# A Mathematical Approach towards the Issue of Synchronization in Neocortical Neural Networks

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When interaction among regularly spiking neurons is simulated, using measured cortical response profiles as experimental input, besides complex network-effects dominated behavior, embedded periodic behavior is observed. This is the starting point for our theoretical analysis of possible emergence of synchronized neocortical neuronal firing, where we start from the model that complex behavior, as observed in natural neural firing, is generated from such periodic behavior, lumped together in time. We address the question of how, during periods of quasistatic activity, different local centers of such behaviors could synchronize, as has been postulated, e.g., by binding theory. It is shown that for synchronization, methods of self-organization are insufficient: additional structure is needed. As a candidate for this task, thalamic input into layer IV is proposed, which, due to the layer's recurrent architecture, may trigger macroscopically synchronized bursting among intrinsically non-bursting neurons, leading in this way to a robust neocortical synchronization paradigm. This collective behavior in layer IV is hyperchaotic and corresponds well with the characterizations obtained from *in vivo* time series measurements of cortical response to visual stimuli.

## 1 Introduction

In mankind's struggle to understand its own intellectual capacity, one question has attracted particular attention. It is the puzzle of how the human cortex can be so variable and efficient, in cognitive tasks and in storage, although the cycle time of cortical computation – if a spike is taken as the basic unit of clock time – is

of the order of ten milliseconds, a time that is far slower than what is currently (easily) achieved by computers. This observation leads to the expectation that there may be hidden, still undiscovered, computational principles within the cortex that, if combined with the speed of modern computers, could lead to a jump in the computational power of artificial computation, from the hardware and software point of view. In the explanation of the computational properties of the human brain, an important issue of current interest is the feature-binding problem, which relates to the cortical task of associating one single object with its different features [1–2]. As a solution to this problem – in opposition to the concept of so-called grandmother cells – synchronization among neuron firing has been proposed.

In order to address what ingredients are needed to obtain synchronized ensembles of firing neurons, we proceed as follows: first, we investigate networks of neocortical circuits of pyramidal neurons, that are endowed with excitatory and inhibitory connections, where we restrict ourselves to quasistatic dynamical conditions. Under these conditions, we obtain a picture of insulated sites that mostly are engaged in locked states, which may be expressing computational results [3]. It has been shown that recurrent connections on these computational circuits can be interpreted as controllers of the periodicity of the locking. In other words, they modify the computational results returned by the circuit [4]. The natural step then is to add second order perturbations among these sites. For this refined case, we find strong indications that self-organized synchronization, needed to support the binding by synchronization hypothesis, is virtually impossible. However, when we turn our attention to layer IV, the picture changes. As is known, this layer's task is more centered on amplification and coordination, than on computation. When we perform biophysically detailed simulations of this layer (measurements comparable to those made for the previous layers are difficult to obtain), we find a strong tendency to generate synchronized activity among the participating neurons. As a conclusion, we find that synchronization in neocortical networks – if present at all – will have its origin in layer IV, since synchronization cannot emerge in a self-organized way from the pyramidal neuron circuits alone.

## 2 Absence of Self-Organized Synchronization

To prove that self-organized synchronization is virtually impossible, we approximate the cortical network by weakly coupled centers, consisting of more strongly coupled neurons. In the latter, we focus on binary interaction, although the extension to n-ary interaction, or even to interaction among synchronized ensembles, is straightforward. The description of this interaction is by means of maps of the circle

$$f \;:\; \phi_{i+1} = \phi_i + \Omega - T(\phi_i)/T_0 \quad (\mathit{modulo}\ 1)\,. \tag{1}$$

This formula describes the response of a previously regularly spiking neuron upon a perturbation by a (in the biological sense strongly connected) neuron (note, however, that in the mathematical literature, this type of interaction is mostly referred to as weak interaction of oscillators [5]). In this formula, $\Omega$ is the ratio of the self-oscillation frequency over the perturbation frequency, and $T(\phi_i)/T_0$ measures the lengthening/shortening of the unperturbed interspike interval due to the

perturbation, as a function of the phase at which the perturbation arrives. Both quantities can be measured in experiments; this is how we base our derivation upon experimental data. From experiments of increased perturbation strengths, we found that the effect of increased perturbation strength can be parametrized as

