

# Avalanche Dynamics of Human Brain Oscillations: Relation to Critical Branching Processes and Temporal Correlations

Simon-Shlomo Poil,<sup>1</sup> Arjen van Ooyen,<sup>1</sup> and Klaus Linkenkaer-Hansen<sup>1,2\*</sup>

<sup>1</sup>Department of Experimental Neurophysiology, Center for Neurogenomics and Cognitive Research (CNCR), VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

<sup>2</sup>BioMag Laboratory, HUSLAB, Helsinki University Central Hospital, FIN-00029 HUS, Finland

---

**Abstract:** Human brain oscillations fluctuate erratically in amplitude during rest and exhibit power-law decay of temporal correlations. It has been suggested that this dynamics reflects self-organized activity near a critical state. In this framework, oscillation bursts may be interpreted as neuronal avalanches propagating in a network with a critical branching ratio. However, a direct comparison of the temporal structure of ongoing oscillations with that of activity propagation in a model network with critical connectivity has never been made. Here, we simulate branching processes and characterize the activity propagation in terms of avalanche life-time distributions and temporal correlations. An equivalent analysis is introduced for characterizing ongoing oscillations in the alpha-frequency band recorded with magnetoencephalography (MEG) during rest. We found that models with a branching ratio near the critical value of one exhibited power-law scaling in life-time distributions with similar scaling exponents as observed in the MEG data. The models reproduced qualitatively the power-law decay of temporal correlations in the human data; however, the correlations in the model appeared on time scales only up to the longest avalanche, whereas human data indicate persistence of correlations on time scales corresponding to several burst events. Our results support the idea that neuronal networks generating ongoing alpha oscillations during rest operate near a critical state, but also suggest that factors not included in the simple classical branching process are needed to account for the complex temporal structure of ongoing oscillations during rest on time scales longer than the duration of individual oscillation bursts. *Hum Brain Mapp* 29:770–777, 2008. © 2008 Wiley-Liss, Inc.

**Key words:** resting-state; ongoing oscillations; critical networks; branching processes; long-range temporal correlations; power-law scaling; magnetoencephalography (MEG); self-organized criticality (SOC)

---

\*Correspondence to: Klaus Linkenkaer-Hansen, Center for Neurogenomics and Cognitive Research (CNCR), Department of Experimental Neurophysiology, Vrije Universiteit Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands.  
E-mail: klaus.linkenkaer@cncr.vu.nl

Received for publication 18 January 2008; Revised 14 March 2008; Accepted 21 March 2008

DOI: 10.1002/hbm.20590

Published online 2 May 2008 in Wiley InterScience (www.interscience.wiley.com).

© 2008 Wiley-Liss, Inc.

## INTRODUCTION

Neuroscientists are becoming increasingly interested in the concept of criticality. The idea that ongoing or endogenous activity in the brain has quantitative spatio-temporal hallmarks of systems operating at the edge between order and disorder is intriguing [Beggs, 2007; Buzsaki, 2006; Chialvo, 2007; Linkenkaer-Hansen et al., 2001]. It could provide a generic framework for understanding important

aspects of neuronal population activity, such as its high susceptibility to perturbations [Kinouchi and Copelli, 2006; Linkenkaer-Hansen et al., 2004], optimal information transmission [Beggs and Plenz, 2003] and computational abilities [Bertschinger and Natschläger, 2004], the presence of metastable states that could support neuronal representations [Beggs and Plenz, 2004; Haldeman and Beggs, 2005; Hopfield, 1982], and robustness of the dynamic state [Bornholdt and Röhl, 2003]. Heuristic arguments for why neuronal networks may operate in a critical state have been known for some years [Bak, 1997; Chialvo and Bak, 1999], but only in recent years has the relevance of criticality for understanding the nature of endogenous brain activity been supported by empirical [Beggs and Plenz, 2003, 2004; Linkenkaer-Hansen et al., 2001; Mazzoni et al., 2007], and modeling evidence [Abbott and Rohrkemper, 2007; Kinouchi and Copelli, 2006; Levina et al., 2007].

The term “critical” has its roots in statistical physics where it refers to the volatile state of certain materials at the critical temperature of a phase transition [Christensen and Moloney, 2005]. In the seminal paper by Bak et al., [1987], the relevance of criticality was broadened considerably. They showed that systems composed of a large number of elements with nonlinear interactions may self-organize into a state with the statistical hallmarks of critical systems, i.e., spatial and temporal correlations of a power-law form. The power-law form is unique, because it is the only mathematical function that indicates that the system has no typical or “characteristic” scale. A system characterized by power-law statistics is, therefore, said to be “scale-free.”

