Spontaneous cortical activity in awake monkeys composed of neuronal avalanches

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Spontaneous neuronal activity is an important property of the cerebral cortex but its spatiotemporal organization and dynamical framework remain poorly understood. Studies in reduced systems—tissue cultures, acute slices, and anesthetized rats—show that spontaneous activity forms characteristic clusters in space and time, called neuronal avalanches. Modeling studies suggest that networks with this property are poised at a critical state that optimizes input processing, information storage, and transfer, but the relevance of avalanches for fully functional cerebral systems has been controversial. Here we show that ongoing cortical synchronization in awake rhesus monkeys carries the signature of neuronal avalanches. Negative LFP deflections (nLFPs) correlate with neuronal spiking and increase in amplitude with increases in local population spike rate and synchrony. These nLFPs form neuronal avalanches that are scale-invariant in space and time and with respect to the threshold of nLFP detection. This dimension, threshold invariance, describes a fractal organization: smaller nLFPs are embedded in clusters of larger ones without destroying the spatial and temporal scale-invariance of the dynamics. These findings suggest an organization of ongoing cortical synchronization that is scale-invariant in its three fundamental dimensions—time, space, and local neuronal group size. Such scale-invariance has ontogenetic and phylogenetic implications because it allows large increases in network capacity without a fundamental reorganization of the system.

neuronal synchronization | resting state | rhesus monkey | spontaneous activity | ongoing activity

The cerebral cortex displays spontaneous activity, also known as ‘ongoing’ or ‘resting state’ activity, which persists in the absence of sensory stimuli or motor outputs. The ongoing activity is a robust feature of cortical dynamics as it is only modulated to a small extent by stimulus presentation (1), but contributes significantly to the large variability observed in stimulus responses (2–5). In fact, ongoing activity has been found to reflect multiple aspects of neuronal processing. The activity is similar to that observed during stimulus presentation (1, 6–8), incorporates previously acquired information (9), and carries information about the underlying neuronal network [for review see (10)]. Indeed, correlations during resting state activity are altered in disease states such as schizophrenia or chronic pain (11, 12), which raises the question whether there is a general framework that describes the statistics in the spatiotemporal organization of this dynamics.

Recently, we found that spontaneous cortical activity in slice cultures, acute slices, and in the anesthetized rat in vivo has a scale-invariant dynamics called neuronal avalanches (13–15). These spontaneous bursts of synchronized activity occur in clusters of sizes s (where s is the number of active sites in an electrode array) that distribute according to a power law with exponent α:

\[ P(s) \propto s^{-\alpha} \]  

where α usually lies between 1 and 2. Thus, given a burst of size s, a burst double that size will occur 2^α times less often, independent of s. More generally, given synchronized activity bursts of sizes s and k * s (where k is a constant), there will always be a fixed ratio k^α between the corresponding probabilities of occurrence. This scale-invariant dynamics has several key properties: (i) it requires balanced excitatory and inhibitory synaptic transmission (13, 15, 16); (ii) it arises in vitro and in vivo when superficial layers form during development (15); and (iii) it is maintained over many weeks in the isolated cortex in the absence of input (17), suggesting that the dynamics is an intrinsic property of the cortex. Importantly, neuronal avalanches resemble the dynamics observed in other systems at the critical point between an ordered and disordered dynamics, commonly referred to as the critical state (18–20). Simulations of neuronal networks show that in the critical state the dynamic range of inputs is optimized, along with the amount of information that can be processed (21), stored (22), and transferred (15).

To date, neuronal avalanches have been described only in reduced preparations from rat brains. These limitations have led to doubts about their relevance to intact and fully functional nervous systems. Accordingly, the present study examined the generality of avalanche dynamics in awake rhesus monkeys. We demonstrate that ongoing activity is composed of neuronal avalanches by demonstrating its invariance to various scale transformations in space, time, and a third dimension, the nLFP amplitude threshold. This scale invariance is in line with predictions from a critical state dynamics (19, 20); it implies that the ongoing functional linking of cortical sites occurs across all distances and on all time scales with a fractal ordering in the size of participating neuronal groups.