$$g(\phi, K) := T(\phi_i, K)/T_0 = (T(\phi_i, K_0)/T_0 - 1)K + 1\,, \tag{2}$$

where $K_0$ is a normalization, chosen such that at $K = 1$, 75% of the maximal experimentally applicable perturbation strength is obtained. The perturbation response experiments are performed for excitatory, as well as for inhibitory, perturbations. The first experimental finding is that, in biology, chaotic response may be attained from pair interaction, but only if the interaction is of inhibitory nature [6]. This is essentially a consequence of the greater efficacy of inhibitory synapses, a fact that is well known in physiology. Note also that the biology-motivated normalization we are using differs from the usual mathematical one, which sets the value $K = 1$ as the critical value of the map, i.e., when the map $f$ loses invertibility. The second finding is that, as is predicted by the theory of interacting limit cycles, locking into periodic states is abundant, and that the measure of a quasiperiodic firing relation between the neurons quickly vanishes as a function of the perturbation strength $K$. A last finding is that when going from the static to the quasistatic case, lockings into subsequent periodicities are observed, exactly of the type that is predicted by the associated Farey-tree. In fact, our results can be interpreted as the first experimental proof of the limit cycle nature of regularly firing cortical neurons.

While, consequently, the activity within the centers of stronger interacting neurons is described by locking on Arnold tongues (see, e.g., [3]), beyond the bi- or n-ary strong interaction, there is also weaker exchange of activity. This weaker exchange can be modeled as diffusive coupling-mediated interaction, among the more strongly coupled centers. In this way, we arrive at a coupled map lattice model, which we base on measured binary interaction profiles at physiological conditions (including all kinds of variability, e.g., interaction, coupling strengths)

$$\phi_{i,j}(t_{n+1}) := (1 - k_2 k_{i,j}) f_{K\Omega}(\phi_{i,j}(t_n)) + \frac{k_2}{nn} k_{i,j} \sum_{nn} \phi_{k,l}(t_n)\,, \tag{3}$$

where $\phi$ is the phase of the phase-return map, at the indexed site, and $nn$ again denotes the cardinality of the set of all next-neighbors of site $i, j$. $k_2$ describes the overall coupling among the site maps. This global coupling strength is locally modified by realizations $k_{i,j}$, taken from some distribution, which may or may not have a first moment (in the first case, $k_2$ can be normalized to be the global average over the local coupling strengths). In Eq. 3, the first term reflects the degree of self-determination of the phase at site $\{i, j\}$, the second term reflects the influence by next-neighbor centers, which are again understood in the sense of strongest interaction.

The corresponding statement of synchronized behavior, as we understand it, would be observable emergence of non-local structures within the firing behavior of the neurons in the network. In the case of initially independent behavior, we may expect that due to the coupling, a simpler macroscopic behavior will be attained, which could be taken as the expression of corresponding perceptional state.

Extended simulations, however, yield the result that, for biologically reasonable parameters, the response of the network is, based on this understanding, essentially unsynchronized, despite the coupling. Extrapolations from simpler models, for which exact results are available [7], provide us with the explanation why. Generically, from weakly coupled regular systems, regular behavior can be expected. If only two systems are coupled, generally a simpler period than the maximum of the involved periodicities emerges. If, however, more partners are involved, a competition sets in, and high periodicities most often are the result. Typically, synchronized chaotic behavior, results from coupling chaotic and regular systems, if the chaotic contribution is strong enough. Otherwise, the response will be regular. When chaotic systems are coupled, however, synchronized chaotic behavior as well as macroscopically synchronized regular behavior, may be the result (e.g., [7]). For obtaining fully synchronized networks, the last option is the one to focus on. The evolution of cyclic eigenstates deserves particular attention, as it shows how novel collective behavior may emerge.

We performed simulations using 2-d networks, diffusive coupling between $20 \times 20$ to $100 \times 100$ local maps of excitatory/inhibitory interaction. In agreement with the above expectations, we found no signs of macroscopic, self-organized synchronization, using physiologically motivated variability on the parameters (type of site maps, excitability expressed by means of $K$, locally varying diffusive coupling strength, etc.). To understand this in more detail, we compared it with an idealized model that should be a better candidate for collective synchronization. This model is a diffusively coupled model with tent maps as sites. It corresponds to a situation where all site maps are identical (a situation that also can be implemented in our numerical simulations). In this comparison, it first may be objected that in distinction from the maps derived from the experiments, the model is hyperbolic, which is a non-generic situation. Through simulations, however, it can be shown that the corresponding model with nonhyperbolic site maps (parabola, e.g.), share the primary properties of the tent-map model, i.e., the phenomenology is due to the coupled map model. The advantage of the model of coupled tent maps is that it can be solved analytically. In our case we want to derive the largest network Lyapunov exponent [8]. This can be achieved by using the approach of thermodynamic formalism as follows. First, it must be realized that the coupled map lattice can be mapped onto a matrix representation of the form:

