Scale-specific dynamics of high-amplitude bursts in EEG capture behaviorally meaningful variability

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A B S T R A C T

Cascading high-amplitude bursts in neural activity, termed avalanches, are thought to provide insight into the complex spatially distributed interactions in neural systems. In human neuroimaging, for example, avalanches occurring during resting-state show scale-invariant dynamics, supporting the hypothesis that the brain operates near a critical point that enables long range spatial communication. In fact, it has been suggested that such scale-invariant dynamics, characterized by a power-law distribution in these avalanches, are universal in neural systems and emerge through a common mechanism. While the analysis of avalanches and subsequent criticality is increasingly seen as a framework for using complex systems theory to understand brain function, it is unclear how the framework would account for the omnipresent cognitive variability, whether across individuals or tasks. To address this, we analyzed avalanches in the EEG activity of healthy humans during rest as well as two distinct task conditions that varied in cognitive demands and produced behavioral measures unique to each individual. In both rest and task conditions we observed that avalanche dynamics demonstrate scale-invariant characteristics, but differ in their specific features, demonstrating individual variability. Using a new metric we call normalized engagement, which estimates the likelihood for a brain region to produce high-amplitude bursts, we also investigated regional features of avalanche dynamics. Normalized engagement showed not only the expected individual and task dependent variability, but also scale-specificity that correlated with individual behavior. Our results suggest that the study of avalanches in human brain activity provides a tool to assess cognitive variability. Our findings expand our understanding of avalanche features and are supportive of the emerging theoretical idea that the dynamics of an active human brain operate close to a critical-like region and not a singular critical-state.

1. Introduction

Cognition is believed to require a widespread coordination of spatiotemporal neural activity. Though such coordination appears to be ubiquitous across tasks and conditions, the underlying principles of how this coordination occurs and how it may relate to individualized behavior are not yet well understood. Previous studies have proposed that cascading high-amplitude bursts in neural activity, also known as avalanches, provide a novel marker of characteristic complex dynamics that relate to brain function (Ariv et al., 2015; 2016; Beggs and Plenz, 2003; Fukunaga et al., 2006; Palva et al., 2013; Priesemann et al., 2013; Shew et al., 2015; Shriki et al., 2013; Tagliazucchi et al., 2012). In terms of analysis of avalanches in the human brain activity, the focus has been on resting state activity, where several groups have demonstrated power-law probability distributions of avalanche sizes and durations (Meisel et al., 2013; Priesemann et al., 2013; Shriki et al., 2013; Tagliazucchi et al., 2012). Power-law distributions are interesting in that they imply the absence of a characteristic scale of activity or scale-invariance. Systems with scale-invariant characteristics demonstrate efficient integration and segregation of information both locally and globally. Another observed attribute of neural avalanches has been that their branching process, i.e., how the dynamics evolve over time, demonstrates a balance between ongoing and upcoming neural activity (Lombardi et al., 2012), which is thought to be indicative of a macroscopic balance in excitation and inhibition (Poil et al., 2012). Interestingly, these statistical features of avalanche dynamics observed at the macro-scale (measured...
during resting state (fMRI, MEG, and EEG) were found consistent with what has been observed in smaller scale neuronal assemblies (Beggs and Plenz, 2003; Friedman et al., 2012; Mazzoni et al., 2007; Pasquale et al., 2008) and in vivo studies (Gireesh and Plenz, 2008; Miller et al., 2019; Petermann et al., 2009; Ponce-Alvarez et al., 2018; Shew et al., 2015). These observations of brain dynamics, based on analyses adopted from statistical physics (Beggs and Timme, 2012; Sethna et al., 2001), have been the basis for the hypothesis that the brain operates near criticality (Beggs and Plenz, 2003; Cocchi et al., 2017; Linkenkaer-Hansen et al., 2001), a special point in system’s dynamical phase space, that separates order from disorder, providing for scale-invariance and subsequently, dynamical and functional diversity (Beggs, 2008; Haldeman and Beggs, 2005; Shew and Plenz, 2013; Shew et al., 2009).