Whereas the power-law is inherently linked to the statistical behavior of a system poised at criticality, it offers little more than a phenomenological description; it shows that event sizes are broadly distributed and, thus, that the system must have a rich dynamical behavior. The branching ratio is another important index of criticality, which provides a better understanding of the mechanism underlying the dynamics at criticality. The branching ratio ( $\sigma$ ) of a neuronal network is defined as the average ratio of current to past activity (Fig. 1A–C). Thus, if the branching ratio is smaller than one ( $\sigma < 1$ ), activity dies out before it has propagated far, whereas a ratio larger than one ( $\sigma > 1$ ) leads to an explosion of activity. These networks are termed sub- and super-critical, respectively. In the critical state, the ratio is close to one ( $\sigma = 1$ ) and the activation of  $N$  neurons will, on average, lead to the activation of another  $N$  neurons [Chialvo, 2006]. Thus, activity in a critical network may be sustained considerably longer than in a sub-critical network and does not suffer from the run-away excitation of the super-critical network. To increase our understanding of the putative link between activity propagation in networks with a critical connectivity and the temporal fluctuations of resting-state oscillations, we simulated a variety of branching processes and compared their dynamics with that of brain oscillations in humans.

## METHODS

### Recordings and Experimental Conditions

Ongoing electrical brain activity in sessions of 20 min was measured with magnetoencephalography (MEG) from 13 normal subjects (aged 20–30 years, two females). Five of the subjects were measured 2–4 times giving a total of 20 data sets; however, statistics are based only on one recording per subject. Eleven data sets were recorded with a system containing 122 planar gradiometers used in a previous study [Linkenkaer-Hansen et al., 2001]; the other nine data sets were recorded with 204 planar gradiometers and have been used in [Linkenkaer-Hansen et al., 2004]. The studies were approved by the Ethics Committee of the Department of Radiology of the Helsinki University Central Hospital.

During the recording sessions, the subjects were seated in a magnetically shielded room and instructed to relax and sit still with eyes closed. The data were sampled at 900 Hz and decimated off-line to 300 Hz with a passband of 0.1–100 Hz (6th order Butterworth digital filters). The off-line decimation was performed to speed up computations and did not influence the amplitude of the 10 Hz oscillations that are the signals of interest in this study. The four channels with the largest mean amplitudes in the parietal and right sensorimotor regions were selected in each subject.

### Computational Modeling of Branching Processes

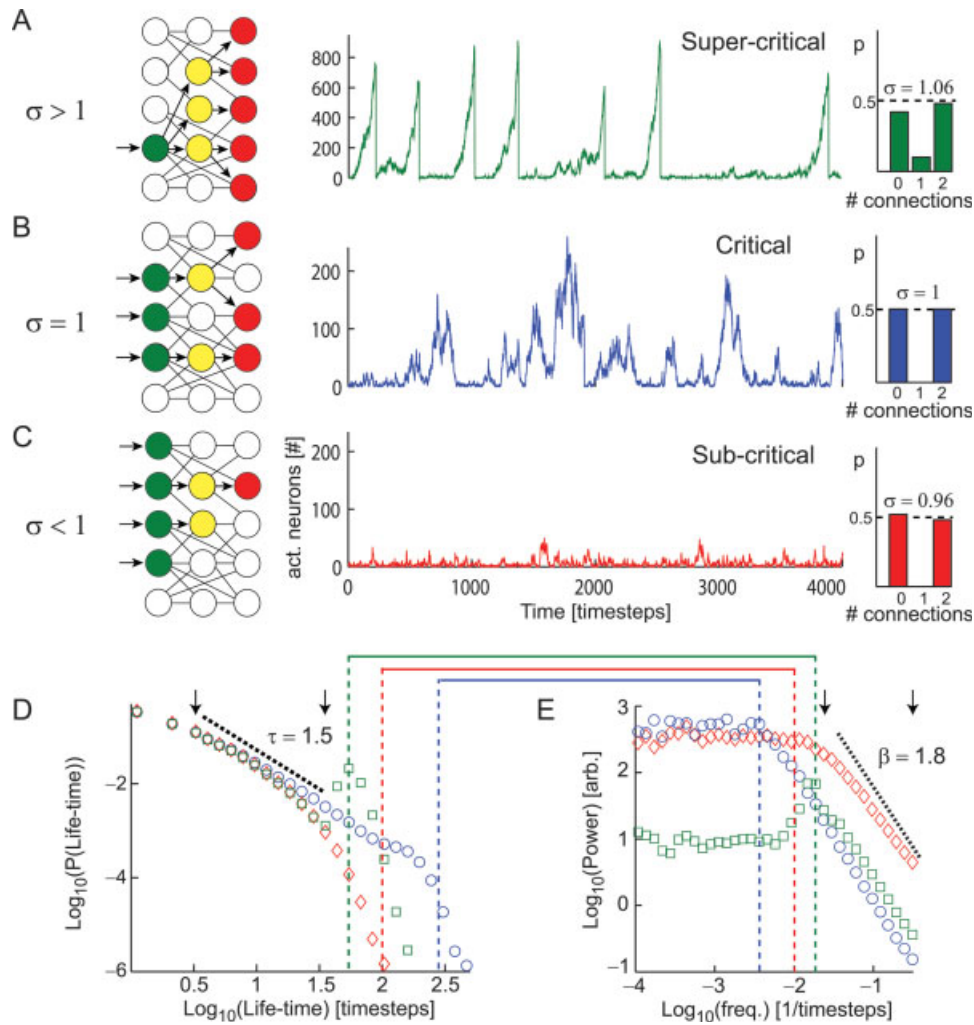
The simulation of a branching process is based on probabilistic activity propagation among units in a network with a fixed probability distribution for each unit (Fig. 1A–C, right column). The average number of units that each active unit activates per time step is the branching ratio ( $\sigma$ ). For example, if the probability of the units to activate 0, 1, or 2 other units in the next time step is 0.5, 0.0, and 0.5, respectively, then  $\sigma = 0 \times 0.5 + 1 \times 0.0 + 2 \times 0.5 = 1$ . A unit is only active during one time step, and the branches are not interacting. Each process begins with one active unit and ends either when no units are active, or when an avalanche-size of 10,000 activated units is reached. This cut-off was introduced to prevent the super-critical process to create unphysiologically large avalanches. We modeled 10 branching processes containing  $10^6$  avalanches for each branching ratio in the MATLAB<sup>TM</sup> environment (The MathWorks, 7.3.0.267).