$$M(a, k_2) = \begin{pmatrix} |(1-k_2)a| & \frac{k_2}{4}a & 0 & \dots & \frac{k_2}{4}a & 0 & \frac{k_2}{4}a & 0 & \frac{k_2}{4}a \\ \frac{k_2}{4}a & |(1-k_2)a| & \frac{k_2}{4}a & 0 & \frac{k_2}{4}a & \dots & 0 & \frac{k_2}{4}a & 0 \\ \vdots & & & & \ddots & & & & \vdots \\ \frac{k_2}{4}a & 0 & \frac{k_2}{4}a & 0 & \frac{k_2}{4}a & \dots & 0 & \frac{k_2}{4}a & |(1-k_2)a| \end{pmatrix}, \tag{4}$$

where $a$ is the slope of the local tent maps, and $k$ is the diffusive coupling strength. The thermodynamic formalism formally proceeds by raising the (matrix) entries to the (inverse) temperature $\beta$, and focusing, as the dominating effect, on the largest

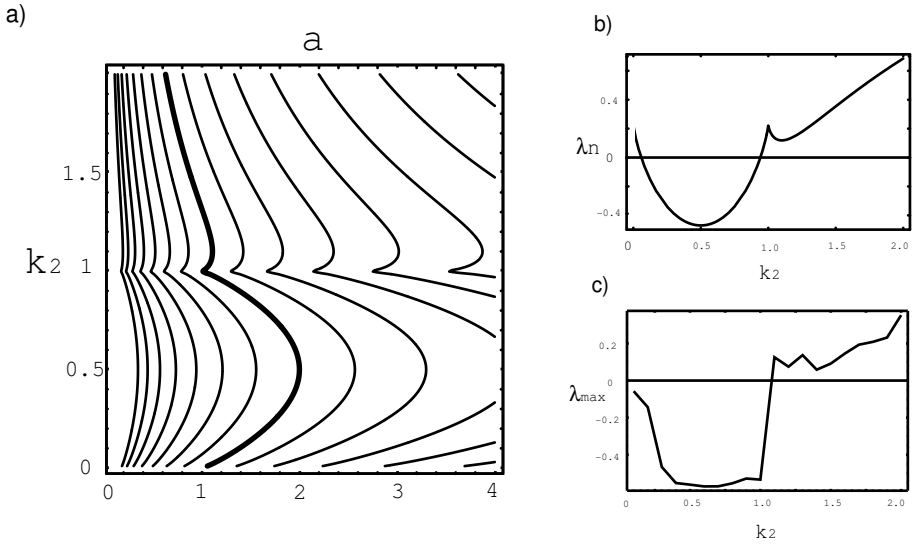



Figure 1 (a) Network Lyapunov exponent $\lambda_n$ describing stability of patterns of a network of coupled tent maps, as a function of the (identical) site map slopes $a$ and coupling $k_2$. Contour lines of distance 0.5 are drawn light, where stable network patterns evolve ($\lambda_n < 0$), bold where unstable patterns evolve; (b) Maximal site-Lyapunov exponent $\lambda_{max}$ of a network of locked inhibitory site maps, as a function of the coupling $k_2$. For the network, the local excitability is $K = 0.5$ for all sites and $\Omega$ is from the interval $[0.8, 0.85]$. The behavior of this network closely follows the behavior predicted by the tent-map model; (c) Cut through the contour plot of (a), slightly above $a = 1$.