Despite these observations that critical-like features appear in experimental recordings across systems, questions surrounding the ‘criticality’ hypothesis have not been fully explored. For example, the effect of stimulus and task-evoked activity on avalanche dynamics is not well understood (Papo, 2014) and has only been partially investigated (Arviv et al., 2015; Fagerholm et al., 2015; Shew et al., 2015; Yu et al., 2017) with some studies indicating deviation from a critical state during task demands (Fagerholm et al., 2015; Shew et al., 2015). Additionally, the proposition that a single universality class exists and serves as a unifying mechanism for observed scale-invariance and criticality (Fontenele et al., 2019; Friedman et al., 2012) theoretically requires identical scaling features and a single critical point for all neural systems. However, given the variability of neural systems, compared to more traditional physical systems studied using this analytical approach (e.g. magnetic systems) (Yeomans, 1992), the ‘universality’ proposition fails to provide an explanation for the variability often observed in the study of neural avalanches (Dehghani et al., 2012; Hahn et al., 2017; Yaghoubi et al., 2018). Existence of criticality requires a delicate balance in system’s dynamics and a single critical point requires a fine tuning of parameters to achieve this balance. Such a fine tuning, although can be modeled to emerge through local synaptic connections (Zeraati et al., 2021), appears unlikely in an entire complex system like the active brain, considering the inherent nonstationarity of brain processes (Kaplan et al., 2005), its functional modularity (Chavez et al., 2010), and the inhomogeneity of neuronal elements (Moretti and Muñoz, 2013). Moreover, a global organization of avalanches, probed by studying the probability distribution of avalanche sizes and durations, does not provide insight into the spatiotemporal cascading dynamics itself, which is of neuroscientific importance.

Here, we aim to address several of these issues by asking how previously observed scale-invariant, near-critical dynamics of avalanches in the ‘resting’ brain (i.e., no controlled task) is related to state changes during stimulus-driven cognitive processing. We examined avalanches of neuronal activity from multi-channel scalp EEG, while participants underwent three sequential experimental conditions (Fig. 1A). The conditions systematically varied in cognitive complexity, ranging from (i) resting state (eyes open), (ii) passive viewing of emotionally charged images, and (iii) active viewing of negatively charged images before rating the emotional intensity. Emotional responses are ubiquitous in our everyday lives and have been shown to affect brain activity by predominantly engaging neural activity in frontal and parietal regions of the brain at distinguishable timescales (Buhle et al., 2014; Kohn et al., 2014). Our relatively simple experimental design allowed us to investigate avalanche properties as a function of cognitive complexity, and enabled us to consider aspects of the ‘criticality’ hypothesis as it relates to behaviorally meaningful variability.

2. Methods

2.1. Participants

36 healthy adults were recruited with average age 32.2 ± 7. This study was carried out in accordance with the accredited Institutional Review Board at US Army Research Laboratory and conducted in compliance with the US Army Research Laboratory Human Research Protection Program (32 Code of Federal Regulations 219 and Department of Defense Instruction 3216.01). All participants gave informed, written consent.

2.2. Experimental design

Participants performed three sequential experimental conditions (Fig. 1A). The conditions systematically varied in cognitive complexity, ranging from (i) resting state (eyes open) with no explicit task, (ii) passive viewing of emotionally charged images with no explicit judgment, and (iii) active viewing of emotionally charged images before rating the emotional intensity. For passive viewing, subjects viewed images with positive, negative, and neutral valence. For the active viewing task, only negatively charged images were shown. Participants used the numeric keypad on the keyboard to rate their emotional intensity in response to each image, for a total of 60 images, on a scale ranging from 1 (low emotional intensity) to 9 (high emotional intensity). Experimental timelines for these tasks are shown in Fig. 1A and further details can be found in reference (Roy et al., 2019) which included a subset of participants from this current study.

2.3. EEG data acquisition and pre-processing

Continuous EEG recordings were captured via the Biosemi ActiveTwo EEG system (Amsterdam, Netherlands) equipped with standard Ag/AgCl electrodes from 64 sites on the scalp. Reference electrodes were placed on the mastoids. VEOG and HEOG external electrodes were used around the eyes during passive viewing and active viewing to ensure that our analysis was not affected by eye-blinks (see Supplementary Fig. S1). Raw EEG measurements were pre-processed using in-house software in MATLAB (Mathworks, Inc., Natick, MA, USA) and the EEGLAB toolbox (Delorme and Makeig, 2004). The pre-processing pipeline consisted of four steps (the PREP approach, Bigdely-Shamlo et al., 2015): (1) resampling the raw EEG to 256 Hz; (2) line noise removal via a frequency-domain (multitaper) regression technique to remove 60 Hz and harmonics present in the signal; (3) a robust average reference with a Huber mean; and (4) artifact subspace reconstruction to remove residual artifact (the standard deviation cutoff parameter was set to 10). Data from all the 64 sensors were used for further analysis.