### Data Analysis

The amplitude envelope in the alpha-frequency band was extracted using bandpass filters at 8–13 Hz (finite impulse response filters with a Hamming window and filter order 90) and the Hilbert transform (Fig. 2A,B).

### Temporal Correlation Analysis

The power spectral density (PSD) was determined by means of the Welch technique with the Hanning window; it reveals the contribution of different frequencies to the



**Figure 1.**

The branching process: model, time series, life-time probability distributions and power spectra. A branching process may be characterized by its branching ratio ( $\sigma$ ), which is the average number of activations per unit per time step. Branching processes come in three main classes: super-critical ( $\sigma > 1$ , A), critical ( $\sigma = 1$ , B); and sub-critical ( $\sigma < 1$ , C). The branching ratio may be varied by changing the probability distribution of number of connections made by the neurons, as shown to the right of the corresponding time series in A–C. (D) Probability distribution of avalanche durations or “life-times”. The probability distribution of avalanche “life-times” reveal many long-lasting avalanches for the super-critical, but only few long-lasting avalanches for the sub-critical, and no characteristic time scale for the critical process. (E) Double logarithmic power spectra. By compar-

son with the power-spectrum analysis, we see that all three branching processes give rise to temporal correlations ( $1/f^\beta$  type, slopes larger than zero for high frequencies) on time scales up to the longest-lasting avalanche events (vertical lines). Thus, sub-critical processes (red diamond,  $\sigma = 0.9$ ) have shorter correlations than critical (blue circle,  $\sigma = 1.0$ ), whereas the super-critical (green squares,  $\sigma = 1.1$ ) branching process has a characteristic scale due to the cut-off at 10,000 units, corresponding to the finite size of a neuronal network or the instrument. Power spectra are based on a  $4 \times 10^5$  time-step signals and the probability distributions are based on  $2 \times 10^6$  avalanches. Fitting intervals are indicated with arrows. (A–C, left column) adapted with permission from Nature Publishing Group (Chialvo, 2006).

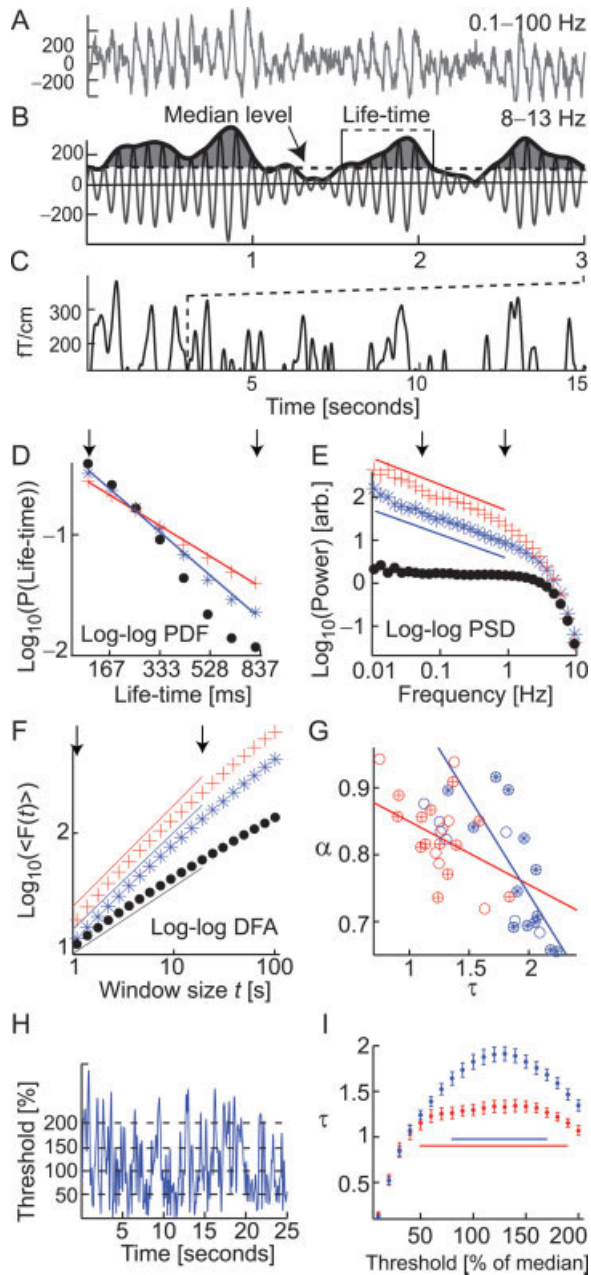
total power of the signal. White-noise signals contain equal power at all frequencies and are uncorrelated, whereas signals with long-range power-law correlations have log-log linear power spectra with a nonzero power-law exponent  $\beta$  ( $1/f^\beta$ -type signal). Periodic signals have peaks in the