eigenvalue as a function of the inverse temperature. For large network sizes, the latter converges towards

$$\mu(\beta, k) = (|(1 - k_2)a|)^\beta + (ak_2)^\beta \,. \tag{5}$$

This expression explicitly shows the contributions to the unstable/stable behavior from the two sources: the coupling ($k_2$) and the local instability at the site ($a$). Using this expression of the largest eigenvalue, we obtain the free energy of our model as $F(\beta) = \log((|a(1-k_2)|)^\beta + (ak_2)^\beta))$. From the free energy, the largest network Lyapunov exponent is derived as a function of the diffusive coupling strength $k_2$ and the slope of the local maps $a$, according to the formula

$$\lambda = -\left.\frac{d}{d\beta} F(\beta, k_2)\right|_{\beta=1} , \tag{6}$$

which yields the final result

$$\lambda(a, k_2) = \frac{a(1 - k_2)\log(|a(1 - k_2)|) + ak_2 \log(ak_2)}{a|1 - k_2| + ak_2} \,. \tag{7}$$

Fig. 1a shows a contour plot of $\lambda(a, k_2)$, for identically coupled identical tent maps, over a range of $\{a, k_2\}$-values. In Fig. 1c, a cut through this contour plot

is shown, at parameters that correspond to results of numerical simulations of the biologically motivated, variable coupled map lattice, displayed in Fig. 1b. The qualitative equivalence of the two approaches is easily seen. Numerical simulations of coupled parabola show furthermore that the behavior is preserved even in the presence of non-hyperbolicities. As a function of the slope $a$ of the local tent map (which corresponds to the local excitability $K$) and of the coupling strength $k_2$, contour lines indicate the instability of the network patterns. As can be seen, due to the coupling, even for locally chaotic maps ($|a| > 1$), stable network patterns may evolve (often in the form of statistical cycling, see [7]). Upon further increasing the local instability, finally chaotic network behavior of turbulent characteristics emerges. The stable patterns, however, are unlikely to correspond to emergent macroscopic behavior, comparable to synchronized behavior. Therefore, in order to estimate the potential for synchronization, we need to concentrate on the parameter region where macroscopic patterns evolve, that is, on the statistical cycling regime. However, the parameter space that corresponds to this behavior is very small, even in the tent map model. When we compare the model situation with our simulations from biologically motivated variable networks, we again observe that the overall picture provided by the tent map model of identical maps still applies. To show this in a qualitative manner, we compare the contour plot of the tent map model with the numerically calculated Lyapunov exponent of the biological network, which shows the identical qualitative behavior. Based on our insight into the tent-map model behavior, we conclude that in the biologically motivated network, a notable degree of global synchronization would require, at least, all binary inhibitory connections to be in the chaotic regime of interaction (excitatory connections are unable to reach this state [3]). Unfortunately, in case of measured neuronal phase return maps, this possibility only exists for the inhibitory connections. Furthermore, the part of the phase space on which the maps would need to dwell is rather small (although of nonzero measure, see [6]). It is then reasonable to expect that for the network including biological variability, statistical cycling is of vanishing measure, and therefore cannot provide a means of synchronizing neuron firing on a macroscopic scale. To phrase it more formally: this implies that by methods of self-organization, the network cannot achieve states of macroscopic synchronization. In addition, we also investigated whether Hebbian [9] learning rules on the weak connections between centers of stronger coupling could be a remedy for this lack of coherent behavior. Even when using this additional mechanism, it does not result in macroscopic synchronization.

## 3 Synchronization via Thalamic Input

Assuming that synchronization – understood as an emergent, not a feed-forward property – is needed for computational and cognitive tasks, the question remains as to what this property may result from. In simulations of biophysically detailed models of layer IV cortical architecture [10], we discovered a strong tendency of this layer to produce coarse-grained synchronization. This synchronization is based on intrinsically non-bursting neurons that develop the bursting property, as a consequence of the recurrent network architecture and the feed-forward thalamic input.