2.4. Identification of avalanches in the EEG activity

Neuronal avalanches are the cascading bursts of neuronal firing, and in macroscopic brain imaging data, avalanches are identified as spatiotemporal clusters of high-amplitude neural activity (Arviv et al., 2015; Meisel et al., 2013; Priesemann et al., 2013). Here, we used 3 minutes of recorded data for each participant and condition to define high-amplitude activity as all the events when the EEG amplitude exceeded a chosen threshold of ±3 standard deviations away from the mean for each EEG sensor (black circles, Fig. 1B) (Shew et al., 2015; Shriki et al., 2013). Next, we identified avalanches as clusters of events combined across all the sensors. These clusters were identified such that the temporally distant events were separated, while the events in close temporal vicinity were included in the same avalanche. We defined temporal vicinity as a pre-identified temporal gap or correlation window  𝛿  , and therefore, an avalanche was identified as a cluster of events such that the temporal interval between any two consecutive events does not exceed  𝛿 . The lowest possible value of  𝛿 is the sampling interval (SI) which in this case is 1/256 s or 3.91 ms. However, following previous work, as shown in Fig. 1C, we chose  𝛿 adaptively within each individual and condition as the average inter-event-interval (  <  𝐼𝐸𝐼 >  ) between all the observed, consecutive events (Priesemann et al., 2013; Shew et al., 2015; Shriki et al., 2013).

\[
\Delta t = \frac{1}{M} \sum_{i=1}^{M} I.E.I
\]
Typically, the average value of IEI (i.e., <IEL>) varied across participants and conditions due to the observed variability in high-amplitude events. Represented as the number of sampling intervals, observed <IEL> values were 6.51±1.01, 7.93±1.72, and 7.3±1.75 for the rest, passive viewing, and active viewing condition, respectively, which corresponded to Δt values of 27.67 ± 4.42 ms, 32.88 ± 7.01 ms, and 30.38 ± 7.06 ms, respectively.

Here, Δt serves as a correlation window in a sense that it determines if two observed events are part of the same avalanche (their interval ≤ Δt) or not. Therefore, a relatively lower (or higher) value of Δt results in relatively smaller (or larger) avalanche sizes. In Supplementary Fig. S2, we discuss the effect of varying Δt and show the robustness of results discussed here.

2.5. Avalanche size and duration

After identifying avalanches, the size of an avalanche (S) was determined as the total number of events within the avalanche. Avalanches of the same size can have different spatiotemporal spreads, as demonstrated by the yellow cluster and the purple cluster in Fig. 1D, both having a size S=11. We also defined avalanche duration (D) as the number of time steps included between the first and the last event. Here, a single time step represents the sampling interval.

2.6. Power-law fitting and quality of fit

To evaluate the global-scale (whole-brain) organization of avalanches, we used a maximum likelihood method to fit a head and tail truncated power-law to the probability distributions of avalanche size and duration as described previously (Klaus et al., 2011; Shew et al., 2015). Avalanche probability distributions were calculated by including all the observed avalanches across all the sensors for a given subject and condition. The fitting function used was

\[ P(S) = S^{-\gamma} \sum_{x_{\text{min}}}^{x_{\text{max}}} x^{-\gamma} \]

(2)

Here, \( r \) is a fitting parameter and is the exponent of the power-law. For fitting, values between 1 and 5 were tried with a step size of 0.01. Another fitting parameter is \( x_{\text{min}} \) which represented the lower bound of the fit. We restricted its value to be <15. Finally, \( x_{\text{max}} \) here denotes the upper bound of the fit and its value was chosen as the maximum value for which the avalanche distribution showed significant fit to a power-law. To ensure the validity of the fitted power-law, we tested the quality of the fit by computing the quality factor \( q \) (Clauset et al., 2009; Shew et al., 2015; Touboul and Destexhe, 2010). For this computation, we used an established approach (Clauset et al., 2009) and constructed 1000 synthetic data sets which had the same number of observations as the fitted experimental data and were drawn from an ideal power-law with the same fitting parameters as the experimental data. We then calculated Kolmogorov-Smirnov (KS) statistics between synthetic data sets and their own power-law fit models. \( q \) is the fraction of these synthetic KS-statistics which were greater than the KS-statistics for the experimental data. A power-law fit was deemed significant with a conservative criterion of \( q \geq 0.1 \) (Clauset et al., 2009; Shew et al., 2015).

2.7. Calculating the branching parameter

We extracted another feature of avalanches termed the ‘branching parameter’ (\( \sigma \)) which represents the progression of events within an avalanche. A branching parameter value close to 1 implies criticality (Arviv et al., 2015; Beggs and Plenz, 2003). We defined a macroscopic branching parameter as the average ratio of events in the second and the first half of the observed avalanches to capture how an avalanche rises and how it dies down, i.e.,

\[ \sigma = 1/N \sum_{i=1}^{N} n_i^{SH}/n_i^{FH}. \]

(3)

Here, \( i \) represents an avalanche, \( n \) represents the number of events in the avalanche \( i \), \( SH \) and \( FH \) represent the second and the first half of the total avalanche duration, and \( N \) represents the total number of avalanches in the given data segment. We defined the avalanche duration as the number of time steps included between the first and the last event of an avalanche. Therefore, the lowest duration for an avalanche can be 1 and in this case, the branching parameter was 0. For avalanches with an odd number of time steps, events at the middle time point were divided equally within SH and FH. For example, if the duration of an avalanche was 9, with 7 events on the 5th time step, 3.5 events were added to both SH and FH.

