Modelling the brain as an Apollonian network

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Networks of living neurons exhibit an avalanche mode of activity, experimentally found in organotypic cultures. Moreover, experimental studies of morphology indicates that neurons develop a network of small-world-like connections, with the possibility of very high connectivity degree. Here we study a recent model based on self-organized criticality, which consists in an electrical network with threshold firing and activity-dependent synapse strengths. We study the model on a scale-free network, the Apollonian network, which presents many features of neuronal systems. The system exhibits a power law distributed avalanche activity. The analysis of the power spectra of the electrical signal reproduces very robustly the power law behaviour with the exponent 0.8, experimentally measured in electroencephalograms (EEG) spectra. The exponents are found quite stable with respect to initial configurations and strength of plastic remodelling, indicating that universality holds for a wide class of brain models.

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I. INTRODUCTION

Neuronal networks exhibit diverse patterns of activity, including oscillations, synchronization and waves. During neuronal activity, each neuron can receive inputs by thousands of other neurons and, when it reaches a threshold, redistributes this integrated activity back to the neuronal network. Recently a neuronal activity based on avalanches has been observed in organotypic cultures from coronal slices of rat cortex [1] where neuronal avalanches are stable for many hours [2]. More precisely, recording spontaneous local potentials continuously by a multielectrode array, has shown that activity initiated at one electrode might spread to other electrodes not necessarily contiguous, as in a wave-like propagation. Cortical slices are then found to exhibit a new form of activity, producing several avalanches per hour of different duration, in which non-synchronous activity is spread over space and time. By analysing the size and duration of neuronal avalanches, the probability distribution reveals a power law behaviour, suggesting that the cortical network operates in a critical state. The experimental data indicate for the avalanche size distribution a slope varying between -1.2 and -1.9, depending on the accuracy of the time-binning procedure, with a value -1.5 for optimal experimental conditions. Interestingly, the power law behaviour is destroyed when the excitability of the system is increased, contrary to what expected since the incidence of large avalanches should decrease the power law exponent. The distribution then becomes bimodal, i.e. dominated either by very small or very large avalanches as in epileptic tissue. The power law behaviour is therefore the indication of an optimal excitability in the system spontaneous activity. Moreover the avalanche time duration is also found to follow a power law behaviour as function of the duration time normalised by the binning time with an exponent equal to -2.0 followed by an exponential cutoff. These results have been interpreted relating spontaneous activity in a cortical network to a critical branching process [3], indeed the experimental branching parameter is very close to the critical value equal to one, at which avalanches at all scales exist.

On the other hand, the dynamics observed in spontaneous brain activity is very similar to self-organized criticality (SOC) [4, 5, 6, 7]. 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 distribution of avalanche sizes is a power law obtained without fine tuning: no tunable parameter is present in the model. 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 SOC. For instance, SOC has been proposed to model earthquakes [3, 8, 10], the evolution of biological systems [11], solar flare occurrence [12], fluctuations in confined plasma [13], snow avalanches [14] and rain fall [15].

Moreover, power law behaviour is observed in power spectra of different time series monitoring neural activities. Prominent examples are EEG data which are used by neurologists to discern sleep phases, diagnose epilepsy and other seizure disorders as well as brain damage and disease [16, 17]. Another example of a physiological function which can be monitored by time series analysis is the human gait which is controlled by the brain [18]. For all these time series the power spectrum, i.e. the square of the amplitude of the Fourier transformation double logarithmically plotted against frequency, generally features a power law at least over one or two orders of magnitude...
with exponents between 1 and 0.7. Moreover, experimental results show that the neurotransmitter secretion rate exhibits fluctuations with time having power law behaviour \[ ] and power laws are observed in fluctuations of extended excitable systems driven by stochastic fluctuations \[20\].

On the basis of these observations, recently a model based on SOC ideas and taking into account synaptic plasticity in a neural network \[21\] has been proposed. Plasticity is one of the most astonishing properties of the brain, occurring mostly during development and learning \[22, 23, 24\], and can be defined as the ability to modify the structural and functional properties of synapses, properties which are thought to underlie memory and learning. Among the postulated mechanisms of synaptic plasticity, the activity dependent Hebbian plasticity constitutes the most fully developed and influential model of how information is stored in neural circuits \[25, 26, 27\]. Within a SOC approach the four most important ingredients for neuronal activity have been introduced, namely threshold firing, neuron refractory period, activity-dependent synaptic plasticity and pruning.

