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Published online: 16 Apr 2020.

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Network dilution and asymmetry in an efficient brain

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ABSTRACT

The ultimate goal of neuroscience is to ultimately understand how the brain functions. The advancement of brain imaging shows us how the brain continuously alternates complex activity patterns and experimentally reveals how these patterns are responsible for memory, association, reasoning, and countless other tasks. Two fundamental parameters, dilution (the number of connections per node), and symmetry (the number of bidirectional connections of the same weight) characterise two fundamental features underlying the networks that connect the single neurons in the brain and generate these patterns. Mammalian brains show large variations of dilution, and mostly asymmetric connectivity, unfortunately the advantages which drove evolution to these state of network dilution and asymmetry are still unknown. Here, we studied the effects of symmetry and dilution on a discrete-time recurrent neural network with McCulloch–Pitts neurons. We use an exhaustive approach, in which we probe all possible inputs for several randomly connected neuron networks with different degrees of dilution and symmetry. We find an optimum value for the synaptic dilution and symmetry, which turns out to be in striking quantitative agreement with what previous researchers have found in the brain cortex, neocortex and hippocampus. The diluted asymmetric brain shows high memory capacity and pattern recognition speed, but most of all it is the less energy-consumptive with respect to fully connected and symmetric network topologies.

1. Introduction

The human brain contains billions of neurons connected with more than a hundred trillion synapses which build countless structures forming anatomically distinguishable regions. Brain imaging allows us to observe the complex

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dynamical patterns of neural activation which occur while mental processes are executed. In this complex dynamical system perspective [1–6], each cell determines his activation state depending on its internal state, and on the activation state of the cells to which it is connected through synapses. Consequently, the single neuron activities collectively give rise to dynamical patterns. These dynamical patterns are universally acknowledged to be responsible for how the brain functions [3]. Several models [7,8] disregard the collective nature of brain functions, and give quantitative descriptions of single neuron behaviour based on patch-clamp voltage measurements [9]. However, many critical functions such as memory, pattern recognition and mathematical operations are carried out by one (or more than one) circuit rather than individual neurons. Even if it is still mostly unknown how the brain, or any distributed hierarchical-less computational system collective, carries out these complex functions [10,11], Hopfield developed a simplified approach to model how a circuit may store memories and associative behaviours [5,6]. This model demonstrates that discrete-time Recurrent Neural Networks (RNN) with randomly connected networks and McCulloch–Pitts neurons possess attractors (states that periodically repeat) which represent the stored memories or network stored behavioural patterns [12,13]. It is easy to demonstrate that discrete-time RNN with completely connected symmetric networks converge fast and possess many attractors [14]: unfortunately, these networks are efficient but far from a real biological system.

To represent realistic biological systems, however, one has to model asymmetric (mono-directional) connections: i.e. if a neuron A is connected to B, then B is not necessarily connected to A. Unfortunately, completely connected networks with asymmetric connections lead to exponentially long convergence time (inefficient computation) in which the network spends most of its time in a transient state before reaching the attractor [15], and for this reason these networks require enormous computational performance to be simulated. For this reason, standard modelling with asymmetric McCulloch–Pitts approaches fail to represent the cortex and hippocampus which performs pattern recognition in a few milliseconds.

The hippocampus is one of the brain regions responsible for memory, where the elaborated sensory input is driven to internal memory states enabling flexible and context-dependent decisions to be made, rather than simple reflexive actions in response to isolated stimuli. It is surprising that such processes, at the basis of any form of long-term programming and thinking, are located in areas of lower connectivity, if compared for example to the motor cortex and the cerebellum. The probability that anyone hippocampal CA3 neuron will contact another is approximately 0.04 (0.96 dilution) ([16,17]). Moreover, the neocortex has diluted connectivity and the probability that a neocortical pyramidal cell will contact a nearby one is in the order of 0.1 (0.9 dilutions) [18]. Similar values of the dilution are also found in monkey and mouse visual cortex [19,20], and in human cortex [21]: the reason for which evolution selected asymmetric

