# NEUROSCIENCE

# Low-dimensional criticality embedded in high-dimensional awake brain dynamics

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Whether cortical neurons operate in a strongly or weakly correlated dynamical regime determines fundamental information processing capabilities and has fueled decades of debate. We offer a resolution of this debate; we show that two important dynamical regimes, typically considered incompatible, can coexist in the same local cortical circuit by separating them into two different subspaces. In awake mouse motor cortex, we find a low-dimensional subspace with large fluctuations consistent with criticality—a dynamical regime with moderate correlations and multi-scale information capacity and transmission. Orthogonal to this critical subspace, we find a high-dimensional subspace containing a desynchronized dynamical regime, which may optimize input discrimination. The critical subspace is apparent only at long timescales, which explains discrepancies among some previous studies. Using a computational model, we show that the emergence of a low-dimensional critical subspace at large timescales agrees with established theory of critical dynamics. Our results suggest that the cortex leverages its high dimensionality to multiplex dynamical regimes across different subspaces.

#### INTRODUCTION

The ongoing dynamics of neuronal populations in the cerebral cortex are high-dimensional and the nature of the dynamics differs across dimensions. Some dimensions contain large amplitude fluctuations, while other dimensions tend to have smaller fluctuations. Accumulating evidence shows that a relatively small fraction of the total possible dimensionality—i.e., a low-dimensional subspace—contains much of the large amplitude collective fluctuations (1-6). This fact is commonly used to justify simplified views of population activity using just a few dominant dimensions defined by principal components analysis (PCA), for example (7, 8). Less commonly discussed are the smaller amplitude, more desynchronized fluctuations in the higher dimensional subspace, beyond the first few principal components (PCs). These basic observations lead to an interesting possible resolution of a long-standing debate in systems neuroscience.

The debate concerns the answer to a fundamental question: What is the dynamical regime of cortical neural networks in awake animals? Some researchers argue in favor of a desynchronized dynamical regime with weak collective fluctuations. This view is supported by measurements of low correlations of spikes recorded from pairs of neurons. Also, the desynchronized regime comes with potential computational benefits, like low noise and high input discrimination (9-12). Others argue for the importance of synchronized dynamics, based on observed oscillatory brain activity and potentially improved long-range signal transmission (13-15). Of particular importance for our work here, a third camp argues in favor of criticality-a dynamical regime poised at the boundary between uncorrelated and strongly coordinated regimes (16-20). Criticality manifests with moderate correlations and highly diverse spatiotemporal fluctuations and is thought to confer multiple functional advantages, like optimal information transmission, large dynamic range, fluid intelligence, and efficient coding (21-29).

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How might consideration of the high-dimensional geometry of population dynamics help resolve the debate about cortical dynamical regime? Here, we hypothesize that cortical populations could support more than one dynamical regime at the same time by separating different regimes into different subspaces. Criticality could occupy the low-dimensional subspace with large fluctuations (first few PCs) while a more desynchronized regime could occupy the higher-dimensional subspace with weak fluctuations (PCs beyond the first few). If this possibility is correct, then a cortical circuit need not choose between weak and strong correlations; it can have both simultaneously.

Is this hypothesis consistent with previous studies? In particular, how could this hypothesis be consistent with the multiple previous studies that have analyzed recordings of spikes from the awake cortex and concluded that the activity was not consistent with criticality (30-35)? These studies found activity that appeared to be weakly correlated, more consistent with a desynchronized regime. At first glance, these studies seem to contradict our hypothesis here of a low-dimensional critical subspace with large, correlated fluctuations; why might these studies have missed the critical subspace? A likely answer to this question comes from a comprehensive comparison of all attempts to seek evidence for criticality based on recordings with single neuron resolution in awake animals [23 cases in all including the 13 negative cases in references (30-35), a complete list to our knowledge at the time of writing this paper; table S1]. A distinguishing feature of the 10 cases that reported positive evidence for criticality was that they focused on relatively long timescale fluctuations; they considered coarse-grained spike counts in time bins larger than about 10 ms. In some cases, this temporal coarse-graining was a deliberate choice in the data analysis (34, 36, 37) but, more commonly, was due to the limited time resolution of experimental measurements, which is typical for calcium imaging (35, 38-43). The most strongly negative reports were based on analyses at the millisecond timescale, with less temporal coarse-graining. On the basis of this small meta-analysis of previous work and theoretical support for the importance of temporal coarse-graining (more on this in the results below), we refine our hypothesis. We

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hypothesize that desynchronized and critical subspaces coexist, but that the critical subspace is not apparent without temporal coarsegraining. To test this hypothesis, we recorded spike activity from the motor cortex of awake mice and compared our measurements to a ground-truth theoretical model of critical dynamics.

#### RESULTS

We performed extracellular spike recordings of up to 247 units in the motor cortex of awake, behaving mice (4 mice, 19 recordings,  $n = 104 \pm 43$  single units,  $44 \pm 18$  multi-units per recording,  $44 \pm 9$  min recording duration; Fig. 1A; more details in Materials and Methods). Our analysis of each recording begins with generating an  $N \times M$  spike count matrix (Fig. 1B), where N is the number of neurons and M is the number of time bins (M = recording duration divided by time bin duration  $\Delta T$ ). The entry in the *i*th row and *j*th column is the number of spikes fired by the *i*th unit during the *j*th time bin. We performed PCA on each spike count matrix and found that the activity is high-dimensional but much less than N-dimensional;  $45 \pm 0.05\%$  of PCs were needed to explain 95% of the variance (Fig. 1C).

