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NEURONAL SYNCHRONIZATION: FROM DYNAMIC FEATURE BINDING TO OBJECT REPRESENTATIONS

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Abstract

Using two different models of oscillatory activity in the primary visual cortex, we analyze the synchronization properties of the networks by an eigenmode decomposition. Both models use clusters of feature-sensitive neurons representing local object properties like color and orientation. Whereas in the mean-field model oscillators communicate via their current amplitude, in the phase model oscillator interaction was controlled by phase difference. In both cases, eigenmode analysis decomposes the complex synchronization patterns into a time-invariant, spatial component, the eigenmodes, and characteristic functions describing their weight in network state over time. We find that characteristic functions can be associated with representations of objects in a visual scene, and eigenmodes represent different epistemic possibilities.

1. Introduction

Synchronization of neuronal activity is a recurring phenomenon in experiments analyzing cortical activity. In a basic explanation for a functional role it is seen as a mechanism for binding the responses of distributed neuronal populations responding to different properties of a visual stimulus (von der Malsburg, 1981; Gray et al., 1989; Engel et al., 1990). It can dynamically establish relations between neuronal populations (Singer, 1999), obviating the need for a combinatorially prohibitive number of specialized neurons (‘grandmother cells’) representing all possible feature combinations in visual stimuli.

Despite the experimental evidence for the relevance of neuronal synchronization in generating perceptual states (Fries et al., 1997; Engel et al., 1999; Bhattacharya et al., 2001), the particular mechanisms still have to be revealed. In regard to perceptual binding of visual stimuli it is assumed that neurons responding to the shape and other properties of the same object tend to synchronize their activity while the activity of neurons activated by

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different objects remains uncorrelated. However, objects consisting of characteristic parts pose a dilemma for this simple binding mechanism. If synchronization is used to bind the properties within each of the object's parts it cannot be used at the same time to bind the parts into a holistic perception of the object. Otherwise different assignments of the same set of properties to the object parts would not generate different object representations. For example, a brown cow with white legs would be indistinguishable from a white cow with brown legs.

In an accompanying article by Werning and Maye and in (Werning & Maye, 2005) we show how this dilemma can be overcome by looking at synchronization as a mechanism for implementing frame theory. Here we analyze the temporal properties of a neural network using eigenmode decomposition. We argue that eigenmodes reflect different interpretations of a stimulus. The characteristic functions associated with each eigenmode can serve as object representations which take into account hierarchical relations between the different parts of a stimulus. Computing eigenmodes and characteristic functions yields a decomposition of oscillatory network dynamics into a spatial and a temporal component, respectively. Based on these components, in (Werning, 2005) a first order predicate language with identity $PL^{=}$ has been developed to show in detail how oscillatory networks can fully implement the semantics of concepts. There it was concluded that clusters of synchronously activated cells can be interpreted as compositionally structured conceptual representations of visual scenes.

The explanatory power of the eigenmodes relies on the simultaneous analysis of a large number of neurons or neuronal populations. Currently, accordant experimental data are scarce. We therefore used two different models to simulate neuronal oscillatory networks. The mean-field model is biologically inspired and consistent with experimental findings on neuronal synchrony. By reducing this model to its basic functional principles we arrived at a network of phase coupled oscillators producing qualitatively the same results.

The next section describes the models in detail. Section 3. explains eigenmode analysis, followed by a presentation of simulations and results in section 4.. The eigenmodes are interpreted and conclusions are drawn in section 5..

2. Network Models

2.1. Mean-Field Model

The state variables in this model describe the average activity of a small population ($\approx 100\ldots200$) of spatially proximal and physiologically similar biological neurons. Wilson and Cowan (1972) showed that two recurrently connected populations, one of excitatory and the other of inhibitory neurons, can generate stable limit cycle oscillations. In the following time, networks of coupled oscillators have been used to model multidimensional feature binding (Schillen & König, 1994), contour integration and enhancement (Li, 2000), and odor recognition (Li & Hertz, 2000).

Equations describing the dynamics of a single oscillator have been derived using mean-field theory (Wilson & Cowan, 1972; Schuster & Wagner, 1990). Our model focuses on the interaction between coupled oscillators and does not use a mean-field approach in the strict sense. To distinguish this model which is based on equations derived by a mean-field approach from the phase-coupled oscillator model in the next section, we will call it mean-field model.