Results

We measured ongoing LFP and unit activity continuously for approximately 40 min using microelectrode arrays in the cerebral cortex of two awake rhesus monkeys, which were seated in a monkey chair. External sounds were minimized. The monkeys were not required to do any behavioral task or respond to a particular stimulus, while they maintained their body posture and general vigilance. The array configurations covered a range of scales, spanning 64 and 36 mm² of the primary motor and premotor areas in two monkeys (Fig. 1A; one array in monkey A, four arrays in monkey B). The simultaneously recorded LFP traces revealed irregular deflections typical of wakefulness (Fig. 1B). Spike-triggered LFP averages demonstrated that nLFP peak times correlated with unit activity (Fig. S1; 92% of units M1left monkey A; 88 ± 4% of units monkey B) and nLFP peak amplitudes increased with instantaneous local firing rate (number of spikes from all units...
amplitude also increased with local synchronization of unit activity. \( \text{SD} \) monkey A; 0.3 /H11001 \( \text{SD} \) monkey B; 0.15 SD for monkey A; right: four arrays monkey B). Insets: Example average LFP triggered by 10 ms periods with one, two, or three spikes at a single electrode. Left: M1left. Right: PMdright. (Scale bars, 0.4 SD left; 0.2 SD right; 100 ms.) (D) nLFP amplitude increases with number of units that contribute at least one spike per 10 ms (left inset) that is, local spike synchrony (see Fig. S2D for significance of two vs. three units). Right inset: Example average LFP triggered on one, two, or three active units (PMdright). Scale bar, 0.2 SD; 100 ms).

at each electrode within 10 ms) \( \text{Fig. 1C; monkey A; F (3, 73) = 26, } \text{P < 10}^{-31} \text{M1left; monkey B; F (3, 53) = 4.0, } \text{P = 0.01 M1left; F (3, 26) = 6.0, } \text{P = 0.003 M1right; F (3, 38) = 10.0 PMdleft; } P = 5 	imes 10^{-7}; F (3, 37) = 23, P = 10^{-3} \text{PMdright, one-way ANOVA; +0.27 SD for monkey A; +0.16 ± 0.05 SD for monkey B per 100 Hz; R = 0.55 ± 0.7; } P < 0.0001 \text{ all arrays; linear regression.} \) nLFP peak amplitude also increased with local synchronization of unit activity \( \text{Fig. 1D; number of units with at least 1 spike/10 ms; see Fig. S2; 2 vs. 3 units: 0.6 SD monkey A; 0.3 ± 0.1 SD monkey B; } t \text{test; } P < 0.0005. \) These locally synchronized spikes were significantly different from chance occurrence and were correlated across cortical sites over many seconds in time \( \text{Fig. S2).} \) Thus, the peak nLFP amplitudes during ongoing activity provides a good approximation of the instantaneous firing rate and degree of spike synchrony of the local neuronal population.

nLFPs in Vivo Organize into Neuronal Avalanches. We then grouped nLFPs into spatiotemporal clusters based on their occurrence in successive time bins, regardless of the electrode on which they occurred \( \text{Fig. 2A).} \) Such temporal grouping of nLFPs is supported by the strong crosscorrelation between nLFPs at different electrodes \( \text{Fig. 2B).} \) The beginning of a cluster was defined by the occurrence of a time bin (chosen at \( \Delta t = 4 \text{ ms} \)) with at least one nLFP and the end by the next encounter of an empty time bin. Clusters had size \( s \) equal to their number of nLFPs and a lifetime...
$T$, that is, duration, equal to the number of bins times $\Delta t$. We found that $P(s)$ distributed according to the power law in Eq. 1. The power law is readily identifiable as a linear relationship in log-log coordinates, where the slope approximates the power law exponent $\alpha$ (Fig. 2C, open circles). For both monkeys and all arrays, the power law ranged from the lowest cluster size of 1 electrode, i.e., $s = 1$, to the maximal number of electrodes in the array ($s = 32$, monkey A; $s = 16$, monkey B).

