SIMULATION OF LARGE SCALE CORTICAL NETWORKS BY INDIVIDUAL NEURON DYNAMICS

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Understanding the functional dynamics of the mammalian brain is one of the central aims of modern neuroscience. Mathematical modeling and computational simulations of neural networks can help in this quest. In recent publications, a multilevel model has been presented to simulate the resting-state dynamics of the cortico-cortical connectivity of the mammalian brain. In the present work we investigate how much of the dynamical behavior of the multilevel model can be reproduced by a strongly simplified model. We find that replacing each cortical area by a single Rulkov map recreates the patterns of dynamical correlation of the multilevel model, while the outcome of other models and setups mainly depends on the local network properties, e.g. the input degree of each vertex. In general, we find that a simple simulation whose dynamics depends on the global topology of the whole network is far from trivial. A systematic analysis of different dynamical models and coupling setups is required.

Keywords: Neural networks; cortical activity; Rulkov map; Izhikevich neurones.

1. Introduction

Understanding the functional dynamics of the mammalian brain is one of the central aims of modern neuroscience. Apart from developing and improving experimental methods like EEG, fMRI and PET, mathematical modeling and computational simulations of neural networks can help to understand the dynamical behavior of the brain. While the dynamics of single neurones is quite well conceived and their dynamical behavior can be reproduced by differential models [beim Graben et al., 2008; Izhikevich, 2007] e.g. Hodgkin & Huxley [1952] or iterated maps, e.g. Rulkov [2002], a

systematic exploration of the impact of connection topology on the dynamical organization in neuronal networks has barely begun [Markram, 2006; Zemanová et al., 2006; Zhou et al., 2006; Honey et al., 2007; Izhikevich & Edelman, 2008].

In [beim Graben et al., 2008; Zhou et al., 2007] the authors simulated the resting-state of the mammalian cortex using different approaches. The models were implemented using the experimentally known anatomical connectivity of the cat cortex, which consists of a network of 53 cortical areas and 826 long-range fibers connecting them [Scannell et al., 1995; Scannell & Young, 1993]. The first approach was to simulate cortical areas using a

neural mass model [Wendling et al., 2000], which aims to imitate the dynamics of a population of neurones and is capable of reproducing EEG-like oscillations. Hence, it promises to be a biologically plausible model for a brain area. However, it was found that the pairwise correlation between cortical areas depends on the individual characteristics of the areas (number of inputs), and further, network topology is irrelevant. The second approach comprised of a multilevel model (a network of networks) in which each area was represented by a subnetwork of 200 neurones. While the connectivity between the cortical areas remained the same, the internal 200 neurones were connected by a small-world topology [Watts & Strogatz, 1998] in order to minimally reproduce qualitative observations of neuronal connectivity [Sporns et al., 2005]. This model displayed biologically plausible behavior in the range of weak coupling between neurones, meaning that (partial) synchronization and dynamical clustering followed the underlying anatomical topology. Additionally, the mean field signals of the areas showed similarity to real EEG data. In the strong coupling regime, the dynamics of individual areas were characterized by well-defined oscillations (as happened with the neural mass model) and therefore, the patterns of synchronization did not depend on the underlying topology. One of the drawbacks of the multilevel model is its rather large computational cost.

The goal of the present work is to investigate how much of the dynamical behavior of the multilevel model can be reproduced by a strongly simplified model (which is computationally competitive). For that, we have simulated each cortical area as a single neuron. Using two popular neuron models, the Rulkov map [Rulkov, 2002] and the neuron model by Izhikevich [2003], the network is simulated and their outcomes are compared. We find that the network of interconnected Rulkov maps recreates the patterns of dynamical correlations at the multilevel model, while in the simulations performed using the Izhikevich model, the dynamics does not depend on the underlying topology. Among other factors, which are discussed below, the difference might arise from the fact that the Rulkov maps are connected by a linear coupling and the Izhikevich neurones by a pulse coupling.

Nevertheless, we find that in the simulations using the Rulkov map, the neurones have a flexible dynamics permitting them to quickly adapt to the dynamics of their neighbors. In the simulations

performed with the Izhikevich neurones, each element follows mainly its own dynamics and correlates only with the neighbors of strongest input. This observation transcends the particular models and configurations here adopted and should be taken into account when studying synchronization phenoma in complex networks [Arenas et al., 2008; Boccaletti et al., 2006].