At a critical state, temporal distribution of events within an avalanche traces a perfectly symmetric, inverted parabola (Miller et al., 2019) which would lead to a branching parameter of 1. As discussed in Supplementary Fig. S5, the branching parameter was originally defined in smaller neural assemblies as the ratio of events at successive time points (Beggs and Plenz, 2003), however, its adaptation in a macroscopic neural system is not straightforward and must be calculated using different computational methods. In the Supplementary Fig. S5, we compare and discuss these different methods in detail.
2.8. Comparing observed avalanche features between conditions

We used a paired t-test to assess if computed global-level avalanche features demonstrate significant group differences due to the change in experimental condition. These features included fitted power-law exponents and branching parameters.

2.9. Calculating normalized engagement

We analyzed localized features of avalanche dynamics by calculating the ‘normalized engagement’ (NE) of each EEG sensor in producing avalanches. We defined engagement as the average number of ‘events’ that a given sensor contributes to observed avalanches. If \( N_i \) is the total number of avalanches under consideration and \( n_i \) is the total number of events observed on a sensor \( i \) during these avalanches, the engagement of the sensor \( E_i = n_i/N_i \). We computed normalized engagement by normalizing each \( E_i \) by the maximum value of \( E_i \) across sensors, and consequently, obtained values bounded between 0 and 1. For each subject and condition, we calculated NEs during all the observed avalanches as well as during avalanches with specific ranges of sizes namely short (1–10 events), moderate (11–100 events), and persistent (101–1000 events).

2.10. Identifying task-evoked changes in avalanche dynamics

We used NE to identify regions of interest (ROIs) which showed significant task-evoked changes in avalanche dynamics. ROIs were those EEG sensors for which the distributions of NE values were significantly different between rest and active viewing, as per a paired t-test. Across these paired t-tests, we applied the FDR correction for multiple comparisons and used a corrected p-value below 0.05 to define significance.

2.11. Statistical analysis

In order to test the relationship between avalanche dynamics and emotional ratings reported during the active viewing task, multiple regression analyses were conducted. The emotional rating (\( Y \)) for each participant was calculated as the average rating reported across all trials. As independent variables in the regression model, we used average NE values across the identified ROIs. In a data-driven manner, ROIs were defined lobe-wise (frontal, central, occipital) and for different ranges of avalanche size i.e., for short avalanches (S-frontal, S-central, and S-occipital), for moderate avalanches (M-frontal, M-central, and M-occipital), and for persistent avalanches (P-frontal, P-central, and P-occipital). Prior to multiple regression analysis, all the variables were mean-centered and tested to be normally distributed using the Shapiro-Wilk’s test (\( p > .05 \)). We also tested the correlation between these variables to avoid using correlated predictor variables in the model.

3. Results

3.1. Global-scale avalanche features vary between individuals and tasks

In our first analysis, we examined how the global, whole-brain functional activity is potentially represented through EEG avalanche dynamics, and varies across our three experimental conditions. Previous findings have shown that the probability distribution of avalanche size during resting state fits a power-law, such that \( P(S) \sim S^{-\alpha} \), where \( \alpha \) is a positive valued exponent (Meisel et al., 2013; Priesemann et al., 2013; Shokri et al., 2013; Tagliazucchi et al., 2012). We examined if the distributions of avalanche sizes, derived from EEG, fit the power-law behavior both for resting state as well as the two task conditions. As shown in Fig. 2A, in our data (circles), avalanche sizes spanned a little over two orders of magnitude; therefore, we fit the data to a truncated power-law (see Methods) (Clauset et al., 2009; Klaus et al., 2011; Shew et al., 2015; Yu et al., 2014). A fitted power-law is shown by the dashed line.

Here, \( x_{\text{min}} \) and \( x_{\text{max}} \) represent the lower and upper bounds of the fit, describing the minimum and maximum values of avalanche size that can be fitted through power-law probability dynamics. To test the goodness of fit (Touboul and Destexhe, 2010), for each participant and each condition, we calculated the quality of the fit factor (\( \varrho \)) as described by Clauset et al. (2009) (see Methods). We used a conservative criterion and deemed the fit significant if \( \varrho \geq 0.1 \) (Clauset et al., 2009; Shew et al., 2015).