In detail, the dynamics of a single oscillator (see Fig. 1a) with lateral coupling to other oscillators is given by:

$$\tau_x \dot{x}_i = -x_i - g_y(y_i) + J_0 g_x(x_i) + \sum_j J_{ij} g_x(x_j) + h_i + \eta_x \tag{1a}$$

$$\tau_y \dot{y}_i = -y_i + g_x(x_i) - \sum_j W_{ij} g_y(y_j) + \eta_y. \tag{1b}$$

The activity of the excitatory and the inhibitory populations is denoted by x and y, respectively. J_{ij} describes the coupling strength between the excitatory populations of oscillator i and j. Accordingly, W_{ij} is the coupling between inhibitory populations. J_0 models local self-excitation, η is white noise, and time constants τ can be used to match refractory times of biological neurons.

For the transfer functions $g_\alpha, \alpha \in \{x, y\}$, typically sigmoidal functions are used. The saturation property of this function prevents diverging network activity. Reaching saturating activity, however, would be disadvantageous for the neurons from a metabolistic viewpoint. In order to show that non-divergent network dynamics is possible without saturating activity we used semi-linear transfer functions with threshold,

$$g_\alpha(x) = \begin{cases} m_\alpha(x - \theta_\alpha) & \text{if } x > \theta_\alpha \\ 0 & \text{else} \end{cases}. \tag{2}$$

Conditions for non-divergent network activity have been derived analytically by Wersing et al. (2001).

The external input h_i was used to represent the output of feature-sensitive neurons in the visual pathway. Oscillators receiving unimodal feature information of a visual stimulus constitute a feature module. Within a feature module oscillators are arranged on a three-dimensional grid. Neurons within a single layer respond to the same feature value at the respective location in the visual field. Different layers respond to different feature values of the same modality.

Figure 1b shows the coupling scheme. Neighboring oscillators in a layer have connections between their excitatory neurons. These connections reduce phase differences between coupled oscillators, thereby synchronizing their activity. Neighboring oscillators in different layers have connections between their inhibitory neurons. These connections increase phase differences. We consider large phase differences to be equivalent to desynchronized states in biological oscillatory networks. The coupling strength falls off exponentially with increasing distance. The connection scheme can be seen as an implementation of two Gestalt laws of perception (Wertheimer, 1924/1950) according to which elements that are spatially proximal or share similar properties have the tendency to be grouped together. The model was set up to be consistent with anatomical findings in primary visual cortex. There, excitatory projection neurons in layer 2 and 3 are connected to local inhibitory interneurons in layers 2 to 6 (Thomson & Bannister, 2003).

Multi-modal feature integration is attained by coupling different feature modules. Synchronizing connections between any single oscillator in one feature module and all os-