2. Dynamical Simulations of the Cat Cortex

As in [beim Graben et al., 2008; Zhou et al., 2006, 2007] the cortico-cortical connectivity of the cat has been modeled, which is summarized as a weighted adjacency matrix W, Fig. 1. This data is a collation performed by Scannell et al. [1995]; Scannell & Young [1993] based on previous anatomical reports. The network is weighted according to the axonal density of the fibers linking two areas. Thus, 3 means a strong (dense) connection, 2 means intermediate and 1 a weak (sparse) connection. The cases explicitly reported as absent or no information available were treated the same and were weighted as 0. Cortical networks have been reported to have small-world characteristics, i.e.
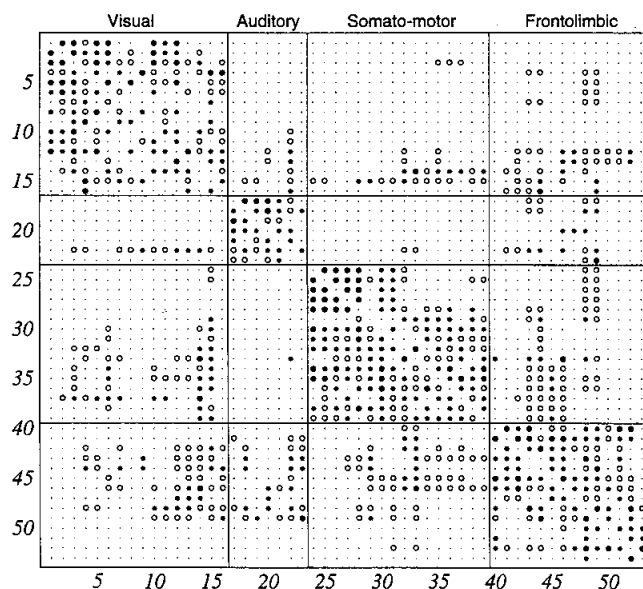

Fig. 1. Weighted adjacency matrix W of the cortico-cortical connectivity of the cat comprising 826 directed connections between 53 cortical areas. The connections are classified as weak (open circles), intermediate (blue stars) and dense (red filled circles) according to the axonal densities in the projections between two areas. For visualization purposes, the nonexisting connections (0) have been replaced by dots.

a high clustering coefficient and a short average pathlength [Hilgetag *et al.*, 2000]. The degree of the nodes is very heterogeneous and ranges from 2 to 35 connections, insofar, the network has a (scale-free-like) broad degree-distribution [Kaiser *et al.*, 2007; Zamora-López *et al.*, 2008]. In Fig. 1, four main clusters called "communities", can be distinguished which have dense connectivity inside. These communities correspond to the functional subsystems *visual* (*V*), *auditory* (*A*), *somato-motor* (*SM*) and *frontolimbic* (*FL*) [Hilgetag *et al.*, 2000; Scannell & Young, 1993; Scannell *et al.*, 1995].

In order to achieve our goal of developing a model that reproduces the main dynamical behavior of the multilevel model and is computationally competitive, we choose to turn back from the multilevel approach and try alternative dynamics for modeling the areas. The dynamics of an area is now simulated by a single neuron, modeled by (i) an iterated map developed by Rulkov [2002], and (ii) a system of two first order differential equations (ODEs) with an additional after spike reseting mechanism, after [Izhikevich, 2003]. Every neuron receives input from its neighbors and is additionally stimulated by an independent Gaussian white noise.

2.1. *Simulation of cortical areas by the Rulkov map*

The Rulkov map is a two-dimensional iterated map, which is capable of replicating the spiking, and spike-bursting behavior of real neurones by the interplay between two dynamical variables, one describing fast dynamics and another slow variable (see details in Appendix 3). To simulate the cortical network of the cat, each area is replaced by one Rulkov map in *chattering* state, i.e. the isolated neuron is characterized by periodic epochs of bursting and inactivity, see Fig. 2 (top). The maps were then coupled following the recommendations in [Rulkov, 2002]. After being coupled, the maps still display a chattering behavior but irregular due to the input from their neighbors, Fig. 2 (bottom).

After running the simulations, the pairwise linear correlation $r(i, j)$ between cortical areas have been computed to characterise the synchronization behavior and the functional clustering. As mentioned in [Ivanchenko *et al.*, 2004; Rulkov, 2002], synchronization is only observed in the low frequency bands of bursts, but not in high frequent spikes, so a low pass filter has been applied
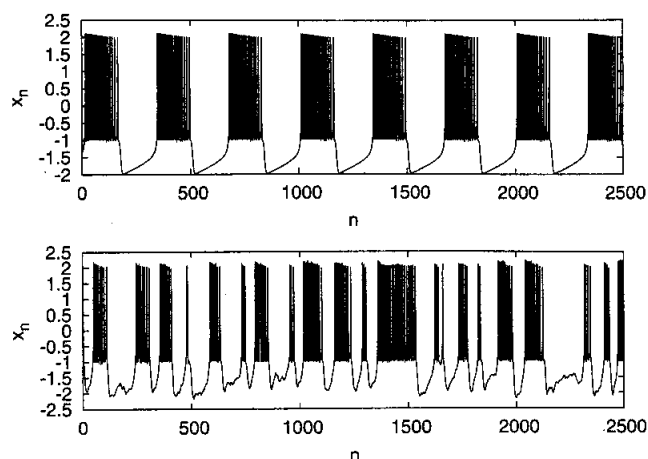