We observed that a majority of the participants showed a significant power-law fit (individual values for \( \alpha \) and \( \varrho \) are shown in Supplementary Fig. S3). We also observed a distribution of the fitted power-law exponent \( \alpha \) across participants for all three conditions, as shown in Fig. 2B. Estimated exponent varied between the range ~1.5 to ~2.5 across subjects for all three conditions. We tested if higher exponents, away from a theoretically expected universal exponent value of 1.5, show a large deviation from power-law, but did not find that to be the case (see Supplementary Fig. S6). In Fig. 2C, we plot the pairwise difference in exponents for individuals who showed significant power-law fits across all three experimental conditions and observed distributed values for each pairing of the conditions. These differences suggest that the global scale-invariant organization may shift based on the cognitive complexity of the task.

In addition to the variability observed in the exponent value of the power-law fits, we also observed that \( \alpha_{\text{max}} \), which represents the upper bound of the fit, decreases from rest to task conditions, as shown in Fig. 2D (rest to PV \( \alpha=2.89, p=0.007 \) and rest to AV \( \alpha=3.20, p=0.003 \); also see Supplementary Fig. S4). Collectively, these results indicate that EEG-derived avalanches that are spatiotemporally distributed within the brain, demonstrate significant power-law dynamics for both rest and our two task conditions, though the form of the power-law varies significantly across both individuals and conditions.

3.2. Avalanche dynamics vary between individuals and task conditions, but in a correlated manner

We computed the branching parameter (\( \sigma \)) to further assess EEG-derived avalanche dynamics and investigate whether the system is near a state of criticality. Previous research has shown that a branching parameter of 1 reflects a balance of inhibition and excitation and suggests the neural system is in a critical state (Beggs, 2008; Beggs and Plenz, 2003). Here, we consider such a critical state across our three experimental conditions.

Branching parameter values demonstrated similar variability as the power-law exponents, both across participants and conditions (also see Supplementary Fig. S5). As shown in Fig. 3A, we observed that the branching parameter show significant increase from the rest to passive viewing (\( \tau(35) = -4.18, p < .001 \)) and to active viewing (\( \tau(35) = -3.60, p =c.001 \)). The means of these values in each experimental condition are close to the theoretical prediction of 1, which, along with the presence of power-law probability distributions, supports the proposition that the system is close to a critical state (Priesemann et al., 2014).

While we observed variability in the values of the branching parameter across individuals, we found significant correlations within an individual between parameters across different experimental conditions (as was also reported in Arviv et al., 2015). In Fig. 3B-D we compared within-individual branching parameter values between all pairings of conditions. For all three pairings, we found a significant positive correlation (rest and passive viewing \( r = 0.58, p < .001 \); rest and active viewing \( r = 0.56, p < .001 \); passive viewing and active viewing \( r = 0.56, p < .001 \)).

Results thus far indicate a consistent interpretation, i.e., EEG activity shows evidence of the brain being at a near-critical state, as quantified via the observed power-law distributions and branching parameter values for the avalanche activity. However, both of these measures reveal the sensitivity of avalanche features to individual and state dependent differences (Figs. 2, 3, and S6). Additional analyses including avalanche durations and their relationship with avalanche sizes also support these
inferences as discussed in Supplementary Fig. S7. In particular, we observed that avalanche durations also show significant fit to power law across majority of participants and conditions, but with varying exponents. Moreover, we found that average avalanche size varies with avalanche duration according to a scaling relationship $S \sim D^\beta$ indicating closeness to criticality (Shew et al., 2015), but with varying values of the scaling exponent $\beta$, indicating individual and task dependent variability.

3.3. Changes in task complexity result in localised changes in avalanche dynamics

We next examined whether avalanche dynamics, defined locally, relate to the task complexity that varies across experimental conditions. Specifically, we characterized the EEG sensors located at spatially distinct positions on the scalp using a metric we term ‘normalized engagement’ (NE, see Methods). Higher NE values indicate more frequent high amplitude activity on the sensor.

We observed differences in the spatial distribution of NE values across the three experimental conditions. Fig. 4A shows the group average of these distributions for three task conditions. We found that higher NE values systematically shifted from posterior areas of the scalp towards anterior areas as the task complexity increased. Interestingly, we found similar results using two different measures previously discussed in literature (see Supplementary Fig. S8).

Next, we evaluated these spatial distributions as a function of avalanche size. We binned avalanches into three scales based on their sizes (short, moderate and persistent) and recomputed the NE measures as a function of task complexity. Fig. 4B displays these results and shows that different avalanche sizes are associated with a different spatial distribution of normalized engagement across the scalp. For short avalanche sizes, there is no substantial difference between the spatial distributions across task conditions. However, for persistent and moderate avalanches, there is a clear shift in the spatial distribution of high NE values from occipital to frontal and central sensors as the task complexity increases, indicating that relatively larger avalanches are informative of the task dependent reorganization of the brain activity. We also found that the observed normalized engagement of persistent avalanches significantly correlates with the global avalanche features, i.e., the power-law exponent and branching parameter (Supplementary Fig. S9), which further establishes the role of larger avalanches in driving individual and task-driven variability in avalanche distributions.