Next, we performed avalanche analysis following previously established methods (*38*, 44–46). We first created a one-dimensional time series by summing spike counts across all *N* neurons. Then, we



Fig. 1. Low-dimensional critical subspace. (A) Mice were head-fixed and placed on top of a wheel, free to run, rest, groom, etc. High-density recordings were performed in the motor cortex, using a Neuropixels 1.0 probe. (B) Example spike count raster plot with 208 units. (C) Cumulative variance of original activity explained by increasing number of PCs. Dashed lines mark the number of PCs needed to explain 95% of the variance. (D) Spike count time series for the entire population (purple), for the subspace defined by PCs 1 to 5 (orange), and for the subspace defined by PCs 6 to 208 (gray). The dashed line represents the avalanche threshold. The shaded suprathreshold excursion represents one avalanche. (E) Distributions of avalanche size (S) for the original data (purple), reconstructed data using the first five PCs (orange), and after removing the first five components (gray). Distributions are shifted vertically for comparison. (F) Same as in (E), but for avalanche durations (T). (G) Avalanche sizes and durations follow the predicted scaling law for original data. (H) Raster and population sum for reconstructed data based on the first five PCs (orange). (I) Scaling laws obeyed for PC1 to PC5 reconstructed data. (J) The power-law range for avalanche size distributions as a function of PCs removed in ascending/descending order (blue/ red). Dimension of the critical subspace is defined as the number of PCs removed before the power-law range drops below 1.5 decades (dashed line). (K) Histogram of critical subspace dimension for all 19 recording sessions. The analyses in all panels were done with  $\Delta T = 50$  ms and an 8% threshold.

defined an avalanche as a period when this summed population activity exceeds a threshold (Fig. 1D; see Materials and Methods). According to theory (46-48), if the neural system operates near criticality, then avalanches should be diverse, with sizes (S) and durations (*T*) distributed according to power laws,  $P(S) \sim S^{-\tau}$  and P(T)~  $T^{-\tau}_{t}$ . We found good agreement with this prediction; avalanche sizes and durations were power-law-distributed over a wide range of scales (Fig. 1, E and F, purple). In addition, theory predicts that the exponents,  $\tau$  and  $\tau_b$  are not independent; they should be related to each other and to a third exponent  $(1/\sigma \upsilon z)$  according to the scaling law  $1/\sigma vz = (1 - \tau_t)/(1 - \tau)$  (46, 47), sometimes called the "crackling noise" scaling law. The third exponent, according to theory, relates avalanche sizes to duration as  $\langle S \rangle(T) \sim T^{1/\sigma \nu z}$ . The avalanches we measured conformed well to all these predictions (Fig. 1G). Thus, we conclude that the awake spike activity we observed here is in good agreement with predictions for a system operating at criticality. (As alluded to in Introduction, this finding depends on the choice of the timescale for the time bins  $\Delta T$ , which was set to 50 ms here and we will investigate further below.)

# Critical subspace is spanned by the first few principal components

Traditional avalanche analysis (Fig. 1, D to G, purple) is based on the one-dimensional population-summed activity, which, by definition, precludes insight into how the dynamics may be distributed across the multiple dimensions revealed by PCA (Fig. 1C). Do the scale-free avalanche dynamics exist in a subspace of the highdimensional population dynamics? If so, then the results of avalanche analysis should be robust to the removal of PCs that are not in the avalanche subspace. We tested this possibility first with an example case (Fig. 1, orange). We generated another  $N \times M$  activity matrix, reconstructed using only the first five PCs, excluding the other 203 dimensions (see Materials and Methods). The populationsummed time series based on the reconstructed data was very similar to the original (Fig. 1, D and H). Moreover, the avalanche statistics for this five-dimensional reconstruction remained in good agreement with predictions for criticality (Fig. 1, E, F, and I, orange). In contrast, if we reconstructed the data using PCs 6 to 208, then the avalanche sizes and durations were not power-law-distributed (Fig. 1, E and F, gray). Thus, for this example, we conclude that the critical dynamics are primarily contained within the subspace spanned by the first five PCs.

This example raises interesting questions. Is the dimensionality of this "critical subspace" exactly 5; is it higher or lower? Is the critical subspace always spanned by the first several PCs? To address these questions, we repeated the avalanche analysis using dimensionally reduced reconstructed data, but systematically varying the cutoff dimension  $d_c$  from 1 to N ( $d_c = 5$  in the example above). For each cutoff dimension, we performed avalanche analysis on two datasets; one was reconstructed using PCs 1 through  $d_c$ , and the other was reconstructed using PCs  $d_c + 1$  through N. For each case, we quantified the range of the avalanche size distribution that was wellfit by a power law. When reconstructed using PCs 1 through  $d_c$ , the power-law range remained high, largely independent of  $d_c$  (Fig. 1J, red). Consistent with the  $d_c = 5$  example above, this suggests that the avalanche statistics are not affected by the activity in the dimensions defined by the high PCs. When we reconstructed the data using PCs  $d_c$  through N, the power-law range markedly dropped when  $d_c$ exceeded a relatively small number (Fig. 1J, blue). Thus, the critical

subspace is strongly dependent on the first few PCs. This observation suggests a convenient quantitative definition for the dimensionality of the critical subspace—the number of PCs that can be removed (starting from PC1) before the power-law range drops below 1.5 decades. Using this definition, we found that the critical subspace rarely had a dimensionality larger than 3 (13 at most; Fig. 1K). Thus, we conclude that the critical subspace is always lowdimensional and is always spanned by the first few PCs.

# Critical subspace is stable and distributed across the population

Next, we sought to test the robustness of the critical subspace, accounting for two potentially important limitations of our experimental measurements. First, there could be slow non-stationarities on timescales comparable to our recording durations (40 to 50 min). Second, the recorded neurons are a tiny fraction of the full population. These facts raise the possibility that the critical subspace might not be stable in time and/or might be sensitive to the particular subset of neurons that was measured.

As a direct test of the temporal stability of the critical subspace, we performed a cross-validation analysis to quantify how similar the critical subspace is in the first half versus the second half of each recording (fig. S1). First, we performed PCA in the first half obtaining one set of PCs. Then, we performed PCA in the second half, obtaining a different set of PCs. If the critical subspace is stable, then we should be able to reconstruct activity equally well using PCs 1 through  $d_c$  from either the first or second half. To test this, we reconstructed the second-half activity in two ways: First, we used the PCs and scores from the second half; second, we used the PCs from the first half and scores obtained by projecting the second-half data onto the first-half PCs. Last, we quantified the similarity of these two reconstructions by creating a population-summed activity time series for each reconstruction and computing the Pearson's correlation of these two time series. We found that this correlation was above 0.9 for nearly every recording (fig. S1). Thus, we conclude that, despite the fact that animals can exhibit substantial changes in behavior and cortical state on long timescales, the critical subspace is stable over ~30 min timescales.