Fig. 2.   Characteristic signal of a cortical area modeled by a Rulkov map. (Top) Before coupling, isolated neurones were setup into a regular *chattering* state, i.e. periodic epochs of bursts and inactivity without noise. (Bottom) After the neuron is coupled to the network with noise, it displays an *irregular* chattering behavior.

to the output signals before computing $r(i, j)$ (Appendix 3). In Fig. 3, a gallery of correlation matrices $r(i, j)$ is shown and the corresponding cluster trees (dendrograms) for coupling strengths ranging from $g = 10$ to $g = 525$. Each correlation matrix is the average of ten realizations. With a very weak coupling, Fig. 3(a), the dynamical clusters are visible although the correlations are weak and noisy. The dynamical clusters in Fig. 3(b) raise from the background with high contrast, while in Fig. 3(c) inter cluster correlation becomes more dominant. Finally, a strong coupling leads to global correlation, Fig. 3(c).

Next, a cluster analysis of the correlation matrices is performed by calculating their corresponding dendrograms. A dendrogram is a graph of many U-shaped lines, which connects nodes in a hierarchical binary tree. The height of each line stands for the *dynamical distance* (euclidean) between two nodes, which is obtained from the correlation matrix: $d_{ij} = \sqrt{\sum_m (r_{i,m} - r_{j,m})^2}$. This technique enables one to visualise which areas are closely connected and how they build up dynamical clusters. As we are concerned about the anatomical clusters (V, A, SM and FL), we concentrate on the hierarchical level where the correlation matrix decomposes into four clusters. Apparently, the stability of hierarchical levels is a function of correlation. By stability, we mean the height of the hierarchical level where there are four clusters in the dendrogram.
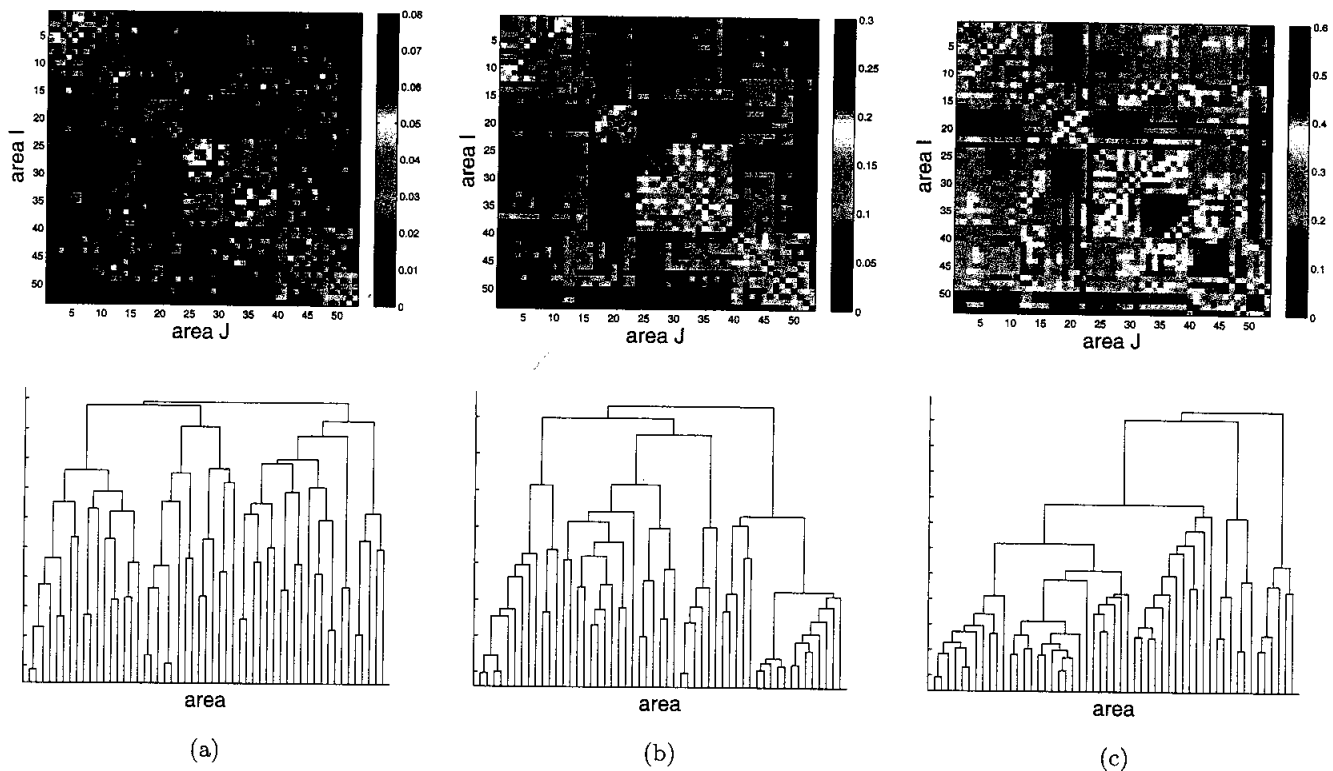
Fig. 3.   Correlation matrices and dendrograms for the Rulkov map with different coupling strengths. (a) $g = 10$, (b) $g = 75$ and (c) $g = 525$.

