DTU Compute

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Dynamics of adaptive neuronal networks
A trip to topology and back

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Contents

Abstract

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Acknowledgements

1 Nomenclature

$\mathrm{i}, e\,(\text{or}\exp)$ Imaginary unit. Euler's number.

$n, \deg(n)$	Network node. Degree of node n.
N	Network degree. The number of neurons in the network.
A_{ij}	Adjacency matrix. Models which neuron i is connected to neuron j and vice-versa.
$\langle k \rangle$	Average node degree in the network.
$\boldsymbol{k}$	Node degree. Vector of the in- and out-degree of a single node as $\left(k^{\mathrm{in}}, k^{\mathrm{out}}\right)$.
$\boldsymbol{k^{\mathrm{in}}}, \boldsymbol{k^{\mathrm{out}}}$	Node degree vector of all in- and out degrees of the network.
$M_{\boldsymbol{k}}$	Number of unique node degrees in the network.
$P(k), P(\boldsymbol{k})$	Univariate and bivariate network degree distribution.
$k_{\mathsf{min}}, k_{\mathsf{max}}$	Smallest and largest degree found in a network.
γ	Degree exponent of a scale-free network.
p	Probability threshold of forming a link in random networks.
c	Assortativity of the network.

$\theta(t)_i$	Phase variable function of the theta model (of neuron i).
$\mathcal{P}_n(\theta)$	Pulse shaped synaptic coupling function.
κ	Macroscopic coupling strength.
$\eta_i, I(t)_i$	Excitability threshold and input current (of neuron i).
$g(\eta|\eta_0, \sigma)$	Excitability threshold distribution with mean η_0 and width σ.

$Z(t)$	Kuramoto order parameter function.
$z(\boldsymbol{k}, t)$	Order parameter function for nodes with degree $\boldsymbol{k}$.
$\bar{Z}(t)$	Mean field order parameter function for arbitrary networks.

$S^{\mathrm{in}}(t)_i, S^{\mathrm{out}}(t)_i$	Spike trains received and emitted by neuron i as a sum of delta functions in time.
K_{ij}	Synaptic connectivity matrix. Strength of the connections between neurons i and j.
Δt_{ij}	Time difference between spikes of neurons i and j.
$W(\Delta t_{ij})$	Learning window. Models the correlation between synaptic strength and spike times.
$\phi(\Delta t_{ij})$	IP learning function. Models correlation between excitability strength and spike times.

$\mathbb{T}$	Set of angles in $[0, 2\pi[$.
$\mathbb{K}$	Set of unique degrees in a network, support of P.
$\mathbb{R}, \mathbb{C}$	Set of real numbers. Set of complex numbers.

$\mathcal{F}, \mathcal{F}^{-1}$	Random permutation and inverse permutation of the elements of a vector.

2   Introduction

In 2013, one of the largest scientific projects ever funded by the European Union was launched. With the Human Brain Project [1], scientists and researchers aimed to reconstruct the human brain through supercomputer-based models and to advance neuroscience, medicine, and computing. Across the globe different fields of science are drawing inspiration from the human brain, through different approaches.

One such approach is to model the behaviour of biological neurons and to quantify the information processes in the brain from stimuli from the senses or from electrical and chemical processes in the body. A given neuron receives hundreds of impulses in the form of neurotransmitters, almost exclusively on its dendrites and cell body. These stimuli add up to an excitatory or inhibitory influence on the membrane potential of the neuron, so that the potential spikes when excitation is higher than an internal threshold. At this point, the neuron releases its own neurotransmitter and joins the interneuronal communication [2]. The neuron dynamics are largely captured by this spiking behaviour, on which most efforts have been concentrated. In 1952, Hodgkin and Huxley described a mathematical model for the action potentials in neurons, using a set of nonlinear differential equations that approximates the electrical characteristics of the neuron elements. In 1963 the authors were awarded the Nobel Prize in Physiology or Medicine [3] for their work.