This stability of the critical subspace could be because the cortical state is not changing much in our mice or it could be because the critical subspace is stable despite a changing cortical state. To sort out these possibilities, we quantified the temporal stability of two established indicators of cortical state: the coefficient of variation of population-summed spike counts [CV<sub>SC</sub>; e.g., (49)] and the coefficient of variation of interspike intervals for the whole population [CV<sub>ISI</sub>; e.g., (50)]. Strongly synchronized states (like in anesthesia or deep sleep) result in large CV<sub>SC</sub> (around 2) and large CV<sub>ISI</sub> (around 2.5). We assessed CV<sub>SC</sub> (using  $\Delta T = 50$  ms) in a sliding 10-s window throughout each of our recordings. We found that the range of CV<sub>SC</sub> was only 0.35 to 0.55 (min-max), which indicates that our mice did not exhibit synchronized states, and is much smaller than previous studies that considered how avalanche statistics depend on cortical state [e.g., Fontenele et al. (49) studied a CV<sub>SC</sub> range of 0.3 to 2.3 due to changes in the cortical state under urethane anesthesia]. We found that CV<sub>ISI</sub>, again in a sliding 10-s window, also had a small range, only 1.05 to 1.25 (min-max), which is small compared to previous studies considering how avalanches depend on state [ e.g., Hahn et al. (50) studied a range of CV<sub>ISI</sub> from 1.1 to 2.6 due to changes in arousal, sleep, and anesthesia]. Our observations of small CV values that did not vary greatly over the recording duration indicate that the mice in our experiments remained in a stable alert state consistently throughout our recordings.

Another type of non-stationarity that could affect our results comes from changes in behavior. Our mice were free to run or rest on the wheel. In some of our recordings, the mice chose to run most of the time, while in other recordings, the mice ran very little (fig. S2). Previous studies suggest that running behavior can result in higher firing rates and less synchronized neural activity compared to resting (51-53). Such changes could alter the statistics of avalanches in the critical subspace or, alternatively, the critical subspace could be stable despite behavioral state changes between running and rest. To distinguish these possibilities, for each recording, we compared the fraction of time spent running to the power-law ranges and exponents for both avalanche sizes and durations. We found that these avalanche statistics were unrelated to time spent running (fig. S2), indicating that the critical subspace dynamics persist whether the mice are running or quiescent. This result is reminiscent of an observation in a previous study of monkeys performing a visuomotor task involving reaching arm movements (54). It was shown that avalanche statistics were mostly unchanged across pretask and task periods despite an increase in body motion.

Next, we tested whether the critical subspace was sensitive to which neurons were recorded, i.e., sensitivity to subsampling. This point is particularly important considering the low dimensionality of the critical subspace. Low dimensionality could indicate that a small number of neurons are involved (e.g., a four-dimensional subspace could simply reflect the activity of four highly active neurons). Alternatively, the critical subspace could be distributed across many neurons, with the low dimensionality reflecting shared variability across many neurons. To distinguish these possibilities, we compared the critical subspace based on the full recorded population to that based on smaller populations. The smaller populations were generated in two ways. First, to directly determine whether a small set of influential neurons is responsible for the critical subspace, we excluded the most important neurons (top 2% loadings) for each PC that was part of the critical subspace. Second, we randomly selected a fraction (0.2, 0.5, or 0.8) of the recorded neurons to be excluded from the analysis. We then ran PCA again on these smaller populations and created a population-summed time series based on a dimensionally reduced reconstruction with the same dimension as the original critical subspace. We found that discarding 20% of neurons caused very little change in the critical subspace (the correlation between the original and subsampled activity was >0.9 for 18 out of 19 recordings). Even discarding half of the recorded neurons resulted in a correlation above 0.8, on average. Similarly, when we excluded the most important neurons based on loadings, the correlation was also above 0.8, on average. These results (fig. S3) demonstrate that the critical subspace is distributed across a large population of neurons and is insensitive to subsampling the population.

# Temporal coarse-graining is required to reveal critical subspace

The activity in the critical subspace manifests as large amplitude fluctuations, coordinated across many neurons. Previous studies suggest that the spatiotemporal structure of such population activity can depend on the timescale of observation (34, 55-57). Moreover, the theory of critical phenomena suggests that temporal coarse-graining, i.e., excluding details at short timescales, may be required

to reveal universal properties of critical dynamics (58). The theory also suggests that systems with true critical dynamics have prominent fluctuations at slow timescales, a concept referred to as "critical slowing down" (58-60). Therefore, we next sought to determine how the critical subspace depends on the timescale of observation  $\Delta T$  (for the results in Fig. 1,  $\Delta T = 50$  ms). In many previous studies of neuronal avalanches based on spike recordings (31, 33, 34, 50), a common approach has been to set  $\Delta T$  to the average interspike interval (ISI) for the entire population of recorded neurons, following the approach pioneered by (61). We note, however, that this approach was originally developed for local field potential (LFP) peak events, not spikes. For our recordings here, the average singleneuron spike rate was about 3 Hz. Thus, for a typical recording of 200 neurons, the (ISI) was about 1.5 ms. Obviously, the population (ISI) will be even smaller in experiments with more recorded neurons. Here, we systematically investigated a range of  $\Delta T$  between 1 and 500 ms.

We first quantified how the importance of the first five PCs depends on  $\Delta T$ . We found that the variance explained by the first five PCs is relatively small for small  $\Delta T$  but rises sharply around  $\Delta T \sim 10$  ms (Fig. 2A). Next, we asked how many neurons are involved in the low dimensional subspace defined by the first  $d_c$  PCs. We measured the number of neurons engaged with (Pearson's correlation, >0.2) the population sum, reconstructed using only the subspace defined by PC1 to PCd<sub>c</sub>. We found that the number of neurons engaged with this low-dimensional subspace is very small when  $\Delta T$  is small but grows to a substantial fraction of the population for larger  $\Delta T$  (Fig. 2B). Thus, the importance of the first few PCs is hidden for small timescales and emerges only after temporal coarse-graining. In our initial example with  $\Delta T = 50$  ms, we saw that the activity of the full population was very similar to that reconstructed from PCs 1 to 5 (Fig. 1D). Next, we asked how the correlation between these two signals depends on  $\Delta T$ . We found that they were not strongly correlated for small  $\Delta T$ ; this correlation sharply increased around  $\Delta T \sim 10$  ms (Fig. 2C).