The power law identifies a scaling relationship in the spontaneous formation of long-range spatial correlations in the system. This can be seen by the greater probability of occurrence of spatiotemporally large clusters relative to random or independent nLFP groupings. Indeed, after random shuffling of nLFPs in time, nLFP clusters distribute exponentially in sizes ($R > 0.999$, all cases; Fig. 2C, broken lines) indicating a rapid decrease in the probability of larger clusters, that is, long-range spatial correlations, and a loss of the scaling relationship.

While the power law was preserved for different choices of $\Delta t$, the absolute value of its corresponding exponent $\alpha$ decreased when $\Delta t$ increased (Fig. 2C and D). This relationship was previously found in vitro as

$$\alpha \sim \Delta t^B,$$  

with $\beta = -0.16 \pm 0.01$ (13). A similar relationship between $\alpha$ and $\Delta t$ was found in vivo with a range of $\beta$ between $-0.04$ and $-0.16$ (Fig. 2D, monkey A; $M_{\text{left}} \beta = -0.15 \pm 0.01, R = -0.98, P < 0.001$; monkey B: $M_{\text{right}} \beta = -0.16 \pm 0.1, M_{\text{left}} \beta = -0.11 \pm 0.02, P_{M_{\text{right}}} \beta = -0.04 \pm 0.02, R = -0.94 \pm 0.04, P < 0.01$ all arrays; linear regression). Formulates 1 and 2 allow for the size distributions $P(s)$ obtained at different $\Delta t$ to be collapsed using a general scaling ansatz (see Materials and Methods) demonstrated for $M_{\text{left}}$ of monkey A in Fig. 2E. The collapse experimentally demonstrates a temporal scale-invariance of the power law in cluster sizes for temporal resolutions of 2–32 ms.

As reported previously in vitro (13), the maximal number of electrodes on the array marked the cut-off of the power law because cortical sites rarely participated in a cluster more than once. Indeed, this cut-off shifted systematically as electrodes were removed from the analysis (Fig. 2F) demonstrating finite-size scaling typical for critical state dynamics (19).

The power law distribution of nLFP clusters is specific to nLFP fluctuations, is not predicted by a 1/1D-decay in LFP frequency power (23) or volume conduction, and is cortical depth specific. First, the power law is not observed for other signal characteristics of the LFP, such as all baseline crossings (Fig. S3A). We note that nLFPs are often followed by positive deflections, which therefore cannot serve as an independent control. Second, phase-shuffling of the LFP, which changes the temporal relationship between frequencies at and between sites without affecting the 1/1D scaling, destroys the power law in nLFP cluster sizes (Fig. S3 B and C). Third, nLFP clusters are most often composed of spatially non-contiguous nLFPs irrespective of the temporal resolution chosen, in contrast to what is predicted for either volume conduction or overlapping signal detection (Fig. S3 D–F). Fourth, the relationship between nLFP and unit activity as shown in Fig. 1C as well as the power law in nLFP cluster sizes is only present in more superficial layers of the cortex demonstrating layer specificity of the organization (Fig. S4A), with the localization of neuronal avalanches to superficial layers in the acute slice (16), slice culture (17), and anesthetized rat (15).

The Avalanche Organization Is Invariant to nLFP Detection Threshold. A remaining and previously unexplored free parameter in the description of nLFP clusters is the threshold $z$ to detect nLFPs. Because nLFP peak amplitudes increase with local firing rate and synchrony (Fig. 1C and D), a threshold operation removes a significant number of suprathreshold, active sites from the analysis. In fact, when $z$ increased from $-1.5$ to $-4.5$ SD the number of extracted nLFPs decayed by almost two orders of magnitude (Fig. 3A; exponential decay, slope $= -2.4$ and $-3.5 \pm 0.4$; monkey A and B respectively; $R = 0.999$). Importantly, the power law in cluster size distribution remained unchanged (Fig. 3B; $\Delta t = 4$ ms; $P > 0.05$; Kolmogorov-Smirnov (KS)-test) including $\alpha$ which remained constant as $z$ increased (Fig. 3C; average slope: $0.07 \pm 0.06/SD; P > 0.1$ all arrays) and accordingly the collapse of $P(s)$ for different $z$ is achieved with $\beta = 0$ (Fig. 3B; Eq. 2). Thus, large nLFPs on the array are parsed into spatiotemporal clusters in exactly the same way after smaller nLFPs are removed. This demonstrates that the neuronal avalanche dynamics is independent of the chosen threshold.