spectrum at frequencies that are inverses of these periods. The power spectra were logarithmically binned with 10 bins per decade.

Whereas PSD analysis is particularly suited for identifying the presence of characteristic scales, the detrended

fluctuation analysis (DFA) [Peng et al., 1994] provides greater accuracy in estimating the decay of temporal (auto-)correlations when the amount of data available is limited [Gao et al., 2006] and, therefore, has been the preferred algorithm in several quantitative studies on long-range temporal correlations (LRTC) in ongoing oscillations [Linkenkaer-Hansen et al., 2007]. The main steps from the broadband MEG signal to the quantification of LRTC using DFA have been explained in detail elsewhere [Linkenkaer-Hansen et al., 2001, 2004; Nikulin and Brismar, 2005]. In brief, the DFA measures the scaling of the root-mean-square fluctuation of the integrated and

linearly detrended signals,  $F(t)$ , as a function of time window size,  $t$ . For signals that are uncorrelated or have persistent power-law correlations, the average fluctuation  $\langle F(t) \rangle$  is of the form  $\langle F(t) \rangle = t^\alpha$ , where  $\alpha$  is the DFA scaling exponent. If  $0.5 < \alpha \leq 1.0$ , this indicates power-law scaling behavior and the presence of temporal correla-



**Figure 2.**

On short to intermediate time scales,  $\alpha$ -oscillation bursts have similar temporal structure to avalanches in a critical branching process. The MEG signals (A) were band-pass filtered from 8–13 Hz (thin line, B) and the amplitude envelope of the oscillations (thick line, B) extracted with the Hilbert transform. The signal exhibits an oscillatory burst structure on longer time scales (C). To quantify differences in oscillation-burst dynamics on short to intermediate time scales ( $< 1$  s), we introduced a threshold at the median amplitude (horizontal dashed line, B) and defined the start and end of an oscillation burst or “avalanche” as the time points of crossing this threshold. Signal from a right sensorimotor channel. (D) Grand-average probability distribution function (PDF) of oscillation-burst life-times in double logarithmic coordinates exhibit a slow power-law decay of oscillation life-times, unlike the empty-room recording (black dots), which has fast-decaying probability of long-lasting events. The life-time exponents (the slopes of the fitted lines in the PDF) were  $\tau = 1.29 \pm 0.06$  (red pluses) and  $\tau = 1.99 \pm 0.06$  (blue stars) in the parietal and right-sensorimotor areas, respectively. (E) Grand-average power spectral density in double logarithmic coordinates (PSD) showing  $1/f^\beta$  spectra with exponents  $\beta = 0.56 \pm 0.05$  (red pluses) and  $\beta = 0.47 \pm 0.07$  (blue stars) in the parietal and right-sensorimotor areas, respectively. These non-zero exponents indicate  $1/f^\beta$ -type of temporal correlations on time scales  $> \sim 1$  s, unlike the empty-room recording, which is characterized by a flat spectrum on these time scales (black dots). Note that the non-zero slopes at frequencies above  $\sim 1$  Hz are caused by the temporal integration of the bandpass filters; however, this filter effect does not lead to long-lasting oscillations, cf. (D). (F) Double logarithmic plots of the DFA fluctuation measure,  $F(t)$ , as a function of window size,  $t$ , display power-law scaling in the time window range of 1–20 s for the parietal area  $\alpha = 0.83 \pm 0.01$  (red pluses), the right-sensorimotor area  $\alpha = 0.78 \pm 0.02$  (blue stars), and for an empty-room recording (black dots). Fitting intervals are indicated with arrows. (G) Scatter plots of life-time ( $\tau$ ) and DFA ( $\alpha$ ) exponents for all subjects indicate a significant correlation between temporal correlations on short ( $\tau$ ) and long ( $\alpha$ ) time scales in the right sensorimotor (blue) region ( $r = -0.77$ ,  $p < 0.002$ ), but only a trend in the parietal region ( $r = -0.45$ ,  $p = 0.12$ ) (red). Open circles are repeated measurements and are not included in the correlation fits. (H) Oscillation-bursts may be defined with respect to an amplitude range of at least  $\pm 20\%$  around the median amplitude without significantly affecting the life-time power-law exponent,  $\tau$ . (I) Life-time exponents (mean  $\pm$  SEM) obtained using different thresholds. Horizontal bars indicate the range of thresholds associated with an insignificant influence on  $\tau$  (ANOVA,  $p < 0.05$ ).

tions, whereas  $\alpha = 0.5$  indicates the case of an uncorrelated signal.