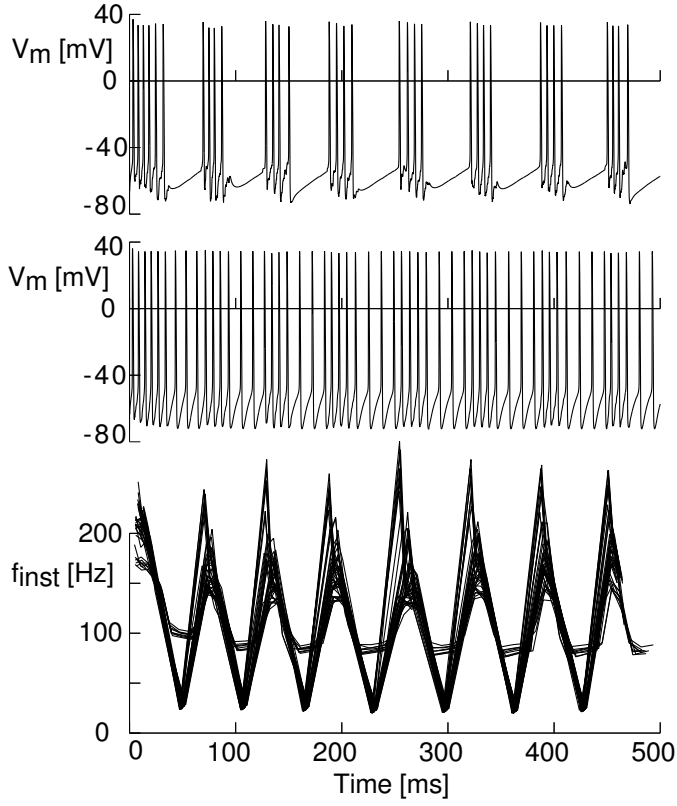



Figure 2 Coarse-grained synchronized activity of layer IV dynamics. Excitatory (upper trace) and inhibitory (lower trace) neuron firing is superimposed (bottom), from several neurons.

Detailed numerical simulations yield the result that, in the major part of the accessible parameter space, collective bursting emerges. That is, all individual neurons are collectivized, in the sense that, in spite of their individual characteristics, they all give rise to dynamics of very similar, synchronized on a coarse-grained scale, characteristics (see Fig. 2). In fact, using methods of noise cleaning (noise, in this sense, is small variations due to the individual neuron characteristics), we find that the collective behavior can be represented in a four-dimensional model, having a strong positive, a small positive, a zero and a very strong negative Lyapunov exponent. This is tantamount saying that the basic behavior of the neuron types involved are identical and hyperchaotic [11]. The validity of the latter characterization has been checked by comparing the Lyapunov dimension ($d_{KY} \sim 3.5$) with the correlation dimension ($d \sim 3.5$). Moreover, different statistical tests have been performed to assess that noise-cleaning did not modify the statistical behavior of the system in an inappropriate way. As a function of the feed-forward input current, we observed an astonishing ability of the layer IV network to generate well-separated characteristic interspike interval lengths.

## 4 Comparison with *in Vivo* Data

When we compared the model data with *in vivo* anesthetized cat measurements (17 time series from 4 neurons of unspecified type from unspecified layers), we found corresponding behavior. Not only were the measured dimensions in the range predicted by the model; specific characteristic patterns found *in vivo* could also be reproduced by our simulation model. Of particular interest are step-wise structures found in the log-log-plots used for the evaluation of the dimensions (see Fig. 3). These steps have previously erroneously been attributed to low dimensions themselves [12] but can be proven to be related to the firing in terms of patterns (the remaining results, although obtained on much smaller data bases, however, agree very well with our findings). These coincidences of modeling and experimental aspects of visual cortex firing lead us to believe that this ability of the network, to fire in well-separated characteristic time scales or in whole patterns, is not accidental, but serves to evoke corresponding responses by means of resonant cortical circuits. Not every neuron, of course, is part of such firing in patterns. In our recent studies of *in vivo* anesthetized cat data, we found essentially three different neuron firing behavior classes upon evoked or spontaneous neuron firing (where the distinction of the stimulation paradigms allowed for no further discrimination of the classes). The first class shows no patterns in their firing at all. The second classes' firing is compatible with the stimulation pattern, whereas the third's firing is incompatible. In the unaffected case, long-tail behavior of the interspike distribution is found. In the compatible case, a clean separation between patterns and individual firing is found, whereas the characteristics of the last class are more associated with the mixture of two behaviors. In all cases, however, the behavior at long interspike interval times is governed by a linear part, i.e., is long-tail.

## 5 Control of Chaotic Network Behavior

Chaotic spiking emerges from my model, as well as from the *in vivo* data that we compared it with. Moreover, nearly identical characterizations in terms of Lyapunov exponents, and of fractal dimensions, emerged. The agreement between Kaplan–Yorke and correlation dimensions [8] corroborates the consistency of the results obtained.