The system consists in an electrical network on a square lattice, on which each site represents the cell body of a neuron, each bond a synapse. Therefore, each site is characterized by a potential and each bond by a conductance. Whenever at a given time the value of the potential at a site is above a certain threshold, approximately equal to \(-55 mV \) for the real brain, the neuron fires, i.e. generates an "action potential", distributing charges to its connected neighbours in proportion to the current flowing through each bond. After firing, a neuron goes back to the resting potential of \(-70 mV \) and remains inactive during the refractory period, when it is unable to send or receive information from other neurons. This time corresponds for real neurons to the physiological time needed to reset ion channels after the transmission of the action potential through the axon. The conductances, on the other hand, represent Hebbian synapses, for which the conjunction of activity at the presynaptic and postsynaptic neuron modulates the efficiency of the synapse \[27\]. To this extent, each time a synapse transmits an action potential between active neurons, its strength is increased proportionally to the intensity of the transmitted signal, whereas synapses inactive during a neuronal avalanche have their strength decreased, as for Hebbian rules. Synapses successively weakened may have their strength finally set to zero, i.e. are "pruned", eliminating that particular connection between neurons. Pruning implies that, as activity goes on, the initial regular lattice is transformed, some patterns are strengthened and the connectivity of some neurons decreased. The system exhibits an avalanche activity power law distributed with an exponent close to \(-1.5\), as measured for spontaneous activity \[1\]. The analysis of the power spectra of the electrical signal reproduces very robustly the power law behaviour with the exponent 0.8, experimentally measured in EEG spectra. The same value of both exponents is found considering leaky neurons or introducing a small percentage of inhibitory synapses, indicating that universality holds for a wide class of brain models.

In real brain neurons are known to be able to develop an extremely high number of connections with other neurons, that is a single cell body may receive inputs from even a hundred thousand presynaptic neurons. One of the most fascinating questions is how an ensemble of living neurons self-organizes, developing connections to give origin to a highly complex system. The dynamics underlying this process should be driven both by the aim of realizing a well connected network leading to efficient information transmission, and the energetic cost of establishing very long connections. The morphological characterization of a neuronal network grown \textit{in vitro} has been studied \[28\] by monitoring the development of neurites in an ensemble of few hundred neurons from the frontal ganglion of adult locusts. After few days the cultured neurons have developed an elaborated network with hundreds of connections, whose morphology and topology has been analysed by mapping it onto a connected graph. The short path length and the high clustering coefficient measured indicate that the network belongs to the category of small-world networks \[29\], interpolating between regular and random networks. However, the system grown \textit{in vitro} necessarily lacks some features of \textit{in vivo} systems, therefore the average node connectivity is found equal only to few units and the "scale-free" feature \[30\] of many real networks was not recovered. Small-world networks are characterized by an efficient information transmission with a small number of long range connections. The activity dependent brain model \[21\] has been implemented on small world networks, by rewiring a small percentage of the square lattice bonds. Again universal scaling behaviour is recovered for both the avalanche distribution and the power spectra. The simple rewiring procedure, however, only allows long range connections leaving the average node connectivity equal to a few units, as for \textit{in vitro} systems.

In this paper we investigate the behaviour of the activity dependent brain model on scale-free networks, whose feature are closer to the morphology of neuronal networks in living brains. Scale-free networks are indeed characterized by a power law distribution of the node connectivity, allowing a high number of connections per neuron. We develop the model on the Apollonian network \[31\], that has the property of being simultaneously small-world and scale-free and therefore exhibits all characteristics found for neuronal networks. Analogously to previous studies, we analyse the behaviour of the avalanche size and duration distribution and the power spectra related to electrical activity. We also study a system composed by both excitatory and inhibitory synapses, to be closer to real brains. The paper is organized as follows: In sect.\[\] the scale-free Apollonian network is described, whereas in section\[11\] the activity dependent brain model is presented and the results on brain activity are discussed in section\[\]. Concluding remarks are given in section\[\].
II. APOLLONIAN NETWORK