### Oscillation “Avalanche” Life-Time Analysis

For each channel and subject, we computed the median amplitude of oscillations as the median amplitude envelope after bandpass filtering and Hilbert transform and used this as the threshold for defining the start and end points of an oscillation burst (Fig. 2B). The duration, or “life-time,” of an oscillation is the time that the amplitude envelope remains above this median level (Fig. 2B). Probability distributions of oscillation life-times were computed using equidistant binning on a logarithmic axis with 10 bins per decade. By visual inspection, it was found that all subjects had probability distributions of life-times that decayed as a power-law in the range of 153–893 ms (Fig. 2D). The life-time power-law exponent,  $\tau$ , is the slope of the straight line in double-logarithmic coordinates and was computed using least-square fitting in this range in all channels and subjects.

### Reference Data

Broadband environmental noise is often temporally correlated. To verify that intrinsic sensor noise or environmental disturbances did not cause any of the effects reported here, a 20-min recording was performed without a subject in the MEG device. These reference data were subjected to identical analyses as the rest of the data.

### Statistical Analysis

We used two-tailed *t*-test that assumed equal variance with significance level  $P < 0.05$ . The exponents for individual subjects were based on the average across the four channels from each anatomical location. Pearson’s coefficient of correlation was used to test for linear correlations among the various measures derived from the data. The numerical results in the text are reported as mean  $\pm$  standard-error-of-mean (SEM) based on the average values across subjects ( $n = 13$ ). Thus, only one recording was included for each subject in the statistics. One-way ANOVA was used to investigate the threshold dependence of the life-time exponent.

## RESULTS

### The Temporal Structure of Branching Processes

A branching process is characterized by its branching ratio ( $\sigma$ ), which is the average number of activations per unit per time step. We generated branching processes corresponding to the three main classes: super-critical ( $\sigma > 1$ ), critical ( $\sigma = 1$ ), and sub-critical ( $\sigma < 1$ ) (Fig. 1; for details, see “Computational modeling of branching processes” in Methods). The probability distributions for each neuron to

make a functional connection with another neuron (i.e., to activate another neuron) are shown in the rightmost column of Figure 1A–C.

The conspicuous differences in dynamics are captured by the probability distribution function of avalanche life-times (Fig. 1D). The super-critical process has a characteristic time scale related to the cut-off of avalanches reaching 10,000 activations, the sub-critical process exhibits an exponential decay of long-lasting avalanches, whereas the critical branching process (Fig. 1B,D, blue traces and circles, respectively) is characterized by a power-law decay with an exponent  $\tau = 1.54 \pm 0.00$  for short life times ( $n = 10$ ). However, if the probability of zero connections in a critical branching process decreases towards 0.05, the life-time exponent decreases towards  $\tau = 1.03 \pm 0.00$  (data not shown). Fitting power laws to the distributions of sub- or super-critical processes in the approximately log–log linear interval used for fitting the critical distribution led to significantly larger exponents than the critical process. Sub-critical:  $\tau = 2.00 \pm 0.00$ ,  $P < 0.005$  (Fig. 1D, red diamonds); and super-critical:  $\tau = 1.93 \pm 0.00$ ,  $P < 0.005$  (Fig. 1D, green squares).

As expected for a causal sequence of events, PSD analysis indicated temporal correlations at high frequencies (corresponding to 1–40 time steps) for all the avalanche processes (critical:  $\beta = 1.80 \pm 0.00$ ; sub-critical:  $\beta = 1.50 \pm 0.00$ ; and super-critical:  $\beta = 1.71 \pm 0.00$ ,  $2 \times 10^5$  time steps) (Fig. 1E). However, the shorter avalanches in the sub-critical process (Fig. 1E, red diamonds) is reflected in the transition to uncorrelated fluctuations at shorter time scales (i.e., higher frequencies) than for critical processes (Fig. 1E, blue circles), and super-critical processes (Fig. 1E, green squares) have a characteristic scale (cf. the peak in the PSD) corresponding to the cut-off followed by uncorrelated fluctuations on longer time scales (lower frequencies). We conclude that power-law scaling both in the life-time distribution and in the PSD is restricted to the largest individual avalanche event and, thus, cannot explain temporal correlations on time scales corresponding to several events.