and diluted connectivity for these areas is still today an open question, which has been so far nearly unexplored [22–24]. In our previous research [25], we found that a discrete-time RNN with McCulloch–Pitts neurons possess two network conditions with optimal memory storage, a completely connected and symmetric condition and a diluted asymmetric condition. Furthermore, we show that the optimal RNN condition of dilution and asymmetry corresponds to the dilution and asymmetry values found in the hippocampus and the neocortex. We propose that evolution selected this condition among the two possible, because it requires the formation of fewer neuron connections, and it is therefore more feasible from a structure-development point of view. A completely connected network would be biologically unfeasible because the high number of connections it would require could not be accommodated in a realistic living brain since the number of connections would grow as the square of the number of neurons.

Here, we propose a numerical model, which, given arbitrary values of dilution and symmetry, allows us to simulate several networks and for each of them to retrieve all the attractors representing memory states. With this approach, we are able to analyse three main cortex properties: memory capacity, association speed, and energy consumption. We study four regions of dilution and symmetry: a complete-connected symmetric network, a complete-connected asymmetric network, a diluted symmetric network, and a dilute asymmetric network. In this paper, we call a complete-connected symmetric network the Hopfield network, and diluted symmetric network the diluted Hopfield network. We reproduce the fact that the Hopfield networks and the diluted asymmetric networks have optimal storage properties and memory retrieval. Moreover, we find that the diluted asymmetric networks have the unexpected characteristic of being more energy-efficient. Although our model is very general, we demonstrate that there exists an optimum degree of connectivity (number of synapses per neuron) for which the circuitry performance is drastically improved. The striking feature is that the optimum connectivity we retrieve both for symmetric and asymmetric networks have a diluted degree of connectivity which is very close to what is found in the mammalian visual cortex, neocortex, and hippocampus.

2. Recurrent neural network model

In this paper, we assume a discrete-time RNN composed of McCulloch–Pitts neurons [3,26] which is one of the most synthetic and minimal models capable of capturing the essential properties of a real cortical neuron network. Monte et al. [27] and Carnevale et al. [28] showed how RNNs can be used to model real cognitive processes, respectively, Monte et al. [27] presented a model that discusses how the prefrontal cortex integrates context information, and Carnevale et al. [28] presented a model that describes the response

modulation of the premotor cortex. This simple model incorporates the notion of multiple inputs (postsynaptic potentials), a threshold, and a single output (action potential). In such model, the state of the ith neuron $\sigma_i(t)$ is described mathematically by a discrete, two valued variable (0, 1), and the dynamic of the system is given by the discrete-time difference equation

$$h_i(t) = \sum_{j=1}^{N} J_{i,j}\sigma_j(t), \tag{1a}$$

$$\sigma_i(t+1) = \Theta[h_i(t) > \eta], \tag{1b}$$

where

- $h_i(t)$ is the total postsynaptic potential of the ith neuron at time t.
- $\sigma_j(t)$ is the state of the jth neuron at time t, 0 (resting state) or 1 (firing state).
- $\Theta = 1$ if $h_i(t) > \eta$ and 0 otherwise, η can be viewed as a threshold.
- $J_{i,j}$ is the connectivity matrix and represents the stored connections.

In such a model, a state of a N neurons neural network is a binary N-dimensional vector which can be regarded as a N digit binary number σ, and each neuron may be in a firing state ($\sigma_i(t) = 1$) or in a resting state ($\sigma_i(t) = 0$). Consequently, the total number of possible network states is 2^N. The evolution Equation (1) determines the network dynamics connecting any state at time t to the following at time $t+1$. Given a connectivity matrix J_{ij} and a threshold η, we get a deterministic dynamics, thus any state $\sigma(t)$ evolves in only a single state $\sigma(t+1)$. Consequently, there are three types of states: transient, recurring, and fixed points. Transient states are visited once by the dynamical system and never recur. Given an initial state that is transient the system travels through a sequence of transient state until it gets to a steady solution (the attractor): one or more states in a sequence that repeats at a specific period. If this steady solution is composed by a single state it is called a fixed point, otherwise we address it as a limit cycle of length L, where L is the number of states composing the period. The states in a limit cycle are recurrent states. Due to the fact that the space that is composed of all network states is discrete and finite, the evolution always brings to a fixed point or a limit cycle. A fixed point can be regarded as a limit cycle with $L=1$.