Next, we determined how  $\Delta T$  affects evidence for criticality based on avalanche analysis. We addressed this question for the full population-summed activity (Fig. 2D and fig. S4) and for the population sum reconstructed from the subspace defined by the first  $d_c$ PCs (Fig. 2, D to I) and found nearly identical results. We quantified the range of good power-law fit (number of decades; see Materials and Methods) for the avalanche size distribution; we interpret a larger power-law range as better evidence for criticality. For both the full population and the PC1 to  $PCd_c$  subspace (Fig. 2D), we found that, at small timescales, the power-law range is small and the avalanche distribution is better fit by an exponential distribution (fig. S5). The power-law range rises around  $\Delta T \sim 10$  ms. If we consider avalanches based on the PC  $d_c$ -N subspace, the power-law range is small for all  $\Delta T$  (Fig. 2D, gray). We note that the emergence of a large power-law range at larger  $\Delta T$  also depends on the threshold used for defining avalanches. Some previous studies have used a median threshold (27, 38), some have used the 35th percentile (35, 36), and many have used a zero threshold (30-34, 49, 50). Here, we found that if the threshold is set to zero, then the emergence of robust power-law statistics at larger  $\Delta T$  will be missed (fig. S4). Setting the threshold to zero does not make sense for reconstructed activity in the critical subspace because that reconstructed activity never reaches zero. This is why the top row of the heat maps in Figs. 2 (E and H) is black. Last, we examined the exponents of the power



**Fig. 2. Temporal coarse-graining reveals critical subspace.** (**A**) Total explained variance for the first five PCs is sensitive to temporal coarse-graining, sharply rising for  $\Delta T > 10$  ms, indicating the emergence of a low-dimensional subspace. (**B**) The number of neurons engaged with the subspace defined by the first  $d_c$  PCs (correlation >0.2) increases with  $\Delta T$ . (**C**) The correlation between the original summed population activity and that reconstructed using the first five PCs increases with  $\Delta T$ . (**D**) The power-law range is less than two decades for  $\Delta T < 10$  ms for the original data and PCs 1 to 5. For PCs 6 to *N*, the power-law range never exceeds two decades. (**E**) Example recording showing how the power-law range in the subspace defined by the first 1 to  $d_c$  PCs depends on  $\Delta T$  and the threshold used for defining avalanches. (**F**) Summary of how avalanche size power-law range depends on the threshold and  $\Delta T$  for all recordings. (**G**) For the 8% threshold, the measured exponent  $\tau$  (solid lines) of the size distribution power law decreases as  $\Delta T$  increases for  $\Delta T < 10$  ms but is relatively steady and close to  $\tau = 1.5$  for  $\Delta T > 10$  ms. Only for  $\Delta T > 10$  ms does the measured  $\tau$  agree with that predicted by the crackling noise scaling law (dashed). Inset shows how  $\tau$  depends on  $\Delta T$  and avalanche threshold for the example in (E). The dashed line marks the region with a large power-law range. (**H** to **J**) Same as (E) to (G), but for avalanche duration statistics. For all panels, solid lines represent the mean across all recordings and shaded areas represent standard error. For (E) to (J), all analyses were done using the subspace defined by PCs 1 through  $d_c$ , which is the critical subspace when  $\Delta T$  is large enough. Figure S4 recapitulates (E) to (J), based on the full population-summed activity instead of the critical subspace.

laws and found that for  $\Delta T < 10$  ms, the exponents did not agree with the crackling noise scaling laws predicted at criticality and varied markedly as  $\Delta T$  changes (Fig. 2, G and J). For larger  $\Delta T$ , the exponents were robust, less dependent on  $\Delta T$ , and were in good agreement with crackling noise scaling laws (Fig. 2, G and J). Consistent with these observations, we further note that the long-term stability of the critical subspace discussed above is apparent only for sufficiently large  $\Delta T$  (fig. S1). Together, the results in Fig. 2 show that evidence for criticality is robust in the critical subspace but will be missed if spike data are not sufficiently coarse-grained in time. In our experiments, the critical subspace emerges for timescales above about 10 ms, but, as we show in the next section, a more general criterion may be that  $\Delta T$  is greater than about 10(ISI).

### Theory of critical dynamics confirms experimental results

Does the necessity of temporal coarse-graining to find the critical subspace agree with the theory? Could the temporal coarse-graining

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we use mislead us, producing apparent critical dynamics from a system that is not actually at criticality? Here, we address these questions showing that our results agree with a simple model—the multivariate Hawkes process (62, 63)—but only if the model is tuned close to criticality. Our model is similar to branching processes and random walks (46, 58, 64), providing an established theoretical case of critical dynamics, but unlike many of these classic models, the Hawkes process treats time continuously. This is helpful for our goals here of studying how the dynamics depend on the timescale  $\Delta T$ . Discrete-time models often have  $\langle ISI \rangle$  well below the duration of one time step, which precludes quantitative comparison to previous studies which often set  $\Delta T = \langle ISI \rangle$ .

We set up our model with  $N = 10^4$  units with fixed, random connectivity. In a multivariate Hawkes process, each unit's spikes are drawn from an inhomogeneous Poisson process. At time *t*, the *i*th unit fires with rate  $\lambda_i(t)$  which depends on the recent history of spikes from other connected units

$$\lambda_i(t) = \mu + \sum_{j=1}^N C_{ij} \sum_{t_j < t} \phi(t - t_j)$$

where *C* is the connectivity matrix. The parameter  $\mu$  determines a baseline rate of noisy or spontaneous firing, independent of interactions among units. The second sum accounts for the spikes fired by the *j*th unit (at times *t<sub>j</sub>*) before time *t* and with a weight that decays exponentially  $\phi(t) = e^{-t}$ . We show numerically (Fig. 3C) that the magnitude of the largest eigenvalue of *C*, called  $\Lambda$  here, determines whether the system operates at criticality. To construct *C*, we first set  $C_{ij} = 1$  with probability 0.1 (otherwise  $C_{ij} = 0$ ) and then multiply *C* 

by a constant to obtain a particular  $\Lambda$ . For  $\Lambda$  well below 1, the units fire asynchronously, the model is subcritical. As  $\Lambda$  approaches 1, firing rates and fluctuations become large and correlated and the autocorrelation time diverges (Fig. 3, B and C);  $\Lambda = 1$  at criticality.