### Critical-Like Power-Law Distribution of $\alpha$ -Oscillation Bursts

To examine whether the temporal structure of oscillation bursts resembles the avalanche structure of a critical branching process and whether LRTC can be explained by very long-lasting oscillation bursts, we introduced an “avalanche analysis” of oscillation bursts (Fig. 2A–C). Power-law scaling of life-time probability distributions was robust across subjects, albeit life-time exponents were significantly larger over sensorimotor cortex  $\tau = 1.99 \pm 0.06$  (Fig. 2D, blue stars) than parietal region  $\tau = 1.29 \pm 0.06$  (Fig. 2D, red plusses;  $P < 0.005$ ,  $n = 13$ ). The life-time exponents were not very sensitive to the chosen threshold (ANOVA,  $P < 0.05$ ; Fig. 2H,I). Further, we did not find significant correlations between the median amplitude and the life-time exponents (Pearson’s correlation,  $P > 0.05$ , data not

shown). The longest oscillation bursts, however, reached life-times one or two orders of magnitude less than the time scales with LRTC according to PSD (Fig. 2E). The PSD had a  $1/f^\beta$ -type signal with power-law exponents  $\beta = 0.47 \pm 0.07$  and  $\beta = 0.56 \pm 0.05$ , for the right sensorimotor and parietal regions, respectively. Together, the life-time distributions and PSD suggest that amplitude dynamics on short to intermediate time scales ( $< \sim 1$  s) resemble the dynamics of a critical process, but that a simple critical branching process cannot account for the rich temporal structure of ongoing alpha oscillations on long(er) time scales (1–20 s).

It has been shown that DFA provides a more accurate estimate of LRTC than PSD, which is particularly important at long time scales, because of the limited amount of empirical data [Linkenkaer-Hansen et al., 2007]. To test whether the life-time exponents that characterize the amplitude dynamics on short to intermediate time scales ( $< \sim 1$  s) are related to the temporal structure on long time scales corresponding to tens of oscillation bursts, we correlated the life-time ( $\tau$ ) and DFA ( $\alpha$ ) exponents (Fig. 2G). The results indicated a significant correlation in sensorimotor ( $r = -0.77$ ,  $P < 0.002$ ), but only a trend in the parietal ( $r = -0.45$ ,  $P = 0.12$ ) regions, suggesting that there may be a relationship despite the difference in time scales.

In summary, a critical branching process has a power-law life-time probability distribution with a power-law exponent around  $\tau = 1.5$ , which is close to the exponents found in the MEG data ( $\tau = 1.3$ – $2.0$ ).

## DISCUSSION

Ongoing or “endogenous” neuronal oscillations in the human brain exhibit erratic amplitude fluctuations that are governed by a slow power-law decay of temporal correlation up to several tens of seconds [Linkenkaer-Hansen et al., 2001, 2007; Monto et al., 2007; Nikulin and Brismar, 2005]. The mechanisms giving rise to this statistical hallmark are poorly understood, but it has been suggested to reflect self-organized activity in critical networks [Linkenkaer-Hansen et al., 2001]. *In vitro* studies in cortical tissue have indicated that population activity may propagate as “neuronal avalanches” and that the branching ratio is close to the critical value of 1 [Beggs and Plenz, 2003; Plenz and Thiagarajan, 2007]. Here, we simulated branching processes and introduced a novel method for characterizing the amplitude fluctuations of ongoing oscillations to compare their temporal dynamics.

### From Bursts of Activity to Temporal Correlations

The models revealed a dramatic influence of the branching ratio on the pattern of activity over time, as reflected in the PSD and the probability distribution function of avalanche life-times, as well as upon visual inspection (see Fig. 1). Analytically, the life-time exponent for a critical branch-

ing process has been derived to be  $\tau = 2$  [Harris, 2002]; however, this result is only valid for long avalanches. Our simulations showed that life-time exponents on short time scales are dependent on the probability of making zero connections and could range from about 1.0 to 1.6 for a critical process. Sub- and super-critical processes were characterized by exponentially decaying life-time probabilities, albeit that the finite-size effect (cut-off) led to a characteristic scale for the super-critical process, as it does in neuronal avalanches *in vitro* when inhibition is pharmacologically reduced [Beggs and Plenz, 2003].

To compare the avalanche life-time statistics of branching processes directly to human oscillations, we introduced a novel analysis based on the quantification of the life-time of individual oscillations bursts (see Fig. 2). For experimental data, it is not possible to unambiguously determine the exact beginning and end of an oscillation burst. We chose an amplitude threshold equal to the median amplitude; however, the threshold could be changed by more than  $\pm 20\%$  without significantly affecting the life-time exponents from the distribution of oscillation bursts, so the exact choice of threshold is less important. We found that resting-state oscillations in the alpha-frequency band (8–13 Hz) have similar scale-free temporal correlations to those of critical branching processes on short to intermediate time scales with life-time exponents in the range of 1.3–2.0, which is comparable with those of critical branching processes, albeit that the upper range of the interval approximates the subcritical process. The results suggest that the individual alpha-burst structure may be explained in terms of a propagation of oscillatory activity through cortical networks with a critical connectivity.