As the human brain contains more than 100 billion neurons [4] it is unfeasible to study complex models at this scale. The topology of neuronal networks displays traits of small-worldness, wiring optimisation, and heterogeneous degree distributions [5], for which it is difficult to pin down one type of network architecture. Through the mean-field reduction (*MFR*) proposed in [6] one can reduce a large network of indistinguishable neurons to a low-dimensional dynamical system, described by the attraction of a mean-field variable to a reduced manifold. In this paper we will study the *MFR* of different types of networks of coupled theta neurons using the generalisations found in [7].

3 Network Topologies

Networks consists of *nodes* n_j, $j \leq N$ connected by *links*. They arise in any context where objects are *related* to each other.

3.1 Representations and properties

We represent a finite network through the adjacency matrix: $A_{ij} = 1$ if there exists a relation from node j to node i and 0 otherwise. This means that A_{ij} can be *undirected* (symmetric) or *undirected*. If we think of the relations between guests at a party, then the social network is directed, as people might not know each other mutually. However, the network of people having shaken hands is symmetric. Self-links are an edge-case that depends on the context, as one generally does not shake hands with himself.

From A_{ij} we can compute the in- and out-degree vectors, which show how many links a node has coming in and out:

$$\boldsymbol{k}_i^{\mathbf{in}} = \sum_{j=1}^{N} A_{ij} \qquad \boldsymbol{k}_j^{\mathbf{out}} = \sum_{i=1}^{N} A_{ij} \qquad \deg(n_j) = \boldsymbol{k}_j = (\boldsymbol{k}_j^{\mathbf{in}}, \boldsymbol{k}_j^{\mathbf{out}}) \in \mathbb{K} \subset \mathbb{N} \qquad (1)$$

The distribution of $\boldsymbol{k}^{\mathbf{in}}$ and $\boldsymbol{k}^{\mathbf{out}}$ is the most defining property of the network:

$$(\boldsymbol{k}^{\mathbf{in}}, \boldsymbol{k}^{\mathbf{out}}) \sim P(\deg(n) = \boldsymbol{k}) \qquad (2)$$

The support of P is the set of unique degrees $\mathbb{K}$ with cardinality $M_{\boldsymbol{k}}$, which consists of integers. For symmetric networks, $\boldsymbol{k}^{\mathbf{in}} = \boldsymbol{k}^{\mathbf{out}}$, so that P is really a univariate distribution.

3.2 Fixed-degree networks

A network consists of nodes, connected by links. The most simple network is one where all the nodes are connected, and so all nodes have a degree of N. In general, we can make networks where all nodes have the same degree, $\langle k \rangle$:

$$P(k) = \begin{cases} \langle k \rangle & \text{if } k = \langle k \rangle \\ 0 & \text{otherwise} \end{cases} \qquad \mathbb{K} = \{\langle k \rangle\} \qquad (3)$$

We will refer to these networks as fixed-degree networks.

3.3 Random / Erdös-Rény networks

In 1959 Erdös and Rény published their work on random graphs [8], where links are established if a random uniformly distributed number is higher than a threshold p. The degrees follow a binomial distribution:

$$P(k) = \binom{N-1}{k} p^k (1-p)^{N-1-k} \qquad \mathbb{K} = [0, N] \qquad (4)$$

with a mean $\mu = p(N-1)$ and standard deviation $\sigma = \mu(1-p)$. For networks where $\langle k \rangle \ll N$, the network can be well approximated by a Poisson distribution:

$$P(k) = e^{-\langle k \rangle} \frac{\langle k \rangle^k}{k!} \qquad \mathbb{K} = [0, N] \qquad (5)$$

with a mean $\mu = \langle k \rangle$ and standard deviation $\sigma = \sqrt{\langle k \rangle}$. Both (4) and (5) describe similar quantities, but the latter is used more often due to its analytical simplicity [9].

3.4 Scale-free networks

What we can often observe in nature is the preferential attachment to nodes with a high degree [5]: the rich or famous tend to get more rich or famous. This trait is also described as the 80/20 rule by Pareto. Networks with this property consist of a small number of highly connected nodes, and a large number of low degree nodes. We can represent this with a power law distribution:

$$P(k) = Ak^{-\gamma} \tag{6}$$

with A is a constant so that $\sum_{k=1}^{\infty} P(k) = 1$. We can also see that $A \sum_{k=1}^{\infty} k^{-\gamma} = 1$ so that $A = \sum_{k=1}^{\infty} k^{\gamma} = 1/\zeta(k)$, the Riemann Zéta function [9].