We performed avalanche analysis on the model population activity, as we did for the experiments. We analyzed the dynamics of a subset of only 200 units, neglecting the rest, to account for subsampling effects that are certainly present in our experiments and may be important for assessing critical dynamics (65–67). We note that our primary results are robust to different degrees of subsampling (fig. S6). When the model was near criticality ( $\Lambda = 0.99$ ), the dynamics closely matched our experimental results. Avalanche sizes



**Fig. 3. Low-dimensional model of critical dynamics agrees well with experiments.** (**A**) We study a multivariate Hawkes process with random connectivity (noise parameter  $\mu = 6$ ). (**B**) When the model is near criticality ( $\Lambda = 0.99$ ), the model generates population activity with large fluctuations (purple), which are abolished if the first PC is projected out (gray). (**C**) As  $\Lambda$  approaches 1 (criticality), the firing rate and the timescales of fluctuations diverge. (**D**) Near criticality and with sufficient temporal coarse-graining, the model avalanche sizes were power-law-distributed ( $\Delta T = 15\langle ISI \rangle$ , purple points), but the power law was obscured for insufficient temporal coarse-graining ( $\Delta T = 1\langle ISI \rangle$ , green points). Subcritical model dynamics were not power-law-distributed, with or without temporal coarse-graining (dashed lines). Experiments (light-colored lines) agree well with the model. The number of avalanches simulated in the model was matched to the average number observed experimentally, specifically for each  $\Delta T/\langle ISI \rangle$ . (**E**) Same as (D), but for avalanche duration. (**F**) With  $\Delta T = 15\langle ISI \rangle$ , the model agrees with the crackling noise scaling law. Inset: The experimentally observed scaling exponents (box plots) match well those from the model with  $\Lambda = 0.99$  (orange). (**G** and **H**) At criticality, the power-law range becomes large only for large  $\Delta T$ . The subcritical model never exhibits more than two decades of power-law range for all  $\Delta T$ . Individual experiments (gray) and mean across experiments (black) agree best with a model with  $\Lambda = 0.99$ . (**I**) The model critical subspace is one-dimensional; the power-law range collapses to less than 1.5 decades after excluding PC1. The inset shows size distributions with (purple) and without (gray) PC1.

and durations were well approximated by a power-law distribution and obeyed the crackling noise scaling law (Fig. 3, D to F), but only after sufficient temporal coarse-graining (approximately  $\Delta T > 10$  (ISI); Fig. 3, D, E, G, and H, and fig. S5). The power-law scaling exponents from the model matched well with our experiments (Fig. 3F, inset) and are consistent with previous experimental reports (49, 68). When the model was subcritical ( $\Lambda = 0.9$ ), the model dynamics were not power-law-distributed for any  $\Delta T$ , demonstrating that temporal coarse-graining does not produce evidence for criticality unless the system is near criticality (Fig. 3, D, E, G, and H, and fig. S5). We note that when we coarse-grained our experimental data using a  $\Delta T$  set to a specified factor of  $\langle ISI \rangle$  (instead of a specified number of milliseconds), the results of different experiments were more consistent with each other and in good quantitative agreement with the model (light colored lines in Fig. 3, D, E, G, and H).

Like the experiments, critical dynamics in the model are confined to a low-dimensional subspace. The model is essentially onedimensional. Removing the first PC fully removes the collective fluctuations in firing rates (Fig. 3B). Moreover, removing the first PC completely abolishes the power-law statistics of avalanches (Fig. 3I). In fig. S7, we show that the model can generate higher dimensional dynamics if we implement spatially dependent local connectivity. This may be similar to critical phenomena in other systems with spatial translational invariance (*69*). However, the neurons recorded from one high-density shank electrode like in our experiments are all within a few hundred micrometers from each other and, thus, are expected to have more spatially independent connectivity. Thus, we conclude that our experimental measurements are well-explained by the theory of low-dimensional critical dynamics.

# Desynchronized subspace coexists with the critical subspace

As discussed in Introduction, the standard point of view is that criticality is not compatible with desynchronized dynamical regimes; it is thought that the cortex must "choose" between criticality and a desynchronized regime. However, the fact that the critical subspace is low-dimensional raises an interesting possibility that challenges the standard view. Could there be a desynchronized dynamical regime that coexists with the critical subspace, in the same neural circuit, but in a different subspace?

As demonstrated in Fig. 1 (C, J, and K), the number of dimensions needed to explain a substantial fraction of the total variance is much greater than the dimension of the critical subspace. This suggests that the additional dimensions beyond the critical subspace are "important," in the sense that they are needed to explain much of the measured variance. What type of dynamics is contained in these additional dimensions? The basic mathematical facts of PCA require that these dimensions outside the critical subspace must have smaller fluctuations because the critical subspace spans the first few PCs. However, PCA does not tell us whether the dynamics in these dimensions have the characteristic features of a desynchronized regime: weak correlations among units, short autocorrelation timescales, and Gaussian distributed population activity. To answer these questions, we reconstructed our measured spike count dynamics in a low-dimensional subspace (PCs  $d_c$  + 1 through  $2d_c$ ) just beyond the cutoff dimension  $d_c$  of the critical subspace, as defined in Fig. 1 (J and K). Figure 4A shows an example recording where each subspace is six-dimensional (i.e.,  $d_c = 6$ ).