In fact, an avalanche identified at a low threshold fragments into multiple avalanches as the threshold increases, but the average size stays close to its original value demonstrating similarity of nLFP amplitudes within avalanches beyond chance (see Fig. S5). As a control, we demonstrate that when nLFPs were extracted at $z = -1.5$ SD and then randomly removed from this raster to arrive at total nLFP numbers that corresponded to a given threshold $z$ (Fig. 3A), the power law in cluster size distribution readily collapsed with an increase in $z$ ($P < 0.05$; KS-test; Fig. 3D; see also Fig. S6 for monkey B $PM_{\text{right}}$).

We visualized the self-similar, hierarchical organization of nLFP amplitudes by reploting nLFP rasters at different temporal and amplitude scales. At $z = -4.5$ SD, the rate of nLFPs was low, but viewing the data at a low temporal scale revealed the spatiotemporal clustering of nLFPs (‘columns’, Fig. 3E). On the other hand, clusters that appeared homogenous at high threshold and low temporal resolution, ‘spawned’ new clusters at successively lower thresholds and increased temporal resolutions (Fig. 3E; $A \rightarrow A’$, $B \rightarrow B’$).

These results clearly demonstrate that proper subsampling of the scale-invariant activity, that is, all events above a given threshold, differs from randomized subsampling of synchronized activity, which underestimates the probability of large clusters (24). For example, when estimating local synchrony using the relatively few extracellular units discriminated successfully at individual electrodes, numerous local, synchronized events as reflected in the nLFP, will not be captured, establishing a condition of partial, random subsampling. Indeed, the resulting distributions of spatiotemporal clusters based on local unit synchrony where heavy-tailed and, while significantly different from an exponential distribution (Fig. S7A), deviated from a power law. The deviation found is in line with the finding of Fig. 3D and Fig. S6, where a scale-invariant organization of nLFPs was subjected to random event removals (cp. transition from the original organization at $-1.5$ SD to an nLFP raster with equivalent nLFP numbers as found at $-2$ SD and $-2.5$ SD by random removal of nLFPs).

Avalanche Lifetimes Are Scale Invariant in Time and nLFP Threshold. For dynamical systems in the critical state, scale-invariance in avalanche sizes is accompanied by scale-invariance in avalanche duration, that is, the lifetime $T$ (18–20). In vivo, $T$ varied greatly even for avalanches of any given size, although large avalanches tended to have longer lifetimes (Fig. 4A). As reported previously in vitro (13, 16), avalanche lifetimes in vivo were significantly longer than when nLFPs were randomized in time (Fig. 4B; broken lines; $P < 0.05$; KS-test; inter nLFP time shuffling) and lifetime distributions collapsed to a similar distribution when $T$ was scaled in multiples of $\Delta t$ ($P > 0.05$; KS-test). Furthermore, similar to avalanche sizes, the lifetime distributions were also scale-invariant with respect to $z$ (Fig. 4C; $P > 0.05$; KS-test).

Discussion

The present data show that ongoing cortical activity in awake monkeys is composed of neuronal avalanches, indicating the universality of these dynamics in the context of cortical activity. nLFPs correlate in time and amplitude with local synchronized spike activity. nLFP power law in nLFP cluster sizes is only present in more superficial layers of the cortex demonstrating layer specificity of the organization (Fig. S4A), with the localization of neuronal avalanches to superficial layers in the acute slice (16), slice culture (17), and anesthetized rat (15).
activity and organize into spatiotemporal clusters with a power-law distribution in sizes. Not only occur these clusters irrespective of spatial and temporal scale, as shown previously for reduced preparations (13–15), but they are also scale-invariant with respect to detection threshold.