The question then arises of what functional, possibly computational, relevance this phenomenon could be associated with? Cortical chaos essentially reflects the ability of the system to express its internal states (e.g., a result of computation) by choosing among different interspike intervals (as in the last example above) or, more generally, among distinct spiking patterns. This mechanism can be viewed in a broader context. Chaotic dynamics is generated through the interplay of distinct unstable periodic orbits, where the system follows a particular orbit until, due to the instability of the orbit, the orbit is lost and the system follows another orbit, and so on. As it is composed of unstable periodic orbits, chaos therefore is not amorphous. It is then natural to exploit this wealth of structures hidden within chaos, especially for technical applications. The task that needs to be solved to do so is the so-called targeting, and chaos control, problem: The chaotic dynamics first

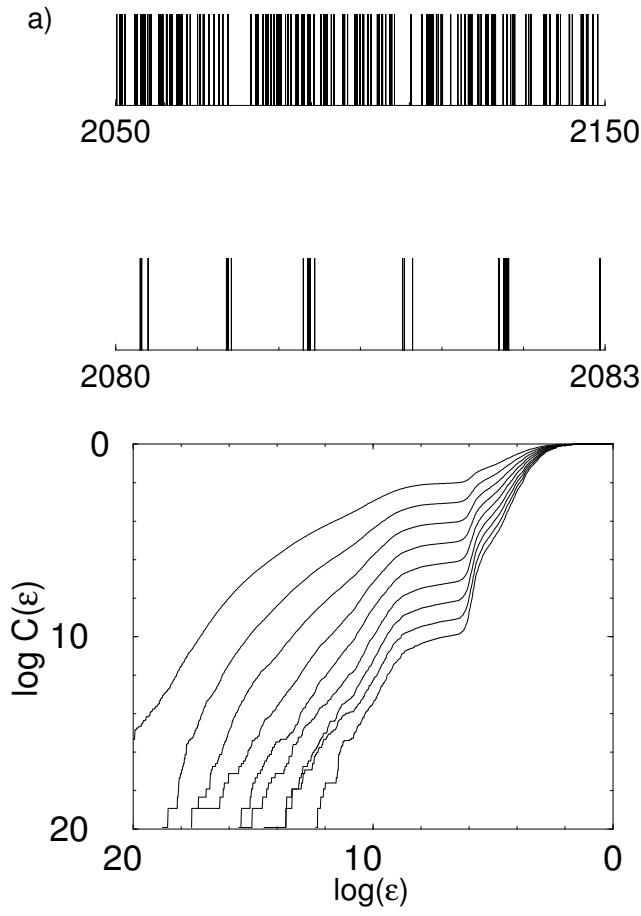



Figure 3 Step-like behavior indicating firing in patterns is observed *in vivo* (picture) and can be reproduced in biologically detailed simulations of layer IV by the interaction of several feed-forward currents to layer IV: (a),(b) from experiments, (c),(d) from corresponding simulations.

needs to be directed onto a desired orbit, on which it then needs to be stabilized, until another choice of orbit is submitted. From an information-theoretic point of view, information content can be associated with the different periodic orbits. This view is related to recent beliefs that information is essentially contained in pattern structures. In the case of the particular *in vivo* measurements discussed above, the different, well-separated interspike interval lengths, can directly be mapped onto symbols (of the same number as there are classes of distinguishable interspike interval lengths). A suitable transition matrix then specifies the allowed, and forbidden, succession of interspike intervals; i.e., this transition matrix provides an approximation to the (in this particular case: almost trivial) grammar of the natural system. In the case of collective bursting, it may be more useful to associate information