First, we summed the reconstructed dynamics across units to obtain a single population-summed activity for each subspace (Fig. 4A). As expected, the reconstructed population activity fluctuated with



**Fig. 4. Desynchronized subspace coexists with critical subspace.** (**A**) Wheel speed (black), and population-summed activity and rasters reconstructed from the critical subspace (top: purple,  $d_c = 6$  in this example) and the desynchronized subspace (bottom: blue). (**B** to **D**) The distribution of population-summed activity is broad, heavy-tailed, and skewed for the critical subspace, but narrow and near Gaussian for the desynchronized subspace. Box plots summarize all experiments (the box spans quartiles, and the white line is the median). (**E**) For the desynchronized subspace, the autocorrelation function drops sharply indicating short-range temporal correlations compared to the critical subspace. Inset: Time constants indicate the lag where the autocorrelation crosses 0.1 (yellow dashed line) for all experiments. (**F**) Mean pairwise correlations among reconstructed single-unit activities are closer to zero for the desynchronized subspace. (**G**) Wheel speed is more strongly correlated with the critical subspace than the desynchronized subspace.

much larger amplitude (larger variance; Fig. 4, C and D) in the critical subspace compared to the desynchronized subspace. In addition, we found that the distribution of population activity in the desynchronized subspace was close to Gaussian (low skewness), while the critical subspace had heavy-tailed, skewed distributions (Fig. 4D). Another defining feature of desynchronized regimes is a lack of longrange temporal correlations. We compared autocorrelation functions for the population activity in the two subspaces and found that the critical subspace had much greater correlations at long timescales (Fig. 4E). Last, we assessed pairwise correlations among units, using the reconstructed spike count rasters (Fig. 4A). Here, some caution is needed; the dimensionality of the subspace affects the basic nature of pairwise correlations for such reconstructed activity. Nonetheless, defining the dimensionality of the two subspaces to be equal allows for meaningful relative comparisons and we found that the critical subspace always had much higher pairwise correlations than the desynchronized subspace. Thus, we conclude that the dynamics in this subspace with the greatest variance, after removing the critical subspace, manifested all the defining features of desynchronized regimes: weak pairwise correlations, short-range temporal correlations, and Gaussian distributed population activity (9, 70).

Last, we asked how the critical subspace and the desynchronized subspace relate to the behavior of the mice. As the mice voluntarily moved their bodies (e.g., spontaneously running or resting), we measured the speed of the wheel that the mice were standing upon (Fig. 1A). We computed the Pearson's correlation of the wheel speed and the summed activity of each subspace (Fig. 4A). We found that the critical subspace was correlated with wheel speed while the desynchronized subspace was not (Fig. 4G). This observation is in line with previous reports that neuronal avalanches are correlated with body movements (*38*) and the first few PCs of cortical population activity are correlated with body movements (*1*).

#### DISCUSSION

We have shown that population spiking activity in the awake mouse motor cortex can be partitioned into different subspaces, each containing fundamentally different kinds of coordinated dynamics. The most prominent subspace—defined by the first few PCs—is home to critical dynamics with long-range temporal correlations, heavytailed distributions of activity, and multifaceted agreement with scaling laws predicted at criticality. This critical subspace is hidden if temporal coarse-graining is insufficient. The next most prominent dimensions contain desynchronized dynamics with weak spatiotemporal correlations and Gaussian distributed population activity.

These observations open several interesting questions and offer answers to several long-standing questions about the fundamental operating regime of cortical neuronal networks. One such longstanding question asks whether cortical circuits operate near criticality or not in the awake cortex. Many previous experiments with strong agreement with criticality theory were based on techniques that measure collective brain signals, like LFP (33, 54, 61, 68, 71, 72), wide field imaging (26, 73), and human brain imaging (71, 74). These collective signals represent an aggregate of the underlying spike activity of many individual neurons. However, when spikes recorded in awake animals have been analyzed directly, results have been less clear—some studies report support for criticality (34, 36, 38-42, 49, 75) while others do not (30-35). Considering that spikes are the fundamental information carriers underlying brain function, the equivocal support for criticality at the level of spike measurements has created skepticism and confusion surrounding the hypothesis (32, 33). Why is evidence for criticality clear in collective signals, but unclear in spike data? As we showed here, one important factor explaining discrepancies among previous spike recordings is that the existence of the critical subspace is clear only at larger timescales, beyond about 10(ISI). Our results suggest that the studies based on spikes with negative reports about criticality missed the evidence for criticality because they did not sufficiently coarse-grain in time (table S1). What about collective signals like LFP? One possibility is that collective signals, by their nature, may carry some degree of overlapping signals (LFP at two nearby locations can reflect signals from the same source neurons), which results in spurious correlations that could be mistaken for criticality (76). Considering our results here, another possibility is that the coordinated activity in the critical subspace is apparent in measurements of collective signals like LFP, but the desynchronized subspace is hidden from collective signals because it is weakly coordinated. Thus, measuring collective signals may effectively filter out the desynchronized subspace, leaving only the critical subspace signals.

What about previous studies of avalanches based on spikes in non-awake animals? One study showed that using  $\Delta T = \langle ISI \rangle$  (i.e., no coarse-graining), anesthetized rats can show strong evidence for criticality (49). Another study also used  $\Delta T = \langle ISI \rangle$  and concluded that sleeping and anesthetized animals were closer to criticality than awake animals (50). Our results here suggest that these previous studies may have found stronger evidence for criticality in the awake state if they used more substantial temporal coarse-graining.

Several recent studies have proposed that critical phenomena in neural systems might be fundamentally high-dimensional (77-81). Do these studies contradict our work here? Several of these previous studies focused on edge-of-chaos (EOC) criticality, which, unlike our results here, is thought to occur without large fluctuations at the population level (77, 80, 81). In other words, EOC criticality would manifest with no avalanches using our definition of avalanches here. In this basic sense, our experimental results are inconsistent with EOC criticality-we observe prominent large amplitude fluctuations and power-law-distributed avalanches. In other studies (69, 77-79), criticality was hypothesized to be high-dimensional based on data analysis and concepts adapted from traditional renormalization groups in systems with spatial translational invariance (similar to the Ising model, for example). Our experimental results do not directly confirm or deny this hypothesis, but our model shows a clear case of low-dimensional criticality; thus, criticality in neural systems is not required to be high-dimensional. We further clarify this point in fig. S7; we show how a transition from low-dimensional to high-dimensional criticality can result from tuning the model connectivity from global to local and introducing approximate spatial translational invariance. (We note that the autocorrelation functions reported in Fig. 4 can also depend on whether connectivity is local or global (82).) These theoretical considerations suggest that we observed a low-dimensional critical subspace in our experiments because we measured neurons from a local patch of cortex (approximately one cortical column) using a single shank Neuropixels probe. Within this small, local population of recorded neurons connectivity is approximately global. Thus, we might expect to find a higher dimensional critical subspace based on more spatially widespread recordings, as found in recent functional magnetic resonance imaging measurements, for example (69).