Scale Invariance in Time, nLFP Amplitude, and Finite-Size Scaling Is Consistent with a Critical State. Power laws in cluster-size distributions can result from numerous mechanisms (14). However, the self-similarity at different scales suggests critical state dynamics as the most likely one. Self-similar hierarchies of events across time, space, and amplitude are universally found in systems that are near a critical point of a phase transition between order and disorder

Fig. 3. The avalanche organization is scale-invariant to nLFP amplitude threshold. (A) Decay in total number of nLFPs with increase in threshold \( z \). (B) Power law distributions in sizes are scale-invariant with respect to nLFP amplitude. Size distributions \( P(s) \) plotted for different \( z \) and two arrays (\( \Delta t = 4 \) ms). (C) The slope \( \alpha \) does not depend on \( z \) (five arrays; color code in A). (D) Random removal of nLFPs differs from threshold-dependent nLFP removal and does not maintain scale-invariance. Filled circles: cluster size distribution at \( z = -1.5 \) SD (original data, monkey A). Open circles: nLFPs are randomly removed from the original \(-1.5 \) SD raster to arrive at rasters with equivalent number of nLFPs as found for \( z = -2, -2.5, \ldots, -4.5 \) SD (see A). Corresponding cluster size distributions rapidly deviate from a power law. (E) Avalanches ‘spawn’ new avalanches when lowering threshold \( z \) (\( \Delta t \) constant). Top: nLFP raster period at \( z = -4.5 \) SD (nLFP clusters appear ‘columnar’). Middle: Raster of expanded time period from top (broken lines) at \( z = -3 \) SD and rescaled for nLFP amplitude (color bar). Segment A (gray) contains more nLFPs some of which form a new cluster A’ (ellipsoid). Bottom: Raster of expanded time period from middle (broken line) for \( z = -1.5 \) SD rescaled in amplitude. Spawn of new cluster in B (middle, gray) indicated by B’ (ellipsoid).

Fig. 4. The scale-invariance of avalanche lifetimes. (A) Avalanche lifetime \( T \) varies widely for a given size \( s \), although longer avalanches tend to have larger sizes. \( P(T,s) \): Probability density. (B) Lifetime distributions (open circles) collapse when scaled in multiples of \( \Delta t \). This scale-invariance is lost for time-shuffled rasters (broken lines, open squares). (C) Lifetime distributions obtained for \( z = -1.5 \) SD to \(-4.5 \) SD are similar demonstrating scale-invariance in nLFP amplitude.

**Scale Invariance in Time, nLFP Amplitude, and Finite-Size Scaling Is Consistent with a Critical State.** Power laws in cluster-size distributions can result from numerous mechanisms (14). However, the self-similarity at different scales suggests critical state dynamics as the most likely one. Self-similar hierarchies of events across time, space, and amplitude are universally found in systems that are near a critical point of a phase transition between order and disorder.
(18–20). Moreover, such a critical state appears to be advantageous for information processing (13, 21, 22).

Alternative dynamic scenarios, where nLFP clusters of small sizes arise by virtue of different mechanisms compared to those responsible for medium- or large-sized clusters, are difficult to translate into different scales. For example, the removal of >90% of nLFPs below a given amplitude threshold (Fig. 3B) demonstrates that the remaining, much fewer, but large nLFPs organize like smaller nLFPs. This property suggests that the generation of large clusters has similar mechanisms as small clusters. Similarly, an equivalent statistical structure after removal of full sections of electrodes implies a common mechanism in space. An analogous argument would apply for different temporal scales.