We find that, with low correlation, Fig. 3(a), the stability of our region of interest is very weak. Here, the correlation between single nodes dominates the synchronization behavior, while an intermediate correlation, Fig. 3(b), leads to the desired synchronization of four stable clusters where each cluster has its particular dynamics and is weakly coupled to other clusters. Very high coupling strength destabilizes the four clusters and "melt" them together, which means that individual dynamics becomes lost, while synchronization of all clusters becomes dominant, Fig. 3(c). Note, that in these dendrograms, areas are generally not ordered by their number. To see which areas form a cluster, we provide another graph (Fig. 4). The dynamical clusters closely follow the anatomical communities, although some of the areas are assigned to a different community. These areas, while belonging to an anatomical community, are hubs with many connections in other communities. Therefore, they also get synchronized with other communities and appear dynamically clustered into a "wrong" community. The presence of such hubs has also been reported in [Honey et al., 2007; Zemanová et al., 2006, 2008; Zhou et al., 2006, 2007].

2.2.   Simulation of areas by Izhikevich neurones

The same analysis has been repeated using the Izhikevich neuron to model the cortical areas [Izhikevich, 2003]. This model consists of a
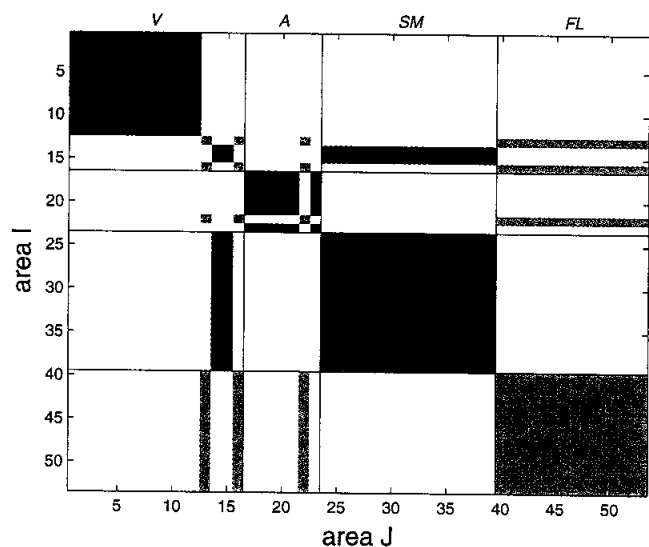

Fig. 4.   The four dynamical clusters of the Rulkov model at an intermediate coupling strength of $g = 75$, resulting from the clustering algorithm described in Sec. 2.
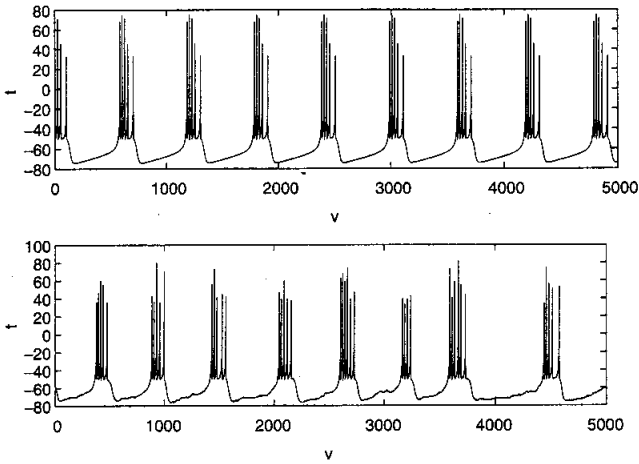
Fig. 5. Characteristic signal of a cortical area modeled by the Izhikevich neuron. (Top) Before coupling, isolated neurones were setup into a regular *chattering* state without noise. (Bottom) After the neuron is coupled into the network with noise, it still displays a chattering behavior, although slightly irregular.

pair of first order ODEs; one variable is denoted as the *membrane potential of the neuron* and the other as *a membrane recovery variable*. Additionally, it contains an after-spike reset to avoid modeling the shape of the spike. This model has been conceived to reproduce a rich range of dynamical behaviors exhibited by real neurones of different classes in a computationally competitive manner [Izhikevich, 2003, 2004].

The model parameters were chosen to simulate the isolated neurones in the *chattering* state as shown in Fig. 5 (top). The network was implemented, setting up the neuron to neuron pulse-coupling as indicated in [Izhikevich, 2003]. See details in Appendix 3. In the coupled configuration, areas still display a chattering behavior, although

only slightly irregular, Fig. 5 (bottom), as compared to the coupled Rulkov maps, Fig. 2 (bottom).

The simulated network also yields synchronization, but as seen in Fig. 6, the clustering behavior is different. Clusters are not concordant with the anatomical communities, regardless of the coupling strength. Here, the SM and FL communities follow almost the same dynamics, together with a large part of the visual cluster. Moreover, the auditory community disappears as a dynamical cluster. These observations are very similar to the patterns of synchronization of the neural mass model discussed in [Zhou et al., 2007].

