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Strobing brain thunders: Functional correlation of extreme activity events

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ABSTRACT

The recent upraise of interest in the dynamics of the brain resting activity opens a number of new and different questions. A fundamental one is related to the character of correlations of healthy large scale brain activity. These studies focus on the linear correlation of the spontaneous activity between brain sites. Here we present a different approach, instead to estimate the average linear correlation of activity between pairs of brain sites, we ask: what are average sequels in space and time of a big event (i.e., a thunder). By strobing these events we find that on average the activity variations with opposite sign are correlated in time, over a temporal scale of few seconds, exposing a critical balance between excitation and depression opposing forces.

1. Introduction

An increasing number of reports deals with spontaneous brain dynamics at large scale. It is known that the brain activity at this coarse scale organizes into relatively few spatio-temporal patterns, as revealed experimentally in recent years [1]. A wide range of experiments using functional Magnetic Resonance Imaging (fMRI) have emphasized that these spatial clusters of coherent activity, termed Resting State Networks (RSN) [2], are specifically associated with neuronal systems responsible for sensory, cognitive and behavioral functions [3]. Furthermore, the pattern of correlations in these networks has been shown to change with various cognitive and pathophysiological conditions [1]. At the same time studies have shown that the RSN activity exhibits peculiar scaling properties, resembling dynamics near the critical point of a second order phase transition [4–6], consistent with evidence showing that the brain at rest is near a critical point [7]. More precisely, these empirical findings are in line with experimental results on spontaneous activity in cortical systems in vitro and in vivo [8–10] and with computational modeling results [11–18]. Indeed, spontaneous neuronal activity generally exhibits slow oscillations between bursty periods, followed by substantially quiet periods. Bursts can last from a few to several hundreds of milliseconds and, if analyzed at a finer temporal scale, show a complex structure in terms of neuronal avalanches. In vitro experiments allow to record avalanche activity [8,19] from mature organotypic cultures of rat somatosensory cortex where they spontaneously emerge in superficial layers. The size and duration of neuronal avalanches follow power law distributions with very stable exponents, which is a typical feature of a system acting in a critical state, where large fluctuations are present and the response does not have a characteristic size. The same critical behavior has been measured also in vivo from rat cortical layers during early post-natal development [20], from the cortex of awake adult rhesus monkeys [10], using microelectrode array recordings, as well as for dissociated neurons from rat hippocampus [21,22] or leech ganglia [21]. Operating at a critical level, far from an uncorrelated subcritical or a too correlated supercritical regime, may optimize information

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management and transmission in real brains, as recently confirmed by experiments [23].

The emergence of power law distributions has been interpreted in terms of self-organized criticality (SOC) [4]. The term SOC usually refers to a mechanism of slow energy accumulation and fast energy redistribution driving the system toward a critical state, where the avalanche extensions and durations follow power law distributions. The simplicity of the mechanism at the basis of SOC has suggested that many physical and biological phenomena characterized by power laws in the size distribution represent natural realizations of the SOC idea. For instance, SOC has been proposed to model earthquakes [24,25], the evolution of biological systems [26], solar flare occurrence [27], fluctuations in confined plasma [28], snow avalanches [29], and rainfall [30]. Understanding the brain electrical activity at large scale is a fundamental issue, which cannot be derived from the abundance of information at the microscopic level. As an analogy, weather forecasting hardly could be inferred from local data in the absence of a good model of large scale atmosphere dynamics.

This special issue is dedicated to our colleague and friend Werner who knew first-hand how important the global picture can be to understand the brain. In multiple occasions in the last years of his long tenure as a brilliant physiologist he insisted on the importance of applying concepts coming from different fields to the understanding of brain dynamics. In particular, Werner adopted in his studies methods coming from critical phenomena and complex systems [31] noticing that "the molecular rearrangement becomes at the macroscopic level manifest as a set of qualitatively new properties that could not be deduced from the microscopic state change, nor could it be anticipated from the prior macroscopic state" [32]. This interdisciplinary approach indeed represents a conceptual framework able to provide new insights into brain dynamics.