Importantly, the PSD analysis revealed persistence of temporal correlations in the critical branching process model only up to time scales corresponding to the longest avalanche (Fig. 1D,E). This reflects that the temporal organization of burst events is random and not correlated on time scales longer than the duration of the longest burst, which is also true for most models of self-organized criticality [Davidsen and Paczuski, 2002]. Thus, if LRTC in neuronal oscillations were to reflect propagation of oscillatory activity in “simple probabilistic critical networks” as simulated here, oscillations would have to last for tens of seconds, which is not the generally accepted view [Lopes da Silva et al., 1997]. Indeed, we observed that correlations in human oscillations persist onto much longer time scales (Fig. 2E,F) than the duration of oscillation bursts (Fig. 2D). Thus, it appears that multiple mechanisms are required for explaining the complex temporal structure of amplitude fluctuations in ongoing alpha oscillations on time scales of tens of milliseconds to tens of seconds.

We propose that the critical connectivity of cortical networks strongly influence burst duration and, thus, the life-time exponents. LRTC, on the other hand, may arise from sub-cortical modulation [Steriade et al., 1990] or other mechanisms affecting cortical excitability [Vanhatalo et al., 2004] that operate on long time scales and give rise to frac-

tal clustering of oscillation bursts on longer time scales than the duration of individual bursts. Another possibility for activity on short time scales to influence long-time scale dynamics is activity-dependent plasticity [Marder and Goaillard, 2006; van Ooyen, 1994; Zhang and Linden, 2003], which is important for the emergence of the self-organized critical state in model neuronal networks [Abbott and Rohrkemper, 2007; de Arcangelis et al., 2006; Levina et al., 2007], but it remains unknown whether this could give rise to correlations on longer time scales than the longest individual events.

Functional magnetic resonance imaging (fMRI) has suggested that also the multi-scale, or fractal, temporal structure of hemodynamic changes during rest is information rich [Bullmore et al., 2004; Maxim et al., 2005]. With the rapid advances in EEG-fMRI [Gonçalves et al., 2006; Mantini et al., 2007], it should soon be possible to address to what extent the fractal structure of ongoing oscillations can be related to the corresponding structure of fMRI data.

### Outlook

The temporal structure of ongoing oscillations has attracted considerable attention in recent years, because it is rich in information and clearly not a form of filtered noise [Leopold et al., 2003; Linkenkaer-Hansen et al., 2001; Nikulin and Brismar, 2005; Stead et al., 2005]. The present model proved useful for determining the life-time exponent of a critical branching process on short-to-intermediate time scales and provided a plausible explanation for the link between functional brain connectivity and alpha-oscillation burst variability. Future studies should address the possible contribution of mechanisms influencing this connectivity on the experimentally observed temporal correlations. We propose that the present method for extracting the life-time exponent of ongoing oscillations may prove useful as a neuroimaging biomarker in clinical studies and for bridging the gap between mechanisms and functions of amplitude fluctuations on short-to-intermediate and long time scales.