3. Summary and Discussion

In this paper, we have explored an alternative and simplified manner to simulate cortical networks which can still recover the dynamical properties of the multilevel approach of [beim Graben et al., 2008; Zemanová et al., 2006, 2008; Zhou et al., 2006, 2007]. We have simulated the cortico-cortical network of the cat by replacing each cortical area by a single excitable oscillator: either a Rulkov map or an Izhikevich neuron. The dynamical correlations between areas, using the Rulkov map (Fig. 3) closely resembles those of the multilevel model. In the weak coupling regime, both models display dynamics which depend on the underlying topology. The dynamical clusters are similar to the anatomical communities (V, A, SM and FL). An example of the dynamical clusters obtained with the multilevel model are shown in Fig. 7 for comparison. In the strong coupling regime of both models, the dynamical clusters melt together leading to global synchronization, a situation which might be considered as
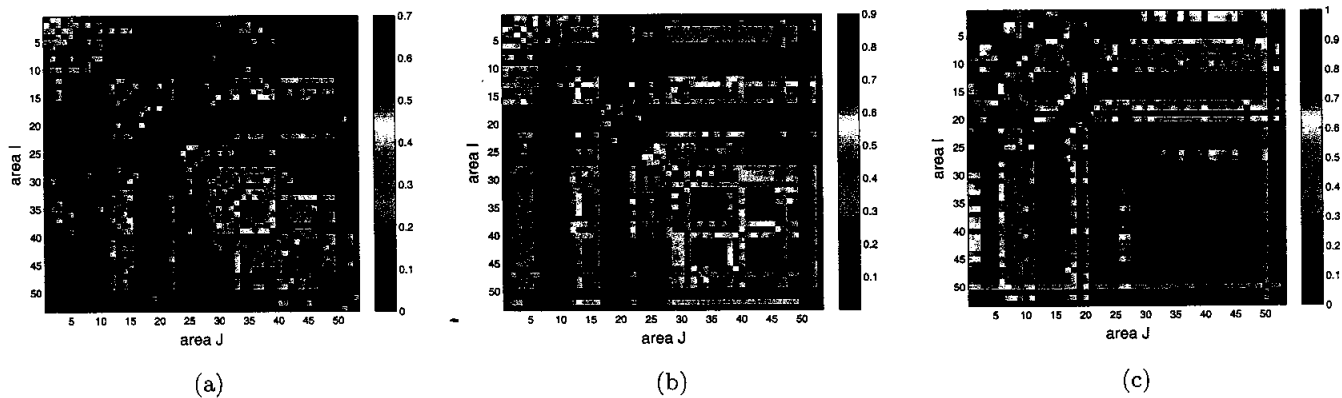

(a)   (b)   (c)

Fig. 6. Correlation matrices for the Izhikevich map with different coupling strengths. (a) $g = 3$, (b) $g = 5$, (c) $g = 10$, at a noise level of $D = 0.1$.

(a)   (b)   (c)
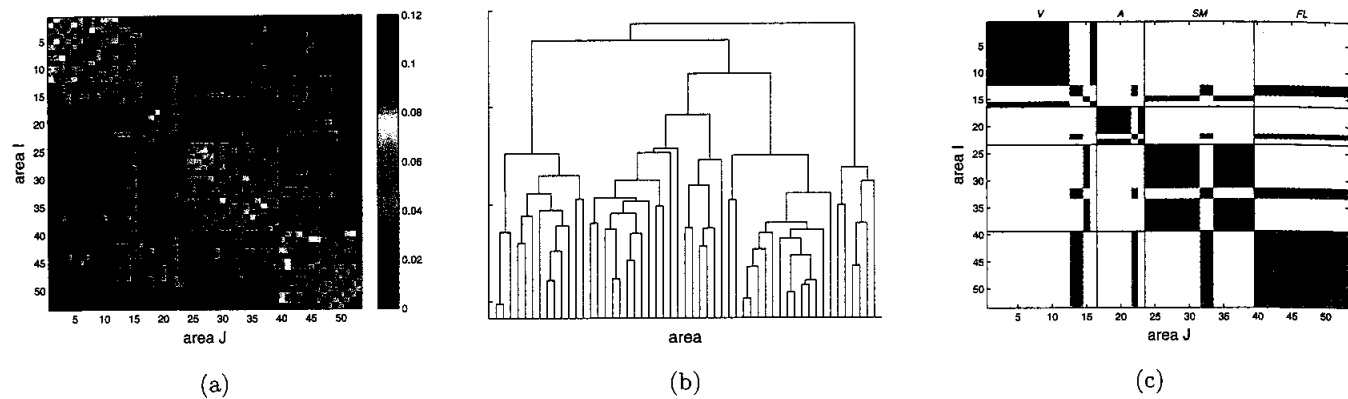
Fig. 7. Multilevel model of [beim Graben *et al.*, 2008; Zhou *et al.*, 2006, 2007] (a) correlation matrix, (b) dendrogram and (c) clustering map in a weak coupling regime.

pathological in brain activity — e.g. during epileptic seizures. On the contrary, in none of the simulations performed using the Izhikevich neurones, we could reproduce this dynamical clustered behavior, see Fig. 6.