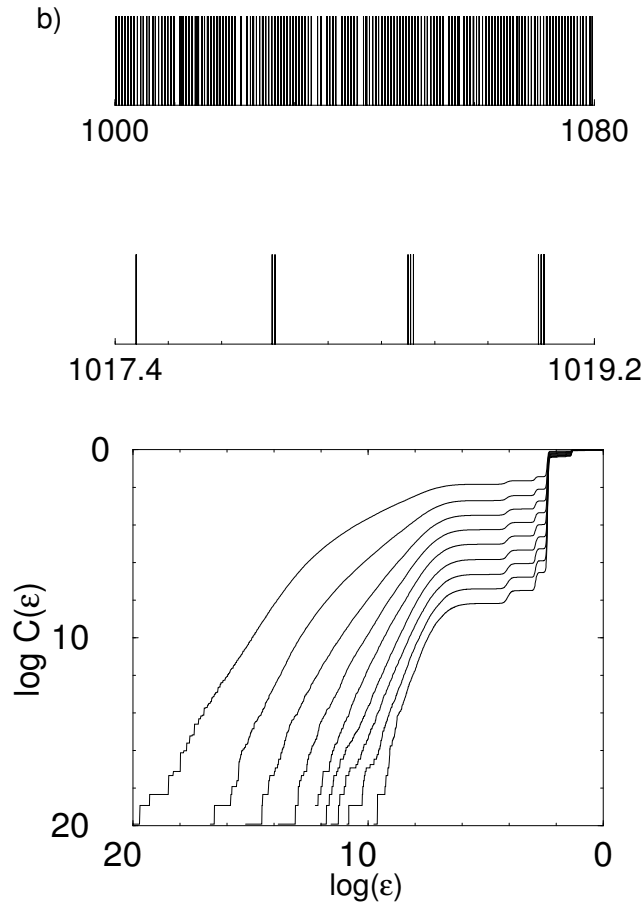
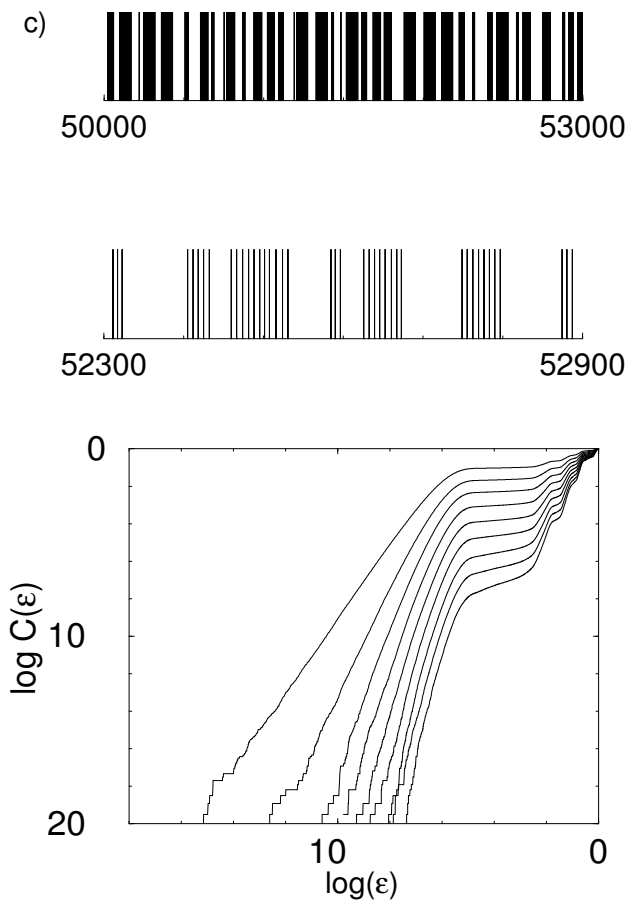



Figure 3 *(continued).*

content with spiking patterns consisting of characteristic successions of spikes. Such an approach has been shown to be optimally tailored to the description of intermittent systems. In a broader context, the two approaches can be interpreted as realizations of a statistical mechanics description by means of different types of ensembles [13–14].

In the case of artificial systems or technical applications, strategies on how to use chaos to transmit messages, and more general information, are well developed. One basic principle used is that small perturbations applied to a chaotic trajectory are sufficient to make the system follow a desired symbol sequence, containing the transmitted message [15]. This control strategy is based upon the property of chaotic systems known as "sensitive dependence on initial conditions." Another approach, which is currently the focus of applications in areas of telecommunications, is the addition of hard limiters to the system's evolution [16–18]. This very simple and robust control mechanism can, due to its simplicity, even be applied to