### REFERENCES

- Abbott LF, Rohrkemper R (2007): A simple growth model constructs critical avalanche networks. *Prog Brain Res* 165:13–19.
- Bak P (1997): *How Nature Works: The Science of Self-organized Criticality*. Oxford: Oxford.
- Bak P, Tang C, Wiesenfeld K (1987): Self-organized criticality: An explanation of the  $1/f$  noise. *Phys Rev Lett* 59:381–384.
- Beggs JM (2008): The criticality hypothesis: How local cortical networks might optimize information processing. *Philos Transact A Math Phys Eng Sci* 366:329–343.
- Beggs JM, Plenz D (2003): Neuronal avalanches in neocortical circuits. *J Neurosci* 23:11167–11177.
- Beggs JM, Plenz D (2004): Neuronal avalanches are diverse and precise activity patterns that are stable for many hours in cortical slice cultures. *J Neurosci* 24:5216–5229.
- Bertschinger N, Natschläger T (2004): Real-time computation at the edge of chaos in recurrent neural networks. *Neural Comp* 16:1413–1436.
- Bornholdt S, Röhl T (2003): Self-organized critical neural networks. *Phys Rev E Stat Nonlin Soft Matter Phys* 67:66118.
- Bullmore E, Fadili J, Maxim V, Sendur L, Whitcher B, Suckling J, Brammer M, Breakspear M (2004): Wavelets and functional magnetic resonance imaging of the human brain. *Neuroimage* 23:234–249.
- Buzsáki G (2006): *Rhythms of the Brain*. New York: Oxford University Press.
- Chialvo DR (2006): Psychophysics: Are our senses critical? *Nat Phys* 2:301–302.
- Chialvo DR (2007): The brain near the edge. *Cooperative Behavior in Neural Systems: Ninth Granada Lectures*. pp 1–12.
- Chialvo DR, Bak P (1999): Learning from mistakes. *Neuroscience* 90:1137–1148.
- Christensen K, Moloney NR (2005): *Complexity and Criticality*. London: Imperial College Press.
- Davidsen J, Paczuski M (2002):  $1/f^\alpha$  noise from correlations between avalanches in self-organized criticality. *Phys Rev E* 66:50101.
- de Arcangelis L, Perrone-Capano C, Herrmann HJ (2006): Self-organized criticality model for brain plasticity. *Phys Rev Lett* 96:028107.
- Gao J, Hu J, Tung W-W, Cao Y, Sarshar N, Roychowdhury VP (2006): Assessment of long-range correlation in time series: How to avoid pitfalls. *Phys Rev E Stat Nonlin Soft Matter Phys* 73:016117.
- Gonçalves SI, de Munck JC, Pouwels PJW, Schoonhoven R, Kuijter JPA, Maurits NM, Hoogduin JM, Van Someren EJW, Heethaar RM, Lopes da Silva FH (2006): Correlating the alpha rhythm to BOLD using simultaneous EEG/fMRI: Inter-subject variability. *Neuroimage* 30:203–213.
- Haldeman C, Beggs JM (2005): Critical branching captures activity in living neural networks and maximizes the number of metastable states. *Phys Rev Lett* 94:58101.
- Harris TE (2002): *The Theory of Branching Processes*. New York: Courier Dover Publications.
- Hopfield JJ (1982): Neural networks and physical systems with emergent collective computational abilities. *Proc Natl Acad Sci USA* 79:2554–2558.
- Kinouchi O, Copelli M (2006): Optimal dynamical range of excitable networks at criticality. *Nat Phys* 2:348–351.
- Leopold DA, Murayama Y, Logothetis NK (2003): Very slow activity fluctuations in monkey visual cortex: Implications for functional brain imaging. *Cereb Cortex* 13:422–433.
- Levina A, Herrmann JM, Geisel T (2007): Dynamical synapses causing self-organized criticality in neural networks. *Nat Phys* 3:857–860.
- Linkenkaer-Hansen K, Nikouline VV, Palva JM, Ilmoniemi RJ (2001): Long-range temporal correlations and scaling behavior in human brain oscillations. *J Neurosci* 21:1370–1377.
- Linkenkaer-Hansen K, Nikulin VV, Palva JM, Kaila K, Ilmoniemi RJ (2004): Stimulus-induced change in long-range temporal correlations and scaling behaviour of sensorimotor oscillations. *Eur J Neurosci* 19:203–218.
- Linkenkaer-Hansen K, Smit DJA, Barkil A, van Beijsterveldt TEM, Brussaard AB, Boomsma DI, van Ooyen A, de Geus EJC (2007): Genetic contributions to long-range temporal correlations in ongoing oscillations. *J Neurosci* 27:13882–13889.
- Lopes da Silva FH, Pijn JP, Velis D, Nijssen PCG (1997): Alpha rhythms: Noise, dynamics and models. *Int J Psychophysiol* 26:237–249.
- Mantini D, Puerucci MG, Del Gratta C, Romani GL, Corbetta M (2007): Electrophysiological signatures of resting state net-

- works in the human brain. *Proc Natl Acad Sci USA* 104:13170–13175.
- Marder E, Goaillard JM (2006): Variability, compensation and homeostasis in neuron and network function. *Nat Rev Neurosci* 7:563–574.
- Maxim V, Sendur L, Fadili J, Suckling J, Gould R, Howard R, Bullmore E (2005): Fractional Gaussian noise, functional MRI and Alzheimer's disease. *NeuroImage* 25:141–158.
- Mazzoni A, Broccard FD, Garcia-Perez E, Bonifazi P, Ruaro ME, Torre V (2007): On the dynamics of the spontaneous activity in neuronal networks. *PLoS ONE* 2:e439.
- Monto S, Vanhatalo S, Holmes MD, Palva JM (2007): Epileptogenic neocortical networks are revealed by abnormal temporal dynamics in seizure-free subdural EEG. *Cereb Cortex* 17:1386–1393.
- Nikulin VV, Brismar T (2005): Long-range temporal correlations in electroencephalographic oscillations: Relation to topography, frequency band, age and gender. *Neuroscience* 130:549–558.
- Peng CK, Buldyrev SV, Havlin S, Simons M, Stanley HE, Goldberger AL (1994): Mosaic organization of DNA nucleotides. *Phys Rev E* 49:1685.
- Plenz D, Thiagarajan TC (2007): The organizing principles of neuronal avalanches: Cell assemblies in the cortex? *Trends Neurosci* 30:101–110.
- Stead M, Worrell GA, Litt B (2005): Frequency and dependence of long range temporal correlations in human hippocampal energy fluctuations. *Complexity* 10:35–44.
- Steriade M, Gloor P, Llinas RR, Lopes de Silva FH, Mesulam MM (1990): Report of IFCN Committee on Basic Mechanisms. Basic mechanisms of cerebral rhythmic activities. *Electroencephalogr Clin Neurophysiol* 76:481–508.
- van Ooyen A (1994): Activity-dependent neural network development. *Network Comput Neural Syst* 5:401–423.
- Vanhatalo S, Palva JM, Holmes MD, Miller JW, Voipio J, Kaila K (2004): Infraslow oscillations modulate excitability and interictal epileptic activity in the human cortex during sleep. *Proc Natl Acad Sci USA* 101:5053–5057.
- Zhang W, Linden DJ (2003): The other side of the engram: Experience-driven changes in neuronal intrinsic excitability. *Nat Rev Neurosci* 4:885–900.