A critical state, as implied by the neuronal avalanche dynamics, does not arise arbitrarily in cortical networks. Instead, this property of spontaneous activity emerges when superficial layers of cortex first differentiate from the cortical plate during development (15). Given the dependence of neuronal avalanches on the balance of fast synaptic excitation and inhibition and the neuromodulator dopamine (13, 15–17), it seems clear that these properties arise from the specific organization of cortical circuitry.

Implications for Large-Scale Cortical Networks. The scale invariance in the spontaneous formation of clusters has important implications for large-scale cortical networks. A large network can support a large diversity of cluster sizes, including those that percolate the maximal extent of the system. This indicates that the maximal cluster size, that is, the long-range correlations established by such a cluster, is constrained by the system size and not system dynamics. Consistent with this, in our experiments, the maximally measured cluster size or area occupied by a cluster was constrained only by the number of electrodes. In these recordings from monkeys, where inter-electrode distances were up to 2 mm, the scale invariance was demonstrated over 64 mm², the area covered by the largest array. This greatly extends the range of scale invariance shown previously, where the arrays and correspondingly the maximal cluster, spanned a maximum of 2 mm² (13, 15). Furthermore, the large number of regions and conditions where neuronal avalanche dynamics have now been observed—motor, premotor, and somatosensory cortex in awake monkeys (present data), somatosensory cortex of anesthetized rats (15), and both rat somatosensory and prefrontal cortex in vitro in acute slices and slice cultures (13, 17)—indicates that this dynamics is likely to be a general property of the cerebral cortex. This also suggests that the dynamics may extend across multiple regions rather than being restricted to specific regions.

As has been shown in well-identified networks, a target dynamics can be achieved by a plethora of different network realizations (25). Indeed, the finding of scale invariance does not exclude long-range or short-range heterogeneous corticocortical projections. Numerical simulations have shown that neuronal avalanches can arise at the critical state in models with scale-free (26), fully connected (27), random (28), and nearest-neighbor (18, 26) topologies, although in each case the conditions to reach criticality can be different. In cortical cultures, the neuronal avalanches establish a functional small-world architecture with specific and highly diverse point-to-point connectivity between cortical sites that is, the network representing these site activations is densely interconnected, globally as well as locally (29). The superficial layers where these dynamics arise in cultures are also where long-range corticocortical connections are most prominent and therefore where information is likely to be integrated across multiple sensory modalities. As discussed above, a hallmark of criticality is the fact that the length of correlations (in space and time) is only limited by the size of the system (18, 19, 30), for instance in the present case the extent of the correlations goes as the size of the largest avalanche, which diverges with system size. Thus an expanding critical system increases the number, the diversity and the maximal cluster size without the necessity to rewire existing connections. This property has significant implications from both a developmental as well as an evolutionary perspective. The ontogenetic and phylogenetic increases in cortical volume would naturally allow for greater functional capacity without requiring a fundamental and sophisticated reorganization of the system (31). Importantly, the superficial layers of cortex, where this dynamics has been identified in vitro and in the anesthetized rat in vivo (15–17), expand most dramatically during both individual development and during the evolution of the cerebral cortex in advanced mammals (32).

Functional Significance. Our results demonstrate that the neuronal avalanche dynamics in awake animals is remarkably similar to that arising in vivo early during development (15) and in explant cortical networks that mature in the absence of external inputs (13, 17). Thus the phenomenon described previously for reduced systems applies to intact ones, as well. The present results also generalize avalanche dynamics across species (including to a primate) and individuals, as well as the broad diversity of cortical areas listed above. Taken together, these findings strongly suggest that criticality is a generic property of cortical network activity. We note that the resting condition of the monkeys in the current experiments is an approximation of the idle state, which would be the proper condition for measuring spontaneous activity as found in vitro preparations and it remains to be compared explicitly to highly active states as for example found during precisely controlled behavioral paradigms.