The Apollonian network has been recently introduced \cite{31} in a simple deterministic version starting from the problem of space-filling packing of spheres according to the ancient Greek mathematician Apollonius of Perga. In its classical version the network associated to the packing gives a triangulation that physically corresponds to the force network of the packing. One starts with the zero-th order triangle of corners $P_1, P_2, P_3$, places a fourth site $P_4$ in the center of the triangle and connects it to the three corners ($n = 0$). This operation will divide the original triangle in three smaller ones having in common the central site. The iteration $n = 1$ proceeds placing one more site in the center of each small triangle and connecting it to the corners (Fig.1). At each iteration $n$, going from 0 to $N$, then the number of sites increases by a factor 3 and the coordination of each already existing site by a factor 2. More precisely, at generation $N$ there are

$$m(k, N) = 3^N, 3^{N-1}, 3^{N-2}, \ldots, 3^2, 3, 1, 3$$

vertices with connectivity degree

$$k(N) = 3, 3 \times 2, 3 \times 2^2, \ldots, 3 \times 2^{N-1}, 3 \times 2^N, 2^{N+1} + 1$$

respectively where the two last values correspond to the site $P_4$ and the three corners $P_1, P_2, P_3$. The maximum connectivity value then is the one of the very central site $P_4$, $k_{\text{max}} = 3 \times 2^N$, whereas the sites inserted at the $N$-th iteration will have lowest connectivity 3.

The important property of the Apollonian network is that it is scale-free. In fact, it has been shown \cite{31} that the cumulative distribution of connectivity degree $P(k) = \sum_{k' > k} m(k, N)/N_N$, where $N_N = 3 + (3^{N+1} - 1)/2$ is the total number of sites at generation $N$, has a power law behaviour with $k$. More precisely, $P(k) \propto k^{1-\gamma}$, with $\gamma = \ln 3/\ln 2 \sim 1.585$. Moreover the network has small-world features. This implies \cite{28} that the average length of the shortest path $l$ behaves as in random networks and grows slower than any positive power of $N$, i.e. $l \propto (\ln N)^{3/4}$. Furthermore the clustering coefficient $C$ is very high as in regular networks ($C = 1$) and contrary to random networks. For the Apollonian network $C$ has been found to be equal to 0.828 in the limit of large $N$. On this basis the Apollonian network appears to have all the features typical of neuronal networks: small-world property found experimentally \cite{28} and possibility of very high connectivity degree (scale-free). Moreover it also presents bonds connecting sites of all lengths. Also this last feature is characteristic of neuronal networks in brain cortex, where the length of an axon connecting the pre-synaptic with the post-synaptic neuron can vary over several orders of magnitude, from $\mu m$ to $cm$.

III. ACTIVITY DEPENDENT MODEL

On a Apollonian network at generation $N$, we assign at each site a neuron at potential $v_i$ and at each bond a synapse of conductance $g_{ij}$. Whenever at time $t$ the value of the potential at a site $i$ is above a certain threshold $v_i \geq v_{\text{max}}$, the neuron generates an action potential, distributing charges to connected neurons in proportion to the current flowing through each bond

$$v_j(t + 1) = v_j(t) + v_1(t) \frac{i_{ij}(t)}{\sum_k i_{ik}(t)}$$

(1)

where $v_j(t)$ is the potential at time $t$ of site $j$, connected to site $i$, $i_{ij} = g_{ij}(v_i - v_j)$ and the sum is extended to all $k$ sites connected to site $i$ that are at a potential $v_k < v_i$. After firing a neuron is set to a zero resting potential.

The conductances can be initially all set equal or else random between 0 and 1, whereas the neuron potentials are uniformly distributed random numbers between $v_{\text{max}} - 2$ and $v_{\text{max}} - 1$. In agreement with the SOC scenario, the initial state for the voltage is not relevant since the system evolves toward the same critical state regardless of the initial condition. The potential is fixed to zero at the three sites 1,2,3 where information can flow out of the system. The external stimulus can be imposed at one input site chosen either fixed or at random, this last case modelling more closely spontaneous brain electrical activity.

The firing rate of real neurons is limited by the refractory period, i.e. the brief period after the generation of an action potential during which a second action potential is difficult or impossible to elicit. The practical implication of refractory periods is that the action potential does not propagate back toward the initiation point and therefore is not allowed to reverberate between the cell body and the synapse. In the model, once a neuron fires, it remains quiescent for one time step and is therefore unable to accept charge from firing connected neurons. This ingredient indeed turns out to be crucial.
for a controlled functioning of the numerical model. In this way an avalanche of charges can propagate far from the input through the system.