Additional analyses, investigating the frequency-specificity of these results, showed that the effects were sustained in EEG activity below 20 Hz, indicating they were unlikely linked to muscle artifact and EMG contamination (Goncharova et al., 2003; Muthukumaraswamy, 2013). More interestingly, for persistent avalanches, the spatial distribution disassociated across frequencies, with occipital patterns expressed in the alpha band activity (8–12 Hz) while the frontal patterns were largely in the theta band activity (4–7Hz) (see supplementary Fig. S10).

Resting state EEG is characterized by strong alpha oscillations in occipito-parietal cortex (Basar, 2012; Goldman et al., 2002). Additionally, it has been shown that visual stimuli and emotional judgments typically result in high theta activity in frontal brain regions (Cavanagh and Frank, 2014; Ertl et al., 2013). Importantly, persistent avalanche dynamics provide links between frontal and occipito-parietal activity in
ROIs ($NE_{P-occipital}$) as predictors in the model. The model findings are detailed in Table 1.

\[ Y = 1 + NE_{M-central} + NE_{M-occipital} + NE_{P-occipital}. \]  

As we show in Fig. 5B, two significant relationships were observed: (i) a positive relationship between the emotional rating and average NE of the ROIs for persistent avalanche activity in occipital region ($NE_{P-occipital}$, coefficient $= 3.94$ and $p = .004$) and (ii) a negative relationship between the emotional rating and average NE of the ROIs for moderate avalanche activity in occipital region ($NE_{M-occipital}$, coefficient $= -3.78$ and $p = .036$). We also observed a trending (positive) relationship between the emotional rating and average NE of the ROIs for moderate avalanche activity in central region ($NE_{M-central}$ coefficient $= 1.81$ and $p = .075$). Fig. 5C shows the estimated model fit, and these findings suggest that localized avalanche dynamics explain significant variability in emotional rating ($R^2 = 0.28$).

4. Discussion

We investigated avalanche features in the EEG time series as a way to characterize brain states across individuals and tasks of varying complexity. For the global organization of avalanches, we observed power-law behavior and scale-invariance in the resting state condition as well as in the passive and active viewing conditions. These findings support previous studies that have investigated resting state brain activity (Priesemann et al., 2013; Shriki et al., 2013; Tagliazucchi et al., 2012), as well as studies where there is a presence of a stimulus, both for humans (Arviv et al., 2015; Palva et al., 2013) and non-human primates (Tomen et al., 2014; Yu et al., 2017). The results also suggest that the large-scale neural dynamics within the brain maintain a critical-like state (Cocchi et al., 2017; Linkenkaer-Hansen et al., 2001; Ponce-Alvarez et al., 2018) for different conditions and that this state may be important for optimizing information processing capabilities within the brain (Beggs, 2008; Haldeman and Beggs, 2005; Papa, 2014; Shew et al., 2009).

Though the ‘critical-like’ state was prevalent across conditions and subjects, the corresponding power-law exponents ($r$) displayed substantial variability across individuals and between conditions within an individual. The estimated exponent values in macroscopic experimental data deviated from the exponent value of $r = 1.5$ reported in multiple organisms as well as in-vitro experiments (Beggs and Plenz, 2003; Hahn et al., 2010; Priesemann et al., 2013; Shew et al., 2015; Yu et al., 2017). The estimated value of $r$ can vary as a function of study parameters, e.g., the distance between recording sensors, the chosen threshold for identifying high-amplitude events, and the size of the correlation window $\Delta t$ (Miller et al., 2019; Petermann et al., 2009; Priesemann et al., 2013). Since the first two parameters were fixed during the study, they did not contribute to the observed variability in exponent. The third parameter was adaptively defined for each individual and condition as the mean inter-event-interval (Priesemann et al., 2013; Shew et al., 2015) which allowed a uniform interpretation of estimated avalanche features across individuals and conditions. Additionally, as we show is Supplementary Fig. S2, different choices of $\Delta t$ led to a systematic variation in avalanche features, which consistently showed between individual variability. Therefore, the observed variability in the exponent can be attributed to individual differences in avalanche dynamics.