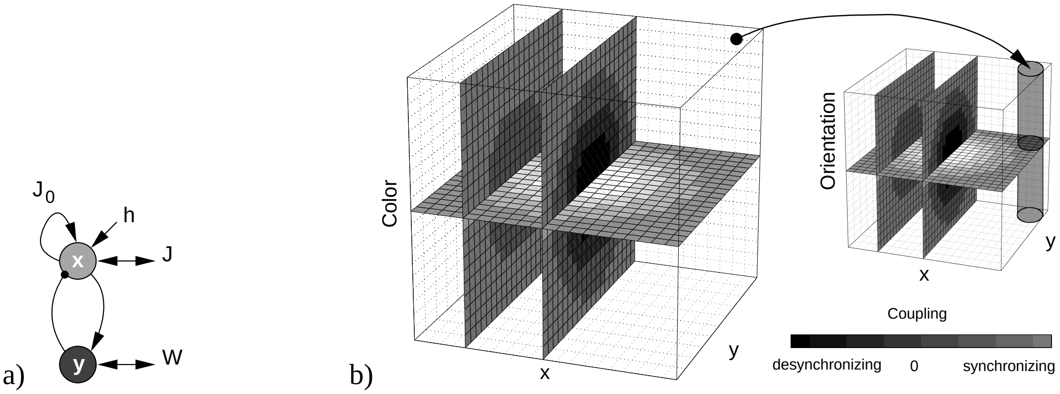

Figure 1. **a)** A single oscillator. **b)** A feature module is composed of a three-dimensional arrangement of oscillators (represented by small cubes). Slices with grey levels visualize connection type and strength of the oscillator at the center of the feature module. Two feature modules have been used, one color module and one orientation module. The arrow between the feature modules symbolizes synchronizing connections between a single oscillator at the origin and all oscillators with the same receptive field position in the other feature module (visualized by a cylinder). This connection scheme is applied to all other positions as well. Parameters: $\tau_x = \tau_y = 1$, $m_x = m_y = 2$, $\theta_x = 2$, $\theta_y = 1$, $h_i = 2$, $J_0 = 0.4$, $J_{ij} = J/\sqrt{2\pi\sigma^2}\exp(-r_{ij}^2/2\sigma^2)$ (W_{ij} accordingly), $J = 0.6$ if i and j are in the same feature module and $J = 0.08$ if j is in a different module, $W = 0.05$, $r = 4$, $\eta = 0.4$.

cillators with the same receptive field position in all other feature modules mediate the synchronization of oscillators activated by different properties of the same object.

2.2. Model with Phase-Coupled Oscillators

In order to verify the results obtained in the mean-field model we performed the same experiments with a model using an alternative description of neuronal oscillators. Models with phase-coupled oscillators do not consider the particular mechanism by which oscillations are generated. A single oscillator is assumed to generate asymptotically stable limit-cycle oscillations (Kuramoto, 1984; Sturm & König, 2001) of frequency ω. Its current state is given by the phase $\phi(t)$ and the amplitude $a(t)$. The output of the neuronal population modeled by a single oscillator is:

$$x_i(t) = a_i(t)\sin(\phi_i(t)).$$

Neighboring oscillators are coupled by synchronizing or desynchronizing connections. They can interact via their phase, their amplitude, or both. The current model is confined to phase interactions only. In the case of synchronizing connections, the phase difference between two oscillators is used to advance the phase of the lagging oscillator and to retreat the phase of the leading oscillator (vice versa for desynchronizing connections). In our model the dynamics of an oscillator is given by:

$$\dot{\phi}_i = \omega - \sum_j s_{ij} a_j \sin(\phi_i - \phi_j) + \eta_i \tag{3a}$$

$$\dot{a}_i = -a_i + h_i. \tag{3b}$$

Weights s_{ij} comprise couplings within a feature module as well as between feature modules. Synchronizing connections have $s_{ij} > 0$, whereas desynchronizing connections are given by $s_{ij} < 0$. The same connection scheme as for the mean-field model is applied. Again, η is a noise term and h_i describes external input from the feature detectors.

Phase-coupled oscillator models have been applied for reproducing experimental results from the visual cortex (Sompolinsky & Golomb, 1991). Apart from a more concise formulation and better analytical amenability, an important advantage of this model is the possibility to separately investigate the effects of phase and amplitude interaction between oscillators. In the current model we included phase interaction only. This is sufficient to reproduce qualitatively the same results as in the mean-field model. Amplitude interaction will be considered in future models.

3. Eigenmode Analysis

Upon stimulation the networks described in the previous section generate oscillatory patterns that simulate oscillatory activity of a larger number of neurons in primary visual cortex. In neurobiological experiments these patters are typically analyzed using pairwise measures like cross-correlation or coherence. Analyzing the temporal dynamics of a larger network using measures that take into account only pairs of oscillators is a very tedious task, though. What we want instead is a method for analyzing all oscillators simultaneously.

From synergetics it is well known that the dynamics of complex systems is often governed by a few dominating states and can, therefore, be described by a small set of corresponding order parameters (Haken, 1990). These states are the eigen- or principal modes of the system, the corresponding eigenvalues designate how much of the variance is accounted for by that mode.

In principle, eq. (1) can be solved analytically by linearization around the fix point and combination of both equations into a second order differential equation (which yields a vectorial form of the fundamental equation of a harmonic oscillator, for that matter). The eigenvectors of the solution constitute a set of eigenstates that characterize the dynamics of the network. Analytic determination of the fix point, however, is possible only for a small and rather uninteresting subset of stimuli, e.g., infinitely long lines or homogeneous activation.