There are two general perspectives that try to explain how memories are stored in the brain. The first is the Hebbian perspective in which memories are stored by rewiring the neural network until each neural pattern associated with a memory becomes a stable attractor [29]. The second is the innate framework in which memories are stored associating to each memory a pre-existing attractor [25] or several lego-like pre-existing attractors [30]. In both perspectives, given an input, a neural network evolves until it reaches the relative

attractor, thus associating an input state (stimulus) to an output attractor (memory). Consequently, the number of attractors can be considered as an upper bound of the number of memories that can be stored [25]. Given this observation, it is reasonable to infer that neural networks with a single or few attractors may be considered to be inefficient memory devices with poor storing capability. On the other hand, neural networks with many attractors are able to classify inputs in many sub-categories. The number of attractors gives us an upper bound estimate of the memory capacity of the network.

We use an exhaustive numerical approach: it enables to retrieve how all the 2^N possible network states are driven to their specific attractors. Practically speaking, we account numerically for all the possible networks dynamics. Differently from previous theoretical approaches, which have focused on the study of fixed points of the network [31], our approach considers all the network attractors including periodic oscillations (limit cycles), which have a relevant role in brain activity [32,33].

In each numerical experiment, we generate the $J_{i,j}$ connectivity matrix randomly and then we retrieve all the network's attractors, by numerically iterating equation (1) for each possible input. An example of the result obtained by our numerical tool is reported in Figure 1 which represents the organisation of the states from a small neural network ($N=6$, $2^6 = 64$ possible states) with a transition graph. The states in the transition graph are represented with three
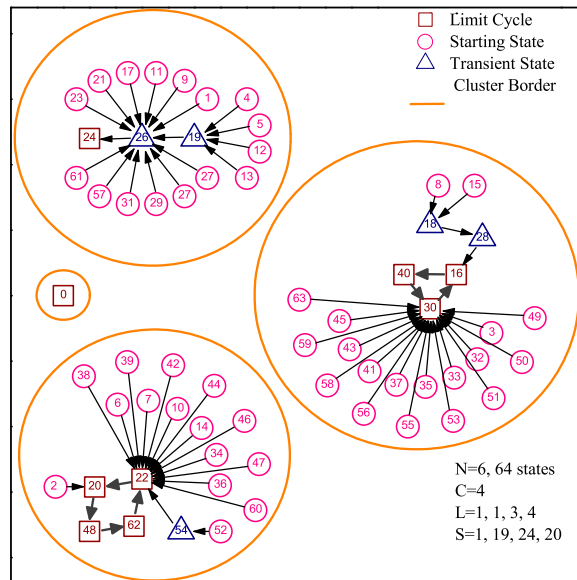
Figure 1. Schematic representation of the dynamic landscape of an asymmetric network. The 64 states of the network are subdivided into their basin (circled areas), each one with its attractor. These are labelled as starting (circles), transient (triangles), and attractors (squares) states. Arrows represent the transitions from any state $\sigma(t)$ to $\sigma(t+1)$.

geometrical markers: limit cycle states (squares), transient states (triangles and circles). The links in the graph represent the transitions from each state $\sigma(t)$ to $\sigma(t+1)$ that are given by the deterministic dynamics of the RNN. This particular realisation of the synaptic matrix produces four limit cycles (C=4). Of these limit cycles one is of length $L=4$, the other is of length $L=3$, and last two limit cycles are fixed points, $L=1$. The set of all transient states that converge to a given attractor is the basin of attraction of that particular attractor. The case in the figure illustrates the attractors' basins that have, respectively, sizes $S=20,24,19$ and 1. In this realisation, the maximum convergence time is 4 evolution steps; the minimum is 0. The dynamical evolution that associates the initial state to the attractor, models a system association process, in which we can assume that the association time is proportional to the number of transient states needed to recover the attractor [12,13]. The number of the attractors C represents an upper bound of the memory capacity of the network, while the number of the transient states represent the time needed to associate the sensory input to the associated limit behaviour.