The absence of a single-valued exponent to describe the avalanche dynamics likely indicates that the scale-invariant organization we see in the EEG is not fine tuned to a single critical state, but instead, varies based on the underlying functional dynamics (Fagerholm et al., 2015; Priesemann et al., 2014; Tomen et al., 2014; Yaghoubi et al., 2018). Therefore, our results suggest that models for criticality in neural systems may need to account for robust individual and task related differences (Moretti and Muñoz, 2013; Priesemann and Shriki, 2018; Williams-Garcia et al., 2014). For example, Moretti and Muñoz (2013) suggested that the inherent hierarchical-modular archi-
Fig. 5. Avalanche dynamics correlate with subject specific emotional ratings in active viewing task. (A) We identified regions of interest (ROIs) as a set of sensors within frontal, central, and occipital lobes which showed significantly different NE values between rest and active viewing (using a paired t-test). Observed ROIs are highlighted with colors for moderate (M) and persistent (P) avalanches. (B) Using multiple linear regression (Eq. (4)), we found that average NEs across these ROIs were predictive of self-reported emotional rating by participants. In particular, we found two significant relationships: a positive relationship between the emotional rating and average NE of the ROIs for persistent avalanche activity in occipital region \( NE_{P,occipital} \) (coefficient = 3.94 and \( p = .004 \)) and a negative relationship between the emotional rating and average NE of the ROIs for moderate avalanche activity in occipital region \( NE_{M,occipital} \) (coefficient = -3.78 and \( p = .036 \)). (C) Circles show the experimental data and the blue line shows the model fit. Dotted lines represent the 95% confidence interval for the fit. Further model details are included in Table 1.

Table 1

Results from the regression model described by Eq. (4) to assess the relationship between localized avalanche features and emotional rating reported by the participants during active viewing task. Here, \( Y \) represents the mean emotional rating for each individual, \( NE_{M,central} \), \( NE_{M,occipital} \), and \( NE_{P,occipital} \) represent average normalized engagement values of regions of interest for moderate avalanches in the central lobe, moderate avalanches in the occipital lobe, and persistent avalanches in the occipital lobe respectively. Results for each model term are presented in different rows of the table and significant effects are highlighted in the bold text.

Linear regression model:

\[
Y \sim \text{Intercept} + NE_{M,central} + NE_{M,occipital} + NE_{P,occipital}
\]

Estimated coefficients:

| Coefficient         | Standard error | t-Stat | p-value |
|---------------------|----------------|--------|---------|
| Intercept           | 3.24           | 0.19   | 17.06   | 1.26e-17 |
| \( NE_{M,central} \) | 1.81           | 0.98   | 1.84    | 0.075    |
| \( NE_{M,occipital} \) | -3.78         | 1.74   | -2.18   | 0.036    |
| \( NE_{P,occipital} \) | 3.94           | 1.26   | 3.12    | 0.004    |

R-Squared: 0.28

F-Statistics vs. constant model: 4.15, p-value: 0.014

Architecture and heterogeneity of cortical networks can replace a singular critical point by an extended critical-like region such that the exponents may vary to capture unique functional connectivity of different neural systems and cognitive states (Dehghani et al., 2012; Yaghoubi et al., 2018). Similarly, in a different line of work, Priesemann et al. (2014) and Tomen et al. (2014) suggested that the cortical networks operate at near-critical states (sub- as well as super-critical) to augment stimulus processing, which can also lead to individual and task dependent variability in avalanche distributions and estimated parameters. Future studies can further analyze avalanches derived from neuroimaging data on case by case basis to establish the cognitive implications of their different deviations from an ideal power-law (i.e., quick decay of large avalanches in case of sub-critical state or the emergence of a peak in case of super-critical state). Despite the variability we see, the observed exponent values are distributed within a similar range across the three experimental conditions, which further suggests a flexible, yet functionally ordered organization within the brain, characteristic to a complex system.

Surprisingly, concurrent with the maintained global scale-invariance, we observed localized dynamics of avalanches to show not only the task-dependent regional patterning, but also the scale-specificity. We found that the avalanches with relatively large sizes (moderate and persistent) carried meaningful information about the task-dependent changes within the brain. Using a metric that quantifies the likelihood of different brain regions to engage in avalanches (i.e., NE), we identified a set of ROIs which were predictive of individual behavior, i.e. emotional rating, through a regression model that included terms pertaining to different scales of avalanche sizes as well as spatially distributed regions. We found these ROIs to be located within
the frontal, central, as well as occipito-parietal regions of the brain. Previous research has also highlighted the activation of these areas during the processing of emotional stimuli (Baumgartner et al., 2006; Buhle et al., 2014; Kohn et al., 2014).

We used a data-driven approach to identify these ROIs and required that they show a significant change of their engagement in producing avalanches, following the change in experimental condition from rest to active viewing. We observed that higher average engagement of occipital ROIs in producing persistent avalanches is indicative of higher emotional rating, and also observed a negative relationship between average engagement of occipital ROIs in producing moderate avalanches and emotional rating. These two observed relationships indicate that when occipital avalanches tended to be larger and sustained, reported emotional intensities were higher.