An answer to this difference may lie in the fact that low dimensional maps are capable of rich dynamics (even 1-D maps can have chaotic behavior) while differential equations can show chaotic behavior only when they are at least three-dimensional. The neurones modeled by the Rulkov map have flexible dynamics as shown in Fig. 2(b). As a consequence, the neurones are able to quickly adapt to the dynamics of their neighbors. For example, the hubs are connected to many areas which might have different time-scales. This adaptability permits the hubs to "keep in synch" with all their neighbors. In the simulations performed with the Izhikevich model, the individual bursting dynamics of the neurones is dominant and they essentially keep their own rhythm. As a result, areas can only synchronise with the groups of neighbors from which they receive the strongest synchronised input.

Another reason for the different behaviors observed lies in the coupling between neurones. In the Rulkov model the neurones are connected by a linear coupling which leads to burst synchronization. As recommended in [Izhikevich, 2003] the connections in the Izhikevich model are modeled by a pulse coupling between the fast variables of both neurones. Hence, the input of a neuron takes only into account the number of neighbors which fire a spike simultaneously.

Whether the dynamical flexibility of the areas arises from the chaoticity of the neuronal model and/or the type of coupling, it seems that when simulating a network of coupled oscillators (generic or excitable) the dynamics of the individual vertices need to be adaptable. Otherwise, the dynamical outcome is not sensitive to the underlying topology of the network, or trivially dependent on the local number of neighbors. Further preliminary observations with different setups, e.g. Izhikevich neurones with electrical coupling (not shown), exhibit dramatic changes in the correlation patterns. These observations suggest that a systematic analysis of different model dynamics and coupling types is required to understand when the outcome of a network simulation will depend on the underlying network topology or not.

Finally, we discuss the reliability of the simplified models presented here in order to simulate cortico-cortical networks. In the multilevel model, the time series signal of individual cortical areas, computed as the mean-field signal of the internal 200 neurones resemble typical EEG data, and thus it can be considered a plausible model for direct comparison to experimental-like data. In the simplified models the signals of individual areas is a spiking or a spike bursting pattern, hence interpreting it as EEG data is implausible. Nevertheless, if we regard the low pass filtered output as the signal (Appendix 3), it might still have some similarities with experimental EEGs. In any case, as the simplified model captures the underlying topology of the network and computes very fast, it seems suitable for applications to investigate network synchronization and other dynamics related properties like information processing. Another promising alternative is to build a multilevel model but using Rulkov maps instead of neuronal models based on differential equations.

As brain areas consist of a large number of neurones, which altogether have a very high-dimensional phase space, in which chaotic behavior is likely, iterated maps could be interpreted as Poincaré-maps of such a high dimensional system and hence, are more suitable to represent them as two-dimensional ODEs.

Acknowledgments

References

Arenas, A., Díaz-Guilera, A., Kurths, J., Moreno, Y. & Zhou, C. S. [2008] "Synchronization in complex networks," *Phys. Rep.* **469**, 93–153.

beim Graben, P., Zhou, C. S., Thiel, M. & Kurths, J. (eds.) [2008] *Lectures in Supercomputational Neuroscience* (Springer-Verlag, Berlin).

Boccaletti, S., Latora, V., Moreno, Y., Chavez, M. & Hwang, D.-U. [2006] "Complex networks: Structure and dynamics," *Phys. Rep.* **424**, 175–308.

Hilgetag, C. C., Burns, G. A. P. C., O'neill, M. A., Scannell, J. W. & Young, M. P. [2000] "Anatomical connectivity defines the organization of clusters of cortical areas in the macaque monkey and the cat," *Phil. Trans. R. Soc. Lond. B* **355**, 91–110.

Hodgkin, A. L. & Huxley, A. F. [1952] "A quantitative description of membrane current and its application to conduction and excitation in nerve," *J. Physiol.* **117**, 500–544.

Honey, C. J., Kötter, R., Breakspear, M. & Sporns, O. [2007] "Network structure of cerebral cortex shapes functional connectivity on multiple time scales," *Proc. Nat. Acad. Sci.* **104**, 10240–10245.

Ivanchenko, M. V., Osipov, G. V., Shalfeev, V. D. & Kurths, J. [2004] "Phase synchronization in ensembles of bursting oscillators," *Phys. Rev. Lett.* **93**, 134101.

Izhikevich, E. M. [2003] "Simple model of spiking neurons," *IEEE Trans. Neural Nets* **14**, 1569–1572.

Izhikevich, E. M. [2004] "Which model to use for cortical spiking neurons?" *IEEE Trans. Neural Nets* **15**, 1063–1070.