We consider two major properties of the connectivity of a recurrent neural network symmetry ε, and dilution ρ. Symmetry expresses the degree to which any couple of neurons i and j with edges, $J_{i,j}$ and $J_{j,i}$ connecting them, have the same strength. Meanwhile, the dilution expresses the fraction of edges $J_{i,j}$ that are missing, $J_{i,j} = 0$. As in [25], to obtain a random network with a certain dilution value ρ and symmetry ε, we perform a convex sum over the matrix elements of a random symmetric matrix S_{ij}, and a random anti-symmetric matrix A_{ij},

$$J_{ij} = \left(1 - \frac{\epsilon}{2}\right)S_{ij} + \frac{\epsilon}{2}A_{ij}, \tag{2}$$

where the random symmetric and anti-symmetric matrices are generated in four steps. First, the upper diagonal elements are randomly generated with values from a uniform distribution defined in the closed interval $[-1, +1]$. Second, these randomly drawn elements are set to zero with probability ρ. Third, the lower diagonal elements are set either as $S_{ij} = S_{ji}$ for the symmetric matrices, or as $A_{ij} = -A_{ji}$ otherwise. Forth the diagonal elements are set to zero.

This model has been extensively studied in the symmetric, $\epsilon = 0$, and completely connected, $\rho = 0$, case, that is for all (i, j), $J_{i,j} = J_{j,i}$ and $J_{j,i} > 0$). In this case, one retrieves only fixed points and limit cycles with $L=2$, and the number of the attractors C (which grows exponentially with N). The opposite is true for asymmetric, $\epsilon = 1$ and completely connected, $\rho = 0$, networks, that is for all (i, j), $J_{i,j} \neq J_{j,i}$ and $J_{j,i} > 0$. These networks produce large average L (longer limit cycles) and store less information (smaller average C), for this reason, they have been disregarded in the majority of previous papers.

3. Results

Here, we present an extensive study of randomly sampled McCulloch–Pitts discrete-time RNN with given symmetry ε and dilution ρ. That is, for each sampled network, we probe all the 2^N states which allow us to reconstruct the full transition graph and to find all the transient states, the attractors, and the attractors' basins. This approach allows the direct comparison of the network properties given different symmetry ε and dilution ρ. Until [25], only completely connected McCulloch–Pitts discrete-time recurrent neural networks were considered, thus only networks that shared synaptic connection between all neurons were considered. Clearly, the assumption that any pair of neurons are connected by a synapse is not realistic if we consider brain regions with several neurons, because there would not be sufficient space for all the required connections.

In Figure 2, we report the number of steady states $\langle C \rangle$ ('$\langle \rangle$' indicate the average over different random synaptic realisations) as a function of the synaptic dilution ρ in the asymmetric case, $\epsilon = 1$. The connection generated by real neurons are usually asymmetric. Consider, that the parameter ρ is approximately the ratio W_0/W, where W is the total number of possible network edges that are not loops, e.g. the number of matrix elements excluded the diagonal terms, and W_0 is the number of missing edges, e.g. the $J_{i,j}$ matrix elements set to 0 excluded the diagonal elements. Thus, ρ determines the percentage of neurons which are not connected. A value of ρ close to 1 represents a set of neurons with no connections. The striking feature is the presence of a peak in C for a value of dilution
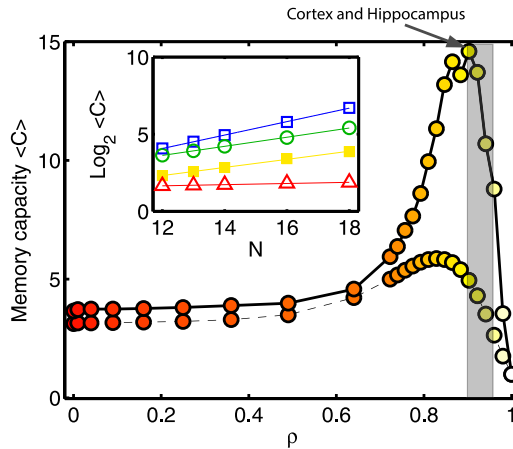