As soon as a site is at or above threshold \( v_{\text{max}} \) at a given time \( t \), it fires according to Eq. (1). Then the conductance of all the bonds, connecting to active neurons and that have carried a current, is increased in the following way

\[
g_{ij}(t+1) = g_{ij}(t) + \delta g_{ij}(t)
\]

where \( \delta g_{ij}(t) = A\alpha i_j(t) \), with \( \alpha \) being a dimensionless parameter and \( A \) a unit constant bearing the dimension of an inverse potential. After applying Eq. (2) the time variable of the simulation is increased by one unit. Eq. (2) describes the mechanism of increase of synaptic strength, tuned by the parameter \( \alpha \). This parameter then represents the ensemble of all possible physiological factors influencing synaptic plasticity, many of which are not yet fully understood.

Once an avalanche of firings comes to an end, the conductance of all the bonds with non-zero conductance is reduced by the average conductance increase per bond, \( \Delta g = \sum_{ij} \delta g_{ij}(t)/N_b \), where \( N_b \) is the number of bonds with non-zero conductance. The quantity \( \Delta g \) depends on \( \alpha \) and on the response of the brain to a given stimulus. In this way the network "memorizes" the most used paths of discharge by increasing their conductance, whereas the less used synapses atrophy. Once the conductance of a bond is below an assigned small value \( \sigma_t \), it is removed, i.e. is set equal to zero, which corresponds to what is known as pruning. This remodelling of synapses mimicks the fine tuning of wiring that occurs during "critical periods" in the developing brain, when neuronal activity can modify the synaptic circuitry once the basic patterns of brain wiring are established [22]. These mechanisms correspond to a Hebbian form of activity dependent plasticity, where the conjunction of activity at the presynaptic and postsynaptic neuron modulates the efficiency of the synapse [27]. To insure the stable functioning of neural circuits, both strengthening and weakening rules of Hebbian synapses are necessary to keep instabilities due to positive feedback [32]. However, differently from the well known Long Term Potentiation (LTP) and Long Term Depression (LTD) mechanisms, the modulation of synaptic strength does not depend on the frequency of synapse activation [22, 33, 34]. The external driving mechanism to the system is imposed by setting the potential of the input site to the value \( v_{\text{max}} \), corresponding to one stimulus. This external stimulus is needed to keep the system functioning and therefore mimicks the living brain activity. The discharge evolves until no further firing occurs, then the next stimulus is applied.

IV. NUMERICAL RESULTS

We consider an Apollonian net at the generation \( N = 9 \) (29527 neurons and 177150 synapses). The three corner sites of the system have always zero potential and represent open boundary conditions. The input site is either chosen at random or fixed. It is worth noticing that the case of random input sites simulates more closely the spontaneous activity of the system. Synapses can be excitatory or inhibitory with probability \( p_{\text{inh}} \). Initial conductances can be either all equal to \( g_0 = 0.25 \) or randomly distributed between 0 and 1. The other parameters in the simulation are: firing threshold \( v_{\text{max}} = 6 \) and conductance cut-off for pruning \( \sigma_t = 0.0001 \). Their value does not influence the simulation results.

Pruning

The strength of the parameter \( \alpha \), controlling both the increase and decrease of synaptic strength, determines the plasticity dynamics in the network. In fact, the more the system learns strengthening the used synapses, the more the unused connections will weaken. We apply a sequence of external stimuli and we measure the total number of pruned bonds at the end of each avalanche, \( N_{pb} \). This quantity in general could depend on the initial conductance \( g_0 \), therefore the two cases of all initial conductances equal to 0.25, and uniformly distributed between 0 and 1, are investigated.

First the case of equal initial conductances is analysed. For each value of \( \alpha \) the average number of pruned bonds, \( N_{pb} \), is monitored as function of time, where a time unit corresponds to the application of an external stimulus. For input sites randomly chosen at each stimulus, Fig.2 shows that pruning starts after a certain time, since all conductances are initially equal to 0.25, and \( N_{pb} \) increases more rapidly with time for larger \( \alpha \). The plateau is reached after about 5000 stimuli (for every \( \alpha \)) after which \( N_{pb} \) increases only of few units in time. From the asymptotic value of each curve we can evaluate the
starts already at $n = 0$, since conductances close to zero are present, and the plateau is reached after about 3000 stimuli. The value of $\alpha$ which now optimizes the number of active bonds is about 0.030. Finally the pruning behaviour for different iterations is similar to the previous case, with the pruning probability also increasing with $n$ exponentially as $N_{pb} \simeq \exp n$.

The effect of pruning on the connectivity degree of the network (Fig.4) has also been analysed, i.e. the number of sites with a given connectivity degree $k$ as function of $t$ for equal initial conductances and $\alpha = 0.020$. In the inset the corresponding behaviour of the number of pruned bonds.