Networks with a distribution like (6) are called *scale-free* networks, as they lack an internal scale to represent the magnitude of the network: we can observe (6) on different scales like the probability of two Hollywood actors appearing in a movie, or the connections between web pages on the internet [10]. One description that comes close is the *natural cutoff* $k_{\max}$, the expected degree of the largest degree in the network. As we only expect the largest hub to be the only hub in the domain $[k_{\max}, +\infty]$:

$$\int_{k_{\max}}^{\infty} P(k)dk = \frac{1}{N}$$

For (6) this results in:

$$k_{\max} = k_{\min} \cdot N^{\frac{1}{\gamma-1}} \tag{7}$$

which shows that there might be large differences in size between the nodes. There are constraints on γ to yield a scale-free network. When $0 < \gamma < 2$ the largest hub grows faster than N, so once its degree exceeds $N-1$ there are no more new nodes to connect to. A rigorous proof is given in [11]. For $\gamma = 2$, the system grows linearly, as we can see in (7). When $2 < \gamma \leq 3$ we find the most scale-free networks, as for $\gamma > 3$ hubs are not sufficiently large and numerous to have much influence on the network [9].

4 The Theta Neuron Model

4.1 Model description

A number of neuron model families have been identified, and often there exists a continuous change of variables from models of the same family into a *canonical* model that can represent the whole family [12]. As the transformation is not required to be invertible, we can study the universal neurocomputational properties of the family in a low dimensional model. It was Hodgkin [13] who classified neurons into two types based on their excitability, upon experimenting with the electrical stimulation of cells. Class 1 models begin to spike at an arbitrarily slow rate, and the spiking frequency increases when the applied current is increased. Class 2 models spike as soon as their internal threshold is exceeded and the spiking frequency stays relatively constant within a certain frequency band [12].

In [14], a class 1 canonical phase model was proposed:

$$\dot{\theta} = (1 - \cos\theta) + (1 + \cos\theta) \cdot I \tag{8}$$

with I a bifurcation parameter on the supplied current. We can visualise the dynamics on the unit circle, like in Figure 1. The neuron produces a spike when θ surpasses π. As I increases, we see the coalescence of a saddle and node and the neuron starts to fire periodically, we can recognise the features of the class 1 model in Figure 2. This makes (8) the normal form of the *saddle-node-on-invariant-circle* (*SNIC*) bifurcation [15].
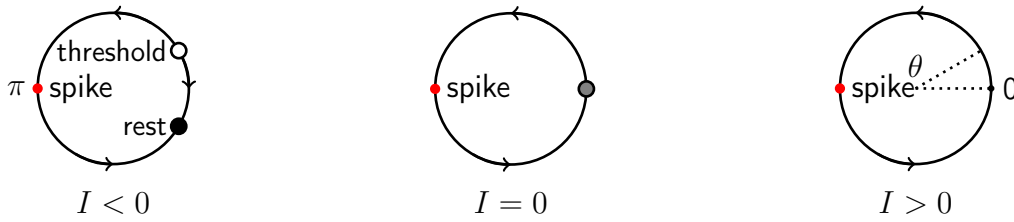

Figure 1: SNIC bifurcation of the theta neuron model. For $I < 0$, the neuron is in a rest state but excitable. For $I > 0$, the neuron spikes regularly. The bifurcation occurs at $I = 0$. A spike occurs when $\theta = \pi$.
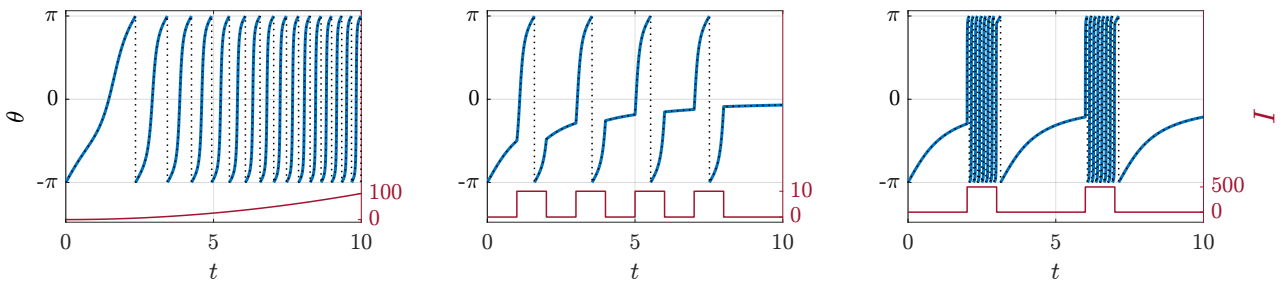