An intuitive functional understanding of the critical state can be obtained by analyzing the internal organization of avalanches, that is, spatiotemporal cascades, within the context of a branching process. We previously demonstrated that during an avalanche, on average, one nLFP (the ancestor) is followed by one nLFP in the near future (the descendant) in line with predictions from theory for a critical system (13). The critical branching ratio σ, which is the number of descendants divided by the number of ancestors is thus precisely 1. For subcritical processes (σ<1), cascades terminate prematurely, whereas for supercritical processes (σ>1), they will quickly engage the whole system in a non-selective manner (similar to an uncontrolled nuclear chain reaction). If systems try to maximize the likelihood of linking distant sites through cascades, while avoiding massive, non-selective activation, criticality is the optimal scenario, and it is from this perspective that the functional significance of the critical state expressed as neuronal avalanches needs to be appreciated. Specifically, modeling studies have shown that critical branching maximizes the mutual information between groups of neurons (13) as well as the ability of a system to respond with diverse internal states to a wide range of inputs (21).

The cerebral cortex in all mammalian species follows a common architectural blueprint and cortical areas must perform, at some level of analysis, an alike function. This function must be more general than the motor, sensory, and associational roles commonly ascribed to particular cortical areas. Thus, independently of the type of inputs that each region of cortex receives, the critical state would endow each spatiotemporal column or patch of cortex with a maximal dynamic range of processing, along with maximizing information transfer to other cortical areas. In addition, since criticality exhibits a mixture of ordered and disordered excitation patterns, neuronal networks at the critical state can generate the largest repertoire of dynamical configurations in a flexible manner. It would be reasonable to think that in some instances those networks with largest repertoires were selected over others throughout evolution. As such, the principles of synchronous, spontaneous activity described here could underlie all cortical functions. The present results open the way to testing this theory and for applying the knowledge gained from reduced systems to awake, behaving animals.
Materials and Methods

Microelectrode Array Positioning. The ACUC of Duke University approved all procedures. Arrays of monopolar tungsten electrodes (30 μm in diameter, 1 MΩ impendence, 0.3 mm spacing) were chronically implanted into the cortex of two adult rhesus monkeys (Macaca mulatta) (33). Monkey A was implanted with a 64-electrode array in the left motor cortex (M1left; leg representation). Monkey B was implanted bilaterally with four 32-electrode arrays in the M1 arm representation (M1Arm; M1Sign) and in dorsolateral premotor cortex (PMdArm; PMdSign).

Areas were identified by cortical landmarks, evoked LFP and unit responses during surgery. Electrodes were placed ~1 mm deep for PMd and ~1.5 mm for M1. Those electrode tips were aligned in a single plane of the array. The study laminar properties, a staggered array was inserted 1–1.5 mm deep in the somatosensory cortex of monkey A (S1left; Fig. S4; electrode tip separation: 4.8 Hz and 5.2 Hz). For the staggered array in M1 left, 37 units were resolved, 24 units on short-shank electrodes and 40 units on long-shank electrodes with 13,300 ± 14,500 and 12,100 ± 12,500 discharges, respectively (4.3 ± 4.8 Hz and 5.2 ± 5.6 Hz). For the four arrays in monkey B, on average 47 ± 13 units were resolved (16 electrodes/array), which fired 16,200 ± 5,200 times during the recording (5.7 ± 1.8 Hz). Unit firing rates were not significantly different between monkeys A and B (Student t test, P = 0.3).

Data Acquisition. Simultaneous recordings were carried out in M1Arm and S1Arm (monkey A) and the four arrays in M1 and PMd (monkey B). LFP and unit activity was sampled simultaneously from every other electrode resulting in 32 electrodes for M1Arm and S1Arm for monkey A and 16 electrodes per array in monkey B using a dual amplifier Plexon system (Fig. 1A and Fig. S4; circled fids). An epidural stainless steel T-bolt, at least 20 mm from all recording areas, served as a common ground.

