed statistics in macroscopic neurophysiological oscillations argues for the need to understand these dynamic and organizational principles, avoiding a selective engagement in one scale, approach, technology or methodology.

Conflict of interest statement

Nothing declared.

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