Izhikevich, E. M. [2007] *Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting* (MIT Press, Cambridge, MA).

Izhikevich, E. M. & Edelman, G. M. [2008] "Large-scale model of mammalian thalamocortical systems," *Proc. Nat. Acad. Sci.* **105**, 3593.

Kaiser, M., Martin, R., Andras, P. & Young, M. P. [2007] "Simulation of robustness against lesions of cortical networks," *Eur. J. Neurosc.* **25**, 3185–3192.

Markram, H. [2006] "The blue brain project," *Nat. Rev. Neurosci.* **7**, 153–160.

Rulkov, N. F. [2002] "Modeling of spiking-bursting neural behavior using two-dimensional map," *Phys. Rev. E* **65**, 041922.

Scannell, J. W. & Young, M. P. [1993] "The connectional organization of neural systems in the cat cerebral cortex," *Curr. Biol.* **3**, 191–200.

Scannell, J. W., Blakemore, C. & Young, M. P. [1995] "Analysis of connectivity in the cat cerebral cortex," *J. Neurosci.* **15**, 1463–1483.

Sporns, O., Tononi, G. & Kötter, R. [2005] "The human connectome: A structural description of the human brain," *PLoS Comput. Biol.* **1**, 0245–0251.

Watts, D. J. & Strogatz, S. H. [1998] "Collective dynamics of 'small-world' networks," *Nature* **393**, 440.

Wendling, F., Bellanger, J. J., Bartolomei, F. & Chauvel, P. [2000] "Relevance of nonlinear lumped-parameter models in the analysis of depth-eeg epiletic signals," *Biol. Cybern.* **83**, 367–378.

Zamora-López, G., Zhou, C. S. & Kurths, J. [2008] "Structural Characterization of networks using the cat cortex as an example," *Lectures in Supercomputational Neuroscience* (Springer-Verlag, Berlin).

Zemanová, L., Zhou, C. S. & Kurths, J. [2006] "Structural and functional clusters of complex brain networks," *Physica D* **224**, 202–212.

Zemanová, L., Zamora-López, G., Zhou, C. S. & Kurths, J. [2008] "Complex brain networks: From topological communities to clustered dynamics," *PRAMANA J. Phys.* **70**, 1087–1097.

Zhou, C. S., Zemanová, L., Zamora, G., Hilgetag, C.-C. & Kurths, J. [2006] "Hierarchical organization unveiled by functional connectivity in complex brain networks," *Phys. Rev. Lett.* **97**, 238103.

Zhou, C. S., Zemanová, L., Zamora-López, G., Hilgetag, C.-C. & Kurths, J. [2007] "Structure-function relationship in complex brain networks expressed by hierarchical synchronization," *New J. Phys.* **9**, 178.

Appendix A

The Rulkov Map

Rulkov introduced a model that replicates the spiking and spike-bursting behavior of real neurones. The model is represented by a two-dimensional map:

$$x_{i,n+1} = f(x_i, y_i + \beta) + \xi_i \tag{A.1}$$

$$y_{i,n+1} = y_{i,n} - \mu(x_{i,n+1}) + \mu\sigma C(x_i, x_j) + \xi_i \tag{A.2}$$

Table 1. Parameter values of the Rulkov map.

Constant	Value
α	6
β	1
μ	0.001
σ	0.3

Table 2. Parameter values for the Izhikevich ODE.

Constant	Value
a	0.02
b	0.2
c	−50.0
d	2
I_0	10

$$f(x_i, y_i) = \begin{cases} \dfrac{\alpha}{1 - x_i} + y_i, & x_i \leq 0 \\ \alpha + y_i, & 0 \leq x_i \leq \alpha + y_i \\ -1 & x_i \geq \alpha + y_i \end{cases} \quad \text{(A.3)}$$

$$C(x_i, x_j) = \frac{g}{N} \sum_{j=1}^{N} \widetilde{W}_{ij}(x_i - x_j) \quad \text{(A.4)}$$

It consists of a fast variable (x), which represents the membrane potential of the neuron and a slow one (y), enabling the possibility to operate on different time scales. For the fast dynamics of x, one can regard y as a control parameter. For some regions of y there exists a stable cycle in the fast dynamics of x, which generates periodic spiking. As y changes slowly, the system will undergo a bifurcation that destroys the stable cycle in the fast dynamics and x will converge to a fixed point, the relaxation regime. After some time y returns to the regime, where a stable cycle in x exists and everything starts over again.

Note that the adjacency matrix $\widetilde{W}_{ij}$ is the normalised weighted matrix after dividing the weight matrix by its largest element i.e. $\widetilde{W}_{ij} = W_{ij}/3$. The constants α, β, σ, μ are model parameters (Table 1) and are all the same for every area, while $\xi = D\Xi_{0,1}(t)$ stands for Gaussian distributed white noise with zero average and variance 1 multiplied by a constant (D) to adjust the noise level. The coupling strength is denoted as g.