LFPs were sampled at 500 Hz and band-pass filtered (1–100 Hz). Using a notch-filter, 60 Hz noise was removed. Extracellular spiking activity was sampled at 40 kHz and band-pass filtered with a two-pole low-cut and a four-pole high cut filter at 0.4–8 kHz. Off-line unit discrimination was based on principal component analysis and spike-template matching (33). The 68 units resolved in M1Arm (32 electrodes) fired on average 11,300 ± 9,700 times (4.3 ± 3.7 Hz). For the staggered array in monkey B, 37 units on short-shank electrodes and 40 units on long-shank electrodes with 13,300 ± 14,500 and 12,100 ± 12,500 discharges, respectively (4.3 ± 4.8 Hz and 5.2 ± 5.6 Hz). For the four arrays in monkey B, on average 47 ± 13 units were resolved (16 electrodes/array), which fired 16,200 ± 5,200 times during the recording (5.7 ± 1.8 Hz). Unit firing rates were not significantly different between monkeys A and B (Student t test, P = 0.3).

Removal of Slow-Wave Activity. To exclude sleep states, we first identified high amplitude, slow-wave activity characteristic of sleep spindles (90% of power at 1–10 Hz; 2 s sliding window at interval steps of 1 s). Periods with >50% channels showing this activity were removed (12.0% of the recorded data in monkey A; 6.8 ± 1.7% in monkey B).

nLFP Detection. LFP activity at each electrode was first normalized by subtracting its mean and dividing by its standard deviation (SD). The detection threshold for negative LFP peaks at each electrode (nLFP) was determined as $-\sigma_{SD}$ (where $n = 1, 2, 3, 4, 5$). Lower temporal resolutions for nLFPs were obtained by down-sampling the original LFP thereby taking every n$th$ value at $\Delta t = 2$ ms ($n = 1, 2, 4, 8, 16$) before nLFP detection. nLFPs from each electrode were combined into nLFP rasters (Fig. 2A). Because such a down sampling can be done in n different ways (e.g., for $n = 4$, one can start with the 1st, 2nd, 3rd, or 4th data point), the resulting distributions of nLFP cluster sizes and lifetimes (see Fig. 2A) were obtained as the averages over the n nLFP rasters.

For controls, up to 80 time-shuffled nLFP rasters were created for each temporal resolution by uniformly redistributing nLFPs for each electrode randomly in time excluding slow-wave periods. This procedure de-correlates nLFPs in space and time, while maintaining the nLFP rate at each electrode. For nLFPs, the cross-correlation functions between cortical sites were calculated from nLFP rasters (temporal resolution 2 ms) for all pair-wise electrode combinations and averaged for each array over a window of 40 ms. As controls, uniformly randomly timelagged nLFP rasters were used.

Scaling of Size Distributions. From 10,000–100,000 clusters contributed to each distribution, thus allowing for robust heavy-tail analysis. Distributions obtained with logarithmic binning were calculated for two parameters, temporal bin width $\Delta t$ and negative threshold $\sigma_{SD}$ (multiples of SD). The slope $\alpha$ of the power law was obtained for each value of $\Delta t$ or $\sigma_{SD}$ using linear regression of log-transformed distributions. The relationship between $\alpha$ and $\Delta t$ at a given value of $\sigma_{SD}$ also reflects the change in the power law relationship with an exponent $\beta$ [Eq. 2 (13, 14)]. Accordingly, the argument $s$ of a size distribution at a given temporal resolution $\Delta t$ can be scaled by $(\Delta t/\Delta t_0)^{\alpha}$ with $\Delta t_0$ constant ($\Delta t_0 = 4$ ms in our experiments; [19, 20]). This results in size distributions with a single slope $\alpha$ ($\Delta t_0$) for any $\Delta t$. For graphs, the collapse of distributions into virtually identical overplots is achieved by scaling $P(s)$ by $\Delta t_0$ where $\gamma$ is estimated by minimizing deviations in $P(s)$ for the various distributions.

Statistical Analysis. Distributions were compared using the two-sided Kolmogorov-Smirnov (KS) test [Matlab (v7)]. ANOVA and linear regression were applied to normal or log-transformed data (Statview v5.0; Origin v7). Significance was established at Pless than or equal to 0.05 and values are given as mean ± SD unless stated otherwise.

For additional information see SI Text.

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