Another way of describing oscillatory network activity by superposition of eigenstates is to determine the principal components of the activity based on a numerical simulation of the network. This is possible for arbitrary stimuli. Computationally, the principal components are eigenvectors of the covariance matrix C:

$$\begin{aligned}
\mathbf{D} &= \begin{bmatrix} x_1(t_1) & x_1(t_2) & \cdots & x_1(t_m) \\ x_2(t_1) & x_2(t_2) & \cdots & x_2(t_m) \\ \vdots & \vdots & \ddots & \vdots \\ x_n(t_1) & x_n(t_2) & \cdots & x_n(t_m) \end{bmatrix} \\
\mathbf{C} &= \mathbf{D}\mathbf{D}^T \\
\mathbf{V}\blacksquare\mathbf{V}^{-1} &= \mathbf{C}
\end{aligned}$$

Matrix **D** contains the activity of oscillators at equidistant time points. **V** is the matrix of eigenvectors and the diagonal matrix ■ contains the corresponding eigenvalues. The eigenmodes constitute an orthonormal coordinate system in which the variance of the network activity in each direction is determined by the magnitude of the respective eigenvalues. The network activity can be described by a superposition of the eigenmodes $\mathbf{v}_i$ with time-dependent weights $c_i(t)$:

$$\mathbf{x}(t) = \sum_i c_i(t)\mathbf{v}_i$$

The weights $c_i(t)$ are determined by projecting the network activity on the respective eigenmode i:

$$c_i(t) = \mathbf{x}(t)^T\mathbf{v}_i.$$

We will call the weights $c_i(t)$ characteristic functions because they correspond to distinct interpretations of the stimulus.

If functions $c_i(t)$ have a sinusoidal time course they can be expressed by $k_i \mathrm{e}^{\lambda_i t+\phi_i}$. Here, k_i is the amplitude of the oscillation and the imaginary part of the complex eigenvalues λ_i is its frequency. The network activity can then be written as

$$\mathbf{x}(t) = \sum_i k_i \mathbf{v}_i \mathrm{e}^{\lambda_i t+\phi_i},$$

which is isomorphic to the analytic solution. In general, the eigenvectors of the covariance matrix will differ from the eigenvectors of the analytic solution of eq. (1). However, if there are strong differences in the variances of the principal directions, they can be considered as approximations of the eigenmodes of the analytic solution. Strong differences of variances are given when the ordered sequence of eigenvalues λ_i is quickly decreasing, which was the case in all our experiments.

4. Results

We investigated multi-dimensional feature binding in networks consisting of two feature modules, one responding to colors and the other to edge orientations. A number of simple (Maye, 2003; Maye & Werning, 2004) and more complex stimuli (Werning & Maye, 2005) have been applied. The network dynamics were determined by numerical integration of eqs. (1) and (3). Figure 2 shows a representative result for a stimulus consisting of a red vertical and a green horizontal (Fig. 2a). Cross-correlation analysis revealed zero-lag phase synchronization between oscillators which are activated by the same object (Fig. 2b). We performed eigenmode analyses on the resulting network activity. The eigenmodes were ordered according to their eigenvalue and reshaped to visualize the contribution of the oscillators in different layers of the feature modules (Fig. 2c).

Eigenmode analysis decomposes the network dynamics into a set of orthogonal states. In the following, we interprete the eigenmodes with the two largest eigenvalues. In the first eigenmode, i.e. the one which accounts for most of the variance, all oscillators activated by the stimulus make the same positive contribution. This corresponds to an oscillation pattern in which all oscillators are synchronized. This in turn can be interpreted as a representation of the stimulus as a single object.

In the second eigenmode, neurons sensitive for red and for vertical orientation make a negative contribution, whereas neurons sensitive to green and horizontal make a positive contribution. This corresponds to an antiphasic oscillation between the oscillators activated by the red vertical and those activated by the green horizontal. This in turn can be interpreted as the network binding the properties red and vertical into one object and green and horizontal into another. Taken together the first two eigenmodes reflect two alternative groupings of the stimulus elements.