As discussed in Introduction, another controversy that our results may help resolve is the question of cortical state: Are cortical population dynamics weakly or strongly correlated? Our results show that this question may be a false dichotomy; we show that weakly correlated dynamics can coexist with relatively strongly coordinated dynamics by separating them into different subspaces. Do these two different subspaces perform different brain functions? While many studies have associated specific functions with specific subspaces (83-87), they typically have not tested whether the dynamics in these subspaces house critical dynamics or more desynchronized dynamics. Our results here suggest that the critical subspace is related to spontaneous, voluntary body movements, while the desynchronized subspace is unrelated to these movements (Fig. 4, A and G). More support for this possibility comes from considering two studies (1, 38). Stringer et al. (1) showed that visual input is encoded in one subspace with relatively small fluctuations (similar to our desynchronized subspace), while some body movements (e.g., running and whisking) are encoded in a different subspace defined by the first few PCs (similar to our critical subspace). Moreover, Jones et al. (38) reanalyzed the data from Stringer et al. (1) and found that subsets of neurons (a subset is a type of subspace) with the strongest correlations to body movements also exhibited power-law avalanche dynamics as we observed in our critical subspace here. Together, these results suggest that sensory input might be encoded in the desynchronized subspace we found here, while motor output may be encoded in the critical subspace. This idea is also in line with a previous study that showed that certain "stiff" dimensions (perhaps like our critical subspace) are responsible for changes in cortical state, while other "sloppy" dimensions (perhaps like our desynchronized subspace) encode sensory responses (88).

The coexistence of a critical subspace and a desynchronized subspace is also consistent with previous studies of population coupling (89, 90). Our Fig. 2C shows that the first few PCs (i.e., the critical subspace) are very strongly correlated with the total populationsummed activity. Thus, neurons with strong population coupling ("chorister neurons") should be interpreted as strongly coupled to the critical subspace. In addition, the soloist neurons (those weakly coupled to the population) are likely to be coupled to the desynchronized subspace. The diversity of population coupling shown by Okun *et al.* (89) is in line with our Fig. 2B, which shows that a substantial fraction of our measured neurons are choristers and implies that many other neurons are soloists, but this observation will be obscured without sufficient temporal coarse-graining.

A line of previous studies of attention and "on-off" dynamics is likely to be related to the critical subspace we identified here (91-93). In these studies, large amplitude fluctuations, coordinated across layers and cortical regions, were observed in the monkey visual cortex. These fluctuations are qualitatively similar to the scale-free dynamics that we observed here in the critical subspace. These studies showed that the degree of coordination depended on visual attention and that the monkey's performance on attention-related tasks varied in time, depending on the peaks and troughs of individual fluctuations. If the "on" periods in these studies are like the avalanches we studied here, then this suggests a previously unappreciated role for critical dynamics and avalanches in attention-related brain function. Moreover, it suggests that such "on-off" dynamics in these studies might coexist with a desynchronized subspace, raising questions about how attention-related functions might be split between these subspaces.

More generally, our results raise many interesting questions about how a neural system might implement the segregation of functions in different subspaces. How do different subspaces interact? How do the subspaces, identified based on measured activity (e.g. using PCA), relate to the anatomical connections among local neurons and/or inputs from distant neurons? How might a neuron selectively interact with the critical subspace rather than the desynchronized subspace? Partial answers to these questions come from considering the nature of synapses and dendrites. Consider a neuron that is downstream from the population we measured in our experiments. Many axons from the measured population might terminate on the dendritic tree of this downstream neuron. Each synapse has a different "strength"; thus, the effective input is a linear combination, weighted according to synaptic strengths. Such a weighted linear combination is nothing more than a projection onto a subspace; with the right combination of synaptic weights, the downstream neuron could selectively sample from the critical subspace. Moreover, the coarse-graining timescale  $\Delta T$  considered throughout our paper can be directly related to the timescale of synaptic integration, which is around 10 to 50 ms. Ultimately, the dendritic tree sums up these weighted inputs conveying a onedimensional signal to the soma, quite similar to the populationsummed activity we study here. Thus, the biophysics of synaptic integration effectively executes an operation that is quite like the data analysis we performed here: coarse grain temporally, project onto a subspace, and sum over the population in that subspace. This reasoning loosely sketches some aspects of how neurons might use subspaces, but further studies will be needed to understand more fully the interesting possible functional implications and implementation mechanics of critical and desynchronized subspaces.

# MATERIALS AND METHODS

# Animals

All procedures followed the Guide for the Care and Use of Laboratory Animals of the National Institutes of Health and were approved by University of Arkansas Institutional Animal Care and Use Committee (protocol 21022). We studied adult male C57BL6/6J mice (The Jackson Laboratory). After acclimatization to handling, a small aluminum plate (0.5 g) was attached to the skull with dental cement. Then, mice were trained for head fixation for 20 sessions, gradually increasing in duration. At the time of recordings, the mice weighed  $\approx$  28 g and were 21 to 23 weeks old. One to 2 days before the first recording for each mouse, a craniotomy (2-mm diameter) was performed over the right motor cortex (anterior-posterior = 0 mm, medial-lateral = 1 mm). Each recording day began with a brief period of isoflurane anesthesia to expose the craniotomy and head fix the mouse. The mice were free to run, sit, groom, and walk for the entire duration (45 min) of each recording. During recordings, after inserting the electrode array, the craniotomy was covered with gel-foam pieces soaked in a sterile phosphate buffer solution.

#### Electrophysiology

The extracellular voltage was recorded using Neuropixels probes (version 1.0, IMEC) consisting of an electrode shank (width: 70  $\mu$ m, length: 10 mm, thickness: 100  $\mu$ m) of 960 total sites laid out in a checkerboard pattern with contacts (18- $\mu$ m site-to-site separation),

enabling up to 384 recording channels. On the recording day, following head fixation, the Neuropixels probe was inserted to a tip depth of approximately 1.2 mm, ensuring that the active recording sites spanned all cortical layers. An Ag/AgCl pellet was used as ground and placed in the saline-soaked gel foam covering the craniotomy. The ground pellet wire was soldered to the Neuropixel midway along the ribbon cable. Electrophysiological data were collected (30 kHz) using SpikeGLX software. Spike sorting was performed using Kilosort 3.0 (https://github.com/MouseLand/Kilosort) and then manually curated using phy (https://github.com/cortex-lab/phy) (94).