Spontaneous activity: avalanche distributions

After training the system applying plasticity rules during $N_p$ external stimuli, we now submit the system to a new sequence of stimuli with no modification of synapse strength. The response of the system to this second sequence models the brain spontaneous activity, which is analysed by measuring the avalanche size distribution $n(s)$, the time duration distribution $n(T)$, and the power spectrum $S(f)$.

The avalanche size distribution $n(s)$ consistently exhibits power law behaviour for different values of model parameters. Fig.5 shows the avalanche size distribution for different values of $N_p$, including also the case $N_p = 0$ (no plasticity training) for random initial conductances. We notice that, for fixed size $s$, increasing $N_p$ decreases the number of avalanches of that size, suggesting that strong plasticity remodelling decreases activity. The ex-

FIG. 3: (Color online) Probability of pruning for bonds of different iterations $n$ as function of time for equal initial conductances. In the inset, the asymptotic $N_{pb}$ (after 5000 stimuli) as function of $n$ with the exponential fit $N_{pb} \simeq \exp 1.2n$.

FIG. 4: (Color online) Connectivity degree distribution $n(k)$ at different pruning stages $t$ for equal initial conductances and $\alpha = 0.020$. In the inset the corresponding behaviour of the number of pruned bonds.
ponent appears to be independent of $N_p$ as long as the number of pruned bonds, $N_{pb}$, is far from the plateau (see inset in Fig.5). Similar results are found for equal initial conductances. The value of the exponent is $\sigma = 1.8 \pm 0.2$ and is stable with respect to variations of the parameter $\alpha$ for both equal and random initial conductance. This value is compatible within error bars with the value found in the experiments of Beggs and Plentz [1], $1.5 \pm 0.4$, and with previous results of the model on both regular and small world lattices. This suggests that the high level of connectivity reduces the probability of very large avalanches but does not change substantially the spontaneous activity behaviour. For larger $N_p$, the distribution exhibits an increase in the scaling exponent and finally looses the scaling behaviour for very large $N_p$ values in the plateau regime for the number of pruned bonds.

It is important to investigate the role of the choice of fixed input site, since in the Apollonian network, contrary to the regular network, sites may have very different connectivity degree. Fig.6 shows the avalanche size distribution for input sites randomly chosen among sites with the same connectivity degree $k$. For connectivity degree $k = 3$ or $k = 6$ exhibits power law behaviour with the same exponents found for random input site: $\sigma = 1.8 \pm 0.2$ for equal and random initial conductances. This value is found to be stable with respect to different $\alpha$ (Fig.7) and $N_p$, provided that the number of pruned bonds $N_{pb}$ is lower than the plateau for that value of $\alpha$. Moreover it does not depend on the choice of the input site, either fixed or random. Finally both values agree within error bars with the value 2.0, exponent found experimentally by Beggs and Plentz [1].

**Power spectra for spontaneous activity**

In order to compare the results of the Apollonian network with EEG medical data, the power spectrum of the resulting time series can be calculated. For this purpose, the number of active neurons is monitored as function of time during spontaneous activity. Fig.8 shows an example of neuronal activity where avalanches of all sizes can be generated in response to the external stimulus. The power spectrum is calculated as the squared amplitude of the Fourier transform as function of frequency, averaged over many sequences of external stimuli.

Fig.9 shows the spectrum for equal initial conductances for different values of $N_p$, random initial conductances, $\alpha = 0.030$ and random input site. In the inset the corresponding behaviour of the number of pruned bonds.
FIG. 7: (Color online) Avalanche duration distribution for different values of $\alpha$ (random initial conductances, random input sites, $N_p = 500$). The dotted line has slope 2.1.