In general, the localized dynamics of avalanching process can be studied through different measures such as event rate and relative avalanches as we discussed in Supplementary Fig. S8. However, the scale-specificity we studied here through NE enabled us to identify cognitively relevant components of the avalanche dynamics. Further, we found that the scalp distributions of NE are robust under sub-sampling of data using a reduced number of sensors (Supplementary Fig. SBD) and believe that this metric could be useful in analyzing even low-density EEG recordings often used in clinical settings. Future studies may be able to further assess the sensitivity of these different measures to a variety of cognitive contexts as well as their robustness for different experimental setups.

Combining our findings across the global and regional scales of the EEG dynamics, we propose that the macro-scale dynamics of the neural activity operates close to criticality whilst simultaneously rapidly changing to match behavioral goals (Karimipanah et al., 2017). Neophysiological mechanisms for the brain to adaptively maintain its macroscopic organization near criticality are not well understood; however, it appears likely that such an adaptive mechanism is a characteristic of healthy human brains (Massobrio et al., 2015). Indeed, it has been previously shown that the features of criticality are more consistently disrupted in the interictal activity of epilepsy patients (Arviv et al., 2016), where, a localized or global inability of the brain to regain its balance may cause uncontrolled activity or seizures. A significant departure from a critical-like state has also been reported during sustained wakefulness over several hours, which reverses back upon the recovery of sleep (Meisel et al., 2013), a necessity for the healthy brain function (Banks and Dinges, 2007). Scale-invariant avalanche dynamics have also been found important during developmental stages of the brain (Iyer et al., 2015) and during recovery after brain insult (Roberts et al., 2014).

In this study, we focused on high-amplitude events and avalanches to investigate scale-invariance and criticality in the brain and established their cognitive relevance, however, such events have also been studied in a variety of other contexts, for example, the propensity of high ‘power’ events in the brain have been shown to predict behavior (Shin et al., 2017). Similarly, scale-invariant brain dynamics have also been observed through different functional features and methodological approaches such as EEG microstates (De Ville et al., 2010) and detrended fluctuation analysis of neural oscillations (Hardstone et al., 2012). While these different methodological approaches lead to similar conclusions, further research is required to establish a connection between them (Willting and Priesemann, 2019).

We believe that the analysis of macroscopic avalanches can provide useful insight into the temporal evolution of brain activity, potentially differentiating the processing of different stimulus types, and might even provide biomarkers when the brain activity becomes abnormal. However, further research will be required to explore these aspects and establish the role of avalanches in cognitive processing and in explaining within and between individual variability. Despite these exciting aspects, the study of avalanches within the human brain presents a number of challenges. Avalanches estimated in EEG recordings allow only a limited neurophysiological interpretation since the EEG represents large population neural activity measured at the scalp, and suffers from volume conduction distortion and artifacts due to the high electrical conductivity of the scalp. Often, source localization is used to identify unique sources in the brain given the measured scalp EEG activity and to rid the data of the artifacts due to volume conduction. However, effective and accurate localization of signal sources is a field of research in itself and the analysis of avalanches in such data would require careful consideration and further work.

4.1. Conclusions

We observed that similar to the resting state activity, EEG-derived avalanches in event-related stimulus-driven activity demonstrate power-law probability distributions and scale-invariance which is characteristic to the global organization of activity in a complex system near criticality. Global avalanche dynamics however varied between individuals, as captured by the exponents of the fitted power-laws and other avalanche features such as the branching parameter. From the analysis of the branching parameter, this global dynamics within an individual seemed to be correlated across experimental conditions. Localized (regional) avalanche dynamics showed scale-specific changes between tasks and also a significant correlation with measured individual behavior. We believe that the analysis of macroscopic avalanches in EEG provides a straightforward yet effective way to study the state dependent dynamics of the human brain, both in health and disease.

Data availability

Data is accessible upon request as far as allowed by the security policy and guidelines established with the ethics committee of the US Army Research Laboratory Human Research Protection Program. Requests should be addressed to K. Bansal. Codes associated with the analyses presented in this article can be found at https://doi.org/10.5281/zenodo.5129034.

Credit authorship contribution statement

Kanika Bansal: Conceptualization, Methodology, Formal analysis, Writing – original draft, Visualization. Javier O. Garcia: Data curation, Writing – review & editing. Nina Lauharatanahirun: Methodology, Writing – review & editing. Sarah F. Muldoon: Methodology, Writing – review & editing. Paul Sajda: Supervision, Methodology, Writing – review & editing. Jean M. Vettel: Funding acquisition, Writing – review & editing.

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Supplementary material

Supplementary material associated with this article can be found, in the online version, at10.1016/j.neuroimage.2021.118425.

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