# **Data analysis**

# PCA

We performed PCA in Python using the function 'decomposition. PCA' from the package 'sklearn'. Let Z be a spike count matrix with *M* rows (number of time bins) and *N* columns (number of neurons). Then, PCA generates V which contains the PCs, i.e., the eigenvectors of the covariance matrix of ZV has N rows and N columns (one column for each eigenvector, i.e., one column for each PC). We calculated the % variance explained by a set of PCs as the sum of their corresponding eigenvalues of V (reported in Figs. 1C and 2A). To reconstruct data based on a subset of PCs (e.g., PCs 1 to K), we first define the  $M \times K$  projection matrix B by , where is  $N \times K$ , including the first K columns of V. Then, the reconstructed activity is  $=B^{T}=Z^{T}$ Avalanche analysis

The first step in avalanche analysis was to create a spike count matrix Z, where  $Z_{ti}$  is the number of spikes fired by unit *j* during time bin t. Next, the population-summed spike count time series X was created by summing spike counts over all neurons at each time bin,  $X_t = \sum_i Z_{ij}$ . The threshold  $\Theta$  used for avalanche detection was

defined as some percentile of X. By definition, an avalanche begins when X exceeds the threshold and ends when X returns below the threshold. The size *S* of an avalanche is defined as  $S = \sum_{t_i}^{t_f} (X_t - \Theta)$ , where the start and end times of the avalanche are  $t_i$  and  $t_f$ , respectively. Avalanche duration is defined as  $T = t_f - t_i$ .

To assess whether avalanche sizes and durations were distributed according to a power law and to obtain power-law exponents and ranges, we built on previously developed maximum likelihood methods (38, 68, 95, 96). Briefly, the fitting algorithm identifies the best fit truncated power law that meets a predefined goodnessof-fit criterion. There are three fitting parameters: the minimum avalanche size  $x_m$ , the maximum avalanche size  $x_M$ , and the powerlaw exponent  $\tau$ . The following steps summarize the algorithm. First, events with a size/duration less than  $x_m$  or larger than  $x_M$  were excluded. Second, the maximum likelihood power-law exponent was calculated. Third, we assessed the goodness of fit. We repeated these four steps for all the possible pairs of  $x_m$  and  $x_M$  values, in the end, identifying the largest power-law range that passed the goodness-of-fit criterion. We define power-law range as the number of decades of power-law scaling  $\log_{10}(x_M/x_m)$ . We note that this algorithm is independent of any choice of bins used to create the PDF plots in the paper.

The primary improvement we made compared to our most recently published methods (38) was to make our goodness-of-fit criterion less sensitive to sample size (number of avalanches) and more computationally efficient. For a given  $x_m$ ,  $x_M$ , and  $\tau$ , goodness of fit was quantified as follows. First, we created a cumulative distribution function (CDF) of the real data (excluding samples outside

the range  $x_m$  to  $x_M$ ). Second, we define a theoretical CDF for a truncated power law with the same range and exponent. Third, we define a region delimited by upper and lower bounds defined as the theoretical CDF +0.03 and -0.03, respectively. Fourth, we resample the real CDF at 10 logarithmically spaced values per decade. Fifth, we calculated the fraction F of resampled points in the CDF of the real data that fell within  $\pm 0.03$  bounds of the theoretical CDF. F is our goodness-of-fit measure. F = 1 means that the entire range of the real data varies less than 3% from a perfect power law. We sought the fit with the largest power-law range that meets the goodness-offit criterion F > 0.8.

### Crackling noise scaling law

In Fig. 2 (G and J), we reported measured exponents  $\tau$  and  $\tau_t$  for avalanche size and duration distributions, respectively. We also reported a predicted exponent based on the crackling noise scaling law, which states  $\langle S \rangle (T) \sim T^{1/\sigma \nu z}$ , where  $1/\sigma \upsilon z = (1 - \tau_t)/(1 - \tau)$  (46, 47). To calculate the predicted exponents we first measured  $1/\sigma vz$ directly from the data, using a linear best fit to log(S) versus log(T)plot (like those in Fig. 1, G and I). The linear fit to measure  $1/\sigma vz$ was limited to the range of avalanche durations identified by the power-law fitting algorithm. Then, we used the empirically determined size exponent,  $\tau$ , to obtain a predicted duration exponent  $\tau_{t,\text{pred}} = 1 - \frac{1-\tau}{\sigma \nu z}$ , and we used the empirically determined duration exponent,  $\tau_t$ , to obtain a predicted size exponent  $\tau_{\text{pred}} = 1 - \sigma \nu z (1 - \tau_t)$ .

Decorrelated subspace

The analysis presented in Fig. 4, began with making a spike count matrix with time bin size  $\Delta T = 50$  ms. Next, the activity was reconstructed using different dimensions as described above. The third step was to perform a band pass filter including 0.1 to 100 Hz on the reconstructed activity time series for each unit. Last, the activity distributions, activity variance and skewness, autocorrelation functions, and pairwise correlations were analyzed. The correlation time for the autocorrelation functions was calculated as the lag beyond which the correlation drops below 0.1. The use of a filter with a lower cutoff frequency avoids potential non-stationarities at long timescales in the experiments. However, close to criticality, there may be relevant timescales slower than 0.1 Hz. Thus, the autocorrelation timescales reported in Fig. 4 for the critical subspace should be interpreted as an approximate lower bound.

#### **Computational model**

The numerical implementation of the multivariate Hawkes process described in Fig. 3 and the corresponding text was carried out using the algorithm developed by Dassios and Zhao (97). Briefly, this algorithm exactly generates a Hawkes process by sampling interspike intervals directly via the underlying analytic distribution functions. Our code for simulating the Hawkes process is freely available for download on Figshare: https://doi.org/10.6084/m9.figshare.24530434.v1.

#### Supplementary Materials

This PDF file includes: Supplementary Text Figs. S1 to S7 Table S1 References

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