The interest for mesoscopic brain dynamics is not new, of course. It is inspiring to read that the father of brain modeling Warren McCulloch, more than 60 years ago, was concerned with the same issues than Werner and us today. Together with Dusser de Barenne, Warren McCulloch and colleagues [36,37] experimented inducing local seizures by applying small drops of strychnine in several regions of the monkey cortex while recording cortical electrical activity simultaneously in twenty sites across the entire cortex. This clever technique, mastered by Dusser de Barenne, received the name of strychnine neuronography, which can be considered the earliest attempt to study brain functional connectivity, by inducing some liminal activity in a given area and recording the co-active cortical sites. Typically, they noticed that the initial activity induced by the strychnine remained local, and did not spread to the entire cortex. However, not without surprise, they noted that, less often, the activity was recorded in very far away locations.

Fig. 1 (redrawn from the original sketches in [35]) summarizes these early observations together with our own rough estimations in Panel D. Filled circles in Panel D represent the distribution of edge lengths, computed from the drawing in Panel A as the Euclidean distance (using arbitrary units) between the location of each strychnine instillation and the resulting activation site/s. Note that, despite the scarcity of the data, the results demonstrate long range correlations, the exponent being similar to the estimations using fMRI [34]. For example an application in the frontal cortex induced sometimes activity as far as to the occipital cortex. Nowadays, is not difficult to admit that frontal activation will evoke visual images and vice versa, however McCulloch knew that much before us.

2. Conditional probability approach

Here we present a statistical analysis of experimental data of functional magnetic resonance inspired by a novel interdisciplinary approach: we apply a method developed to detect correlations in magnitude, time and spatial location between successive earthquakes [38] in seismic catalogs. This analysis is very difficult to perform since statistical noise hides the presence of correlations. The method, comparing probabilities evaluated in the real catalog with a catalog made uncorrelated by reshuffling, is able to subtract the effect of noise. Our aim is to investigate the existence and features of spatio-temporal correlations in activity variations. More precisely, the analysis aims at enlightening the structure of these correlations and their relationship with the spatial and temporal distance between successive variations. The study focuses on correlations between large events, analogously to a recent work [39] that analyzed the gradual and continuous changes in the brain blood oxygenated level dependent (BOLD) signal to estimate functional connectivity from resting BOLD events triggered average. The activity $B(\vec{r}_i, t)$ is monitored at each voxel i as function of time. Data are recorded in time every $\delta t = 2.5$ s, therefore time is measured in unit of δt. We focus our study only on extreme activity events (thunders) and therefore analyze voxels for which $B(\vec{r}_i, t)$ is larger than a given threshold $B_c = 18{,}000$, value that selects the largest 10% of the entire activity range. Namely, we substitute the below-threshold values with zero and leave the above-threshold values of $B(\vec{r}_i, t)$ unchanged. The local activity variations at each voxel are evaluated as $s_i(t) = B(\vec{r}_i, t + \delta t) - B(\vec{r}_i, t)$, which can have positive and negative values. As a first attempt, we simply calculate the average cross-correlation function on the entire set of data as

$$G(\tau) = \langle \overline{(s_i(t+\tau) - \overline{s_i(t)})(s_j(t+\tau) - \overline{s_j(t)})} \rangle \quad (1)$$

where the bar indicates the temporal average, whereas brackets stand for the average over all possible voxel couples. In order to evaluate the role of statistical noise on this quantity, we calculate $G(\tau)$ also in a catalog where $s_i(t)$ values are reshuffled in time and space. In this way, the data set we generate is uncorrelated by construction and therefore should show a cross-correlation function fluctuating around zero. The amplitude of fluctuations is a measure of the statistical noise present in the catalog. In Fig. 2 we plot $G(\tau)$ for both data sets. In the original catalog the cross-correlation exhibits strong fluctuations over a range comparable to the one measured in the uncorrelated data set. It is therefore quite difficult to extract information on