FIG. 8: Total current flowing in the system as function of time. Avalanches of all sizes can be observed.

and different values of $N_p$. For $N_p = 0$, i.e. when no plasticity mechanism is applied, the spectrum has a behaviour $1/f$, characteristic of SOC. For values of $N_p$ different from zero but before $N_{pb}$ reaches the plateau, one can distinguish two different regimes: a power law behaviour with exponent $\beta = 0.8 \pm 0.1$ at high frequency, followed by a crossover toward white noise at low frequency. However, for $N_p = 2000$ (close to the plateau value for $N_{pb}$) the scaling behaviour with exponent 0.8 is detected over a wider frequency range. The difference between $\beta = 1$ for $N_p = 0$ and $\beta \simeq 0.8$ for higher $N_p$, suggests that the existence of plasticity rules reduces the power spectrum exponent reaching agreement with experimental EEG spectrum \[36, 37\]. The stability of the exponent with respect to $\alpha$ has also been verified, finding consistently $\beta = 0.8 \pm 0.1$ at high frequency. Finally the power spectrum for fixed input site shows a scaling exponent $\beta = 0.8 \pm 0.1$ over two orders of magnitude. The measured value for the power spectra exponent is in agreement with the expected relation with the scaling exponent of the avalanche duration distribution $\beta = 3 - \tau$, being $-\tau < -1$.\[5\].

The scaling behaviour of the power spectrum can be interpreted in terms of a stochastic process determined by multiple random inputs \[38\]. In fact, the output signal resulting from different and uncorrelated superimposed processes is characterized by a power spectrum with power law behaviour and a crossover to white noise at low frequencies. The crossover frequency is related to the inverse of the longest characteristic time among the superimposed processes. The value of the scaling exponent depends on the ratio of the relative effect of a process of given frequency on the output with respect to other processes. $1/f$ noise corresponds to a superposition of processes of different frequency having all the same relative effect on the output signal. In our case the scaling exponent is smaller than unity, suggesting that processes with high characteristic frequency are more relevant than processes with low frequency in the superposition \[38\].

**Inhibitory synapses**

In the mature living brain synapses can be excitatory or inhibitory, namely they set the potential of the postsynaptic membrane to a level closer or farther, respectively, to the firing threshold. This ingredient can be introduced by considering each synapse inhibitory with probability $p_{in}$ and excitatory with probability $1 - p_{in}$. The avalanche size and duration distributions show that the exponents $\sigma$ and $\tau$ increase for increasing $p_{in}$, therefore for a high percentage of inhibitory synapses the probability of large avalanches decreases (Fig.10). On the regular lattice for $p_{in} = 0.5$ no longer power law but exponential behaviour is found \[21\]. In the present case scaling behaviour persists due to the very high connectivity

FIG. 9: (Color online) Power spectra for different $N_p$, equal initial conductances, $\alpha = 0.020$ and random input sites.
degree, suggesting that the Apollonian network is better suited to model the neural connections in the brain.

The power spectra for different values of $p_{in}$ exhibit a complex behaviour. In fact, for a small fraction of inhibitory synapses ($p_{in} \leq 0.05$) the power law exponent $\beta$ increases with respect to the case where synapses are all excitatory up to a value 1.2. Then, for $p_{in} \sim 0.10$, the exponent decreases toward values compatible with experimental results, i.e. between 0.7 and 1.0. By increasing further the percentage of inhibitory synapses, to values close or greater than 0.2, the spectrum becomes the one of white noise.

V. CONCLUSIONS

Extensive simulations have been performed for the activity dependent brain model implemented on the scale-free Apollonian network. The results are compared with previous simulations on regular and small world lattices and with experimental data. We first find the striking result that an optimal value of of the plasticity strength $\alpha$ exists with respect to the pruning process. Moreover, it appears that synapses of later generations, deeply embedded in the network, are pruned with higher probability with respect to bonds of the early generations, mostly long range, that optimize information transmission. Moreover the avalanche size distribution shows a power law behaviour with an exponent $\sigma = 1.8 \pm 0.2$ for equal and random initial conductances. This value is compatible with $1.5 \pm 0.4$, experimentally found for neuronal avalanches and recovered by the model on the square lattice and small world networks. Also the avalanche duration distribution exhibits power law behaviour with an exponential cutoff, in agreement with experimental results of Beggs and Plenz [1]. The exponent has value $\tau = 2.1 \pm 0.2$ for equal and random initial conductance, in agreement with 2.0 found experimentally. Furthermore the power spectrum exhibits power law behaviour at high frequency with $\beta = 0.8 \pm 0.1$, in agreement with experimental data [21, 22]. At intermediate frequency the slope becomes greater than unity, crossing over to white noise at low frequencies. None of the scaling exponents for spontaneous activity in the case of excitatory synapses depends on the particular choice for the length or strength of the plasticity training and are quite stable with respect to the initial conductance configurations. These results suggest that also on Apollonian network universal behaviour found for regular and small world networks [21] holds. Furthermore, the scale-free Apollonian net provides an excellent description both of the morphology and the electrical activity properties of the brain.

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