Figure 2: Properties of the theta neuron model. Left: the spike frequency of θ increases as I is increased over time, which is the distinguishing feature of class 1 canonical models. Middle: spikes occur and Right:

4.2 Solutions for static currents

4.3 Networks of theta neurons

We can easily extend the model to networks of neurons:

$$\dot{\theta}_i = (1 - \cos\theta_i) + (1 + \cos\theta_i) \cdot [\eta_i + \kappa I_i(t)] \tag{9}$$

$$I_i(t) = \frac{1}{\langle k \rangle} \sum_{j=1}^{N} A_{ij} \cdot \mathcal{P}_n(\theta_j) \tag{10}$$

where the excitability is drawn from a distribution and $\mathcal{P}(\theta) = a_n(1 - \cos\theta)^n$ models synaptic coupling by a pulse-shaped signal, emitted when a neuron fires. n models the sharpness of the pulse, and a_n is a normalisation constant. We will take $n = 2$ from here in as in [15], [7], [16]. Another type of coupling is proportional to the difference in voltage between neurons [16]. Note that for a fully connected network, (10) reduces to the scenarios in [15] and [16].

5 Mean Field Reductions

5.1 The Ott-Antonsen manifold for fully connected networks

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5.2 Extension to arbitrary network topologies

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6   *Investigation:* Mean Field Reductions for undirected graphs

6.1   Directed graphs as permutations

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6.2   Building the adjacency matrix

We can find an exact solution for A given the degree vectors in (2). A_{ij} represents a directed graph, but $A_{ij} \neq A_{ji}$ is not a necessary condition. For the elements of A_{ij} we need to find N^2 number of variables. We have the following constraints:

1. The column- and row-sums of A_{ij} must be equal to $\boldsymbol{k}^{\mathbf{in}}$ and $\boldsymbol{k}^{\mathbf{out}}$, see (1). $2N$ constraints.

2. Self-coupling is mandatory: $A_{ii} = \mathbf{1}$. N constraints.

3. The total number of links is constant: $\sum_{i=1}^{N} \boldsymbol{k}_i^{\mathbf{in}} \equiv \sum_{j=1}^{N} \boldsymbol{k}_j^{\mathbf{out}} \equiv \sum_{i,j=1}^{N} A_{ij}$. 1 constraint.

This means that there are $N^2 - (3N + 1)$ variables to find. Once a solution has been found, A_{ij} can be switched with element A_{ic} if $A_{ij} \neq A_{ic}$ and A_{rj} with A_{rc}, which yields a new feasible solution. The number of switches one can make is high, and therefore we can simply try a stochastic approach to obtain A:

1. Choose a random row $i \in [1, N]$. $A_{i,i} = 1$, so we need $m = \boldsymbol{k}_i^{\mathbf{in}} - 1$ elements that are 1.

2. Perform $F(\boldsymbol{k}_j^{\mathbf{out}}, j \neq i)$ and therein find the indices $\boldsymbol{\ell}$ of the m first largest elements.

3. Set $A_{il} = 1 \ \forall \ l \in F^{-1}(\boldsymbol{\ell})$.

Algorithms that find the largest value in a vector start from the first or the last element. The permutation allows us to find different maxima every time by shuffling the vector.

6.3   Results

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7 Hebbian Learning

7.1 Fire and Wire

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7.2 Anti-hebbian learning

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8 Plasticity

8.1 Intrinsic plasticity

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8.2 Spike-timing dependant plasticity

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9   *Investigation:* Emerging Network Topologies

9.1   Redefinition of the network

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9.2   Results

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9.3   Discussion

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10 Conclusion and discussion

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12 Appendix