Figure 2. Memory capacity $\langle C \rangle$ as a function of the network dilution ρ for a N=12 neurons network and for a N=18 neurons network (exhaustive sampling), given asymmetric networks, $\epsilon = 1$. The grey shaded area marks the dilution of cortex and hippocampus. The inset shows the scaling of $\langle C \rangle$ as a function of N for four paradigmatic kinds of network: the Hopfield network ($\epsilon = 0$ $\rho = 0$, open circles), the diluted Hopfield network ($\epsilon = 0$ $\rho = 0.9$, open squares), the diluted asymmetric network ($\epsilon = 1$ $\rho = 0.9$, full squares), the glassy completely connected asymmetric ($\epsilon = 1$ $\rho = 0$, open triangles).

ρ of about 0.90: in that region (we name it peak region) every neuron is connected just with the 10% of the total number of neurons N. This number is very close to what found in mammalian cortex and hippocampus. The amount of information that may be stored by this neural circuit increases as $2^{\gamma N}$ with γ equal to 0.26 (full square markers). This value is higher than what is found in non-diluted asymmetric matrices, γ equal to 0.03 (triangle markes). Moreover, if we call Hopfield neural networks completely connected symmetric neural networks, diluted Hopfield networks diluted symmetric networks, then in the diluted asymmetric networks the number of information increases at a lower rate than the Hopfield network and at a higher rate than the diluted Hopfield network (in the inset of the Figure 2, with circle and open square markers, respectively). When ρ is close to 1 the connectivity matrix results entirely filled with zeros, thus at any input follows the 'shutdown state': all neurons are 0 (not firing).

Another important feature is the convergence speed (number of transient states needed to reach the attractor), which is connected to the speed needed to associate the starting state (as a sensory input) to the corresponding attractor. The convergence time T is represented by the number of evolution steps through transient states, needed for the network to reach a limit cycle (or a fixed point). $\langle T \rangle$ (averaged over at least 100 of realisations of the connectivity matrix) is reported in Figure 3. The convergence time decreases with increasing ρ,
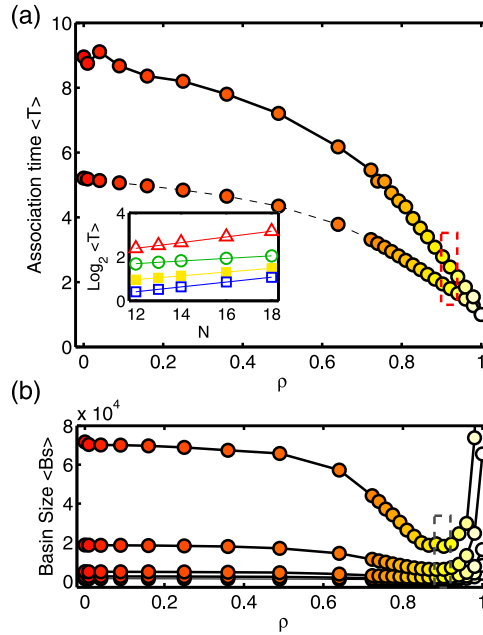
Figure 3. Association time $\langle T \rangle$ (panel a) and Basin size $\langle B \rangle$ (panel b). Lower data point is from an RNN with N=12 and higher data points are from an RNN with N=18. The inset reports the scaling with N for paradigmatic cases. The markers code is the same as in the inset of Figure 2. In panel (b), the different curves are for $N = [12, 13, 14, 16, 18]$ (from lower to higher).
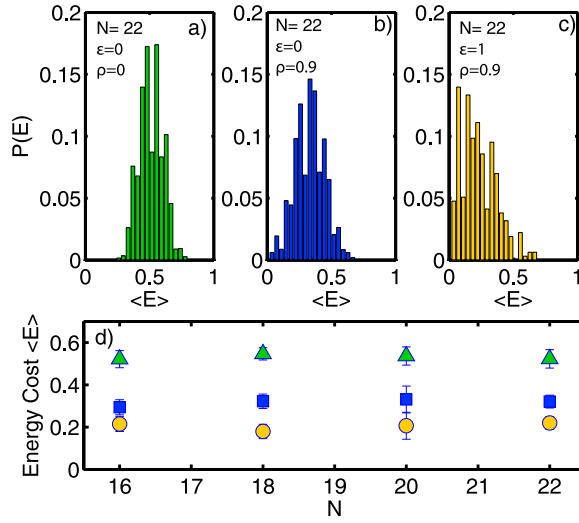
Figure 4. Average energy consumption $\langle E \rangle$ for three paradigmatic brain connectivity. The $P(\langle E \rangle)$ as a function of $\langle E \rangle$ is reported for Hopfield, (panel a), diluted Hopfield (panel b), and brain (panel c). In (d), we report the average values of energy consumption as a function of N in the network for Hopfield (triangles markes), diluted Hopfield (square markes), and brain (circle markers).