Appendix B

The Izhikevich model

The model by Izhikevich [Izhikevich, 2003] consists of a pair of first order ordinary differential equations:

$$\frac{d}{dt}v_i = 0.04v_i^2 + 5v_i + 140 - u_i + I_i \quad \text{(B.1)}$$

$$\frac{d}{dt}u_i = a(bv_i - u_i) + \xi_i \quad \text{(B.2)}$$

with an after spike resetting

$$\text{if } v \geq 30, \text{ then } v := c \text{ and } u := u + d. \quad \text{(B.3)}$$

In our simulations, the equations have been integrated, using the fourth-order Runge–Kutta method with a step size of $dt = 0.1$.[1] This model is also capable of generating spiking and spike-bursting signals, but, as it consists of a system of two first order ODEs, it cannot be chaotic in the uncoupled case. Following the original recomendations, the pulse-coupling between neurones is modeled by replacing the input to the neurones I with:

$$I_i = I_0 \left(1 + \frac{g}{N} \sum_{j=1}^{N} \widetilde{W}_{ij}\Theta(v_j - 20) \right) + \xi_i \quad \text{(B.4)}$$

where $\widetilde{W}_{ij}$ is the adjacency matrix as above, g is the coupling parameter and $\xi = D\Xi_{0,1}(t)$ stands for Gaussian distributed white noise with zero average and variance 1 multiplied with a constant (D) to adjust the noise level. Here $D = 0.1$ was used in all cases. The control parameters (Table 2) were chosen such that the model generates a *chattering* signal $v(t)$, as shown in Fig. 5.

Appendix C

Pre-processing

All simulations started with random initial conditions and the transient (first 10 000 iterations) was discarded. The following 50 000 iterations were saved for data analysis. The correlation matrices exhibited are an average of ten realizations for the Rulkov model and 50 for the cases using the Izhikevich model because of the resolution differences of the models. As a measure for synchronicity of the signals $x_{i,n}$ the linear (zero-lag) correlation coefficient $r(i,j)$ is used. The signal contains two main frequencies: a (fast) occurrence of spikes and a

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[1]For a faster computation, the simple Euler integration method can be used, because its errors do not accumulate due to the after-spike reset.
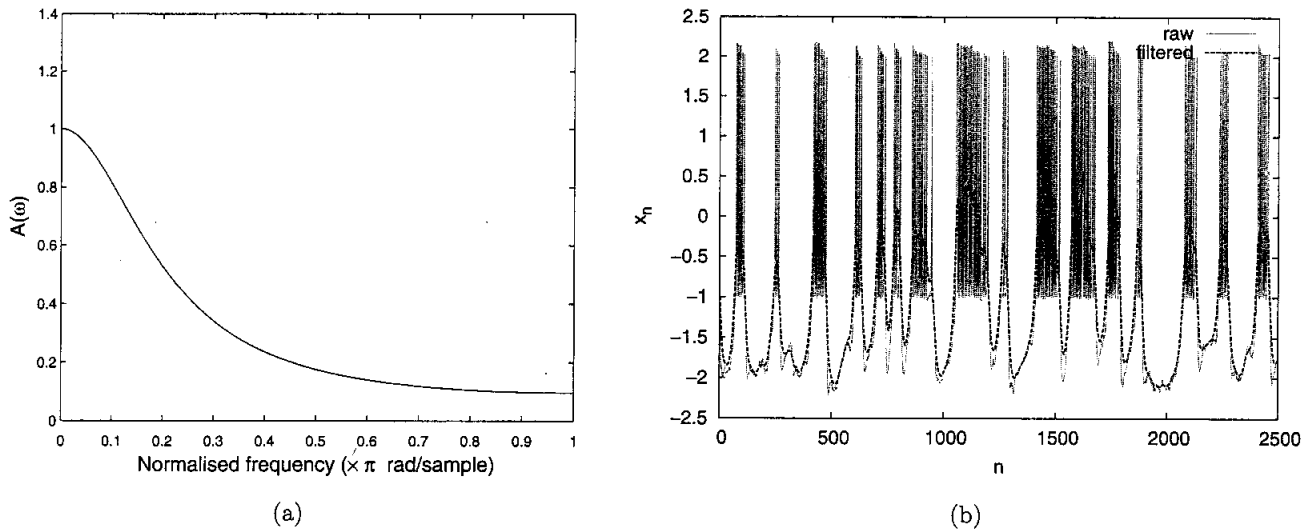
Fig. 8. (a) Filter response, (b) comparison between the filtered and the unfiltered (Rulkov) signals.

(slow) occurrence of bursts. As we are interested in the correlation of bursting activity, the signals have been filtered to eliminate the high frequencies. A recursive filter was chosen:

$$z_n = (a - 1)x_n + az_{n-1} \qquad (C.1)$$

The filter has been applied in both directions (forward and backward) to remove the phase shift that it generates if applied only once. We found $a = 0.9$ as suitable value. Figure 8 shows the effect of the filter on our data.