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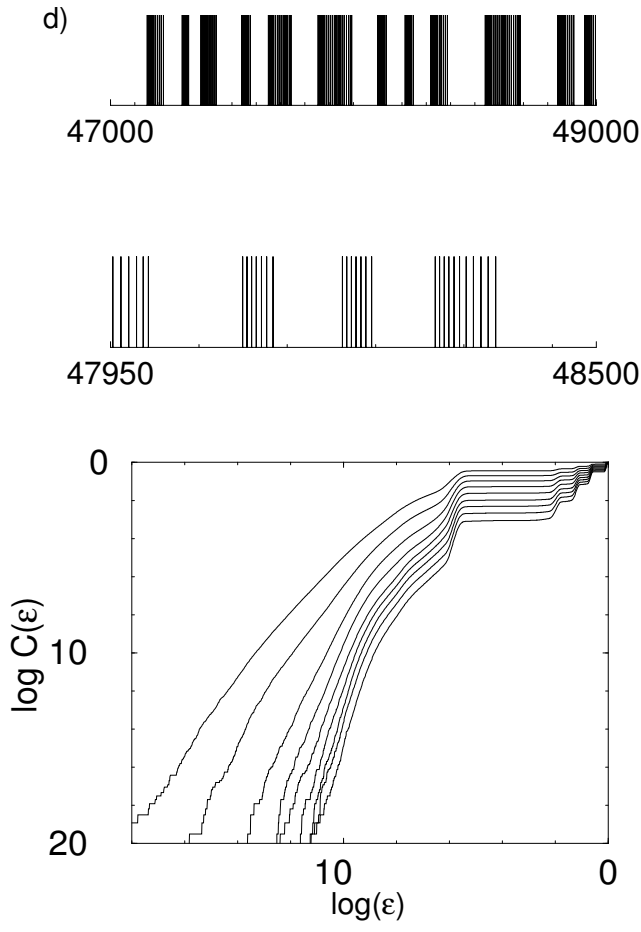
systems running at Giga-Hertz frequencies. It recently has been shown [18] that optimal hard limiter control leads to convergence onto periodic orbits in less than exponential time.

In spite of these insights into the nature of chaos control, which kind of control measures should be associated with cortical chaos, however, is unclear. In the collective bursting case of layer IV, one possible biophysical mechanism would be a small excitatory post-synaptic current. When the membrane of an excitatory neuron is perturbed at the end of a collective burst with an excitatory pulse, the cell may fire additional spikes. Alternatively, at this stage inhibitory input may prevent the appearance of spikes and terminate bursts abruptly. In a similar way, the spiking of inhibitory neurons also can be controlled. Another possibility is the use of local recurrent loops to establish delay-feedback control [4]. In fact, such control loops could be one explanation for the abundantly occurring recurrent connections among neurons. The relevant parameters in this approach are the time delay of the

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re-fed signal, and the synaptic efficacy, where especially the latter seems biologically well accessible.

In addition to the encoding of information, one also needs read-out mechanisms able to decode the signal at the receiver's side. Thinking in terms of encoding strategies, as outlined above, this would amount to the implementation of spike-pattern detection mechanisms. Besides simple straightforward implementations based on decay times, more sophisticated approaches, such as the recently discovered activity-dependent synapses [19–21] seem natural candidates for this task. Also the interactions of synapses, with varying degrees of short-term depression and facilitation, could provide the selectivity for certain spike patterns. Yet another possible mechanism is small populations of neurons, where varying axonal delays, and delays in the propagation time of the synaptic potentials, lead to supra-threshold summation, only for some sequences of input spike intervals.

In conclusion, as we have seen, biological systems provide an abundance of possible information encoding/decoding mechanisms. To explore the contextual dependence in which these alternative strategies are applied in the neocortex will require detailed experimental work in the future. We find that the most appealing explanation of synchronized firing in the cortex originates in layer IV, and is heavily based on recurrent connections and simultaneous LGN feed-forward input. We expect that firing in patterns, in this layer, is able to trigger specific resonant circuits in other layers, where then the actual computation is done (which we propose to be based on the symbol set of an infinity of locked states [22]). In future investigations we will focus on the mathematical properties of the interaction between the two types of networks, and on the relationship of this two-fold structure with the computational task the brain performs. One thing that is easy to predict is that, as a by-product of the network structure, long-range network interactions should emerge. The majority of the interspike interval distributions from *in vivo* cat visual cortex neurons and simple statistical models of neuron interaction, where the emergent long-tail behavior can be traced back to the influence of the inhibitory inputs, support this claim [23]. Long-tail interspike interval distributions are in full contrast to the current assumption of a Poissonian behavior that originates from the assumption of random spike coding. Our conclusion here is that in the cases that can be approximated by Poissonian spike trains, layer IV explicitly shuts down the long-range interactions via inhibitory connections or by pumping energy into new temporal scales that no longer sustain the ongoing activity.

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