meaning that the process to associate the input to the relative limit cycle is much faster when the neuron connection probability is reduced. For ρ close to 0 the mean convergence time $\langle T \rangle$ scales with N as $2^{\gamma N}$ with $\gamma = 0.13$. On the other hand, in the region of the peak ($\rho = 0.9$) $\gamma = 0.08$, this means that in the peak region the brain has a fast memory recovery together with large memory capacity. Correspondingly, we find that the attraction basins becomes smaller in correspondence of the peak region (Figure 3).

We also calculated the energy consumption of the activated cycles. In our model firing neurons have $\sigma_i(t) = 1$ and the neurons at rest have $\sigma_i(t) = 0$. The energy consumed by the system, while it is stuck in an attractor state, is proportional to the number of firing neurons, the number of '1s' in the attractor states. On the other hand, an attractor in which the majority of the neurons remain silent, the '0s' present in the states of the attractors, are preferable because they correspond to lower energy consumption. Consequently, we calculated the total energy consumption, E, as the number of ones per limit cycle N_1 normalised by the network size N and the attractor length: $E = N_1/(N*L)$. Finally, we analyse how E changes as a function of ε and ρ. The probability of retrieving a certain energy consumption is reported in panels 4(a–c) for three paradigmatic cases: Hopfield (a, $(\epsilon, \rho) = (0, 0)$), diluted Hopfield (b, $(\epsilon, \rho) = (0, 0.9)$), diluted asymmetric (c, $(\epsilon, \rho) = (1, 0.9)$). The energy consumption is independent on N (Figure 4(d)), while the more efficient form of connectivity is the one of diluted and asymmetric network, reported with circles in the figure.

4. Conclusions

We proposed an exhaustive McCulloch–Pitts network which allows us to retrieve memory capacity and association speed given an arbitrary connectivity matrix. We demonstrate that in an asymmetric network dilution <mark>increases the rapidity</mark> (the steps needed to associate the input to the attractor) and the <mark>capacity</mark> (number of attractors). Moreover, diluted networks are biologically more plausible because there would not be sufficient space for a network with links connecting all possible couples of neurons. Furthermore, for asymmetric networks there exists an optimum value for the network connectivity, which produces a maximum in the network capacity: this value ($\rho = 0.90$, 10% probability for a neuron to be connected with another of the same region) is <mark>in agreement with the values of connectivity found in nature</mark> for the brain hippocampus and cortical regions. The asymmetric-diluted network also provides a significant advantage <mark>in terms of energy consumption:</mark> neurons fire less than half time with respect to the Hopfield network and about 2/3 times less than the diluted Hopfield networks. Thus providing an explanation for the dilution and asymmetry of certain brain areas specifically connected to the storage of memories and behavioural patterns.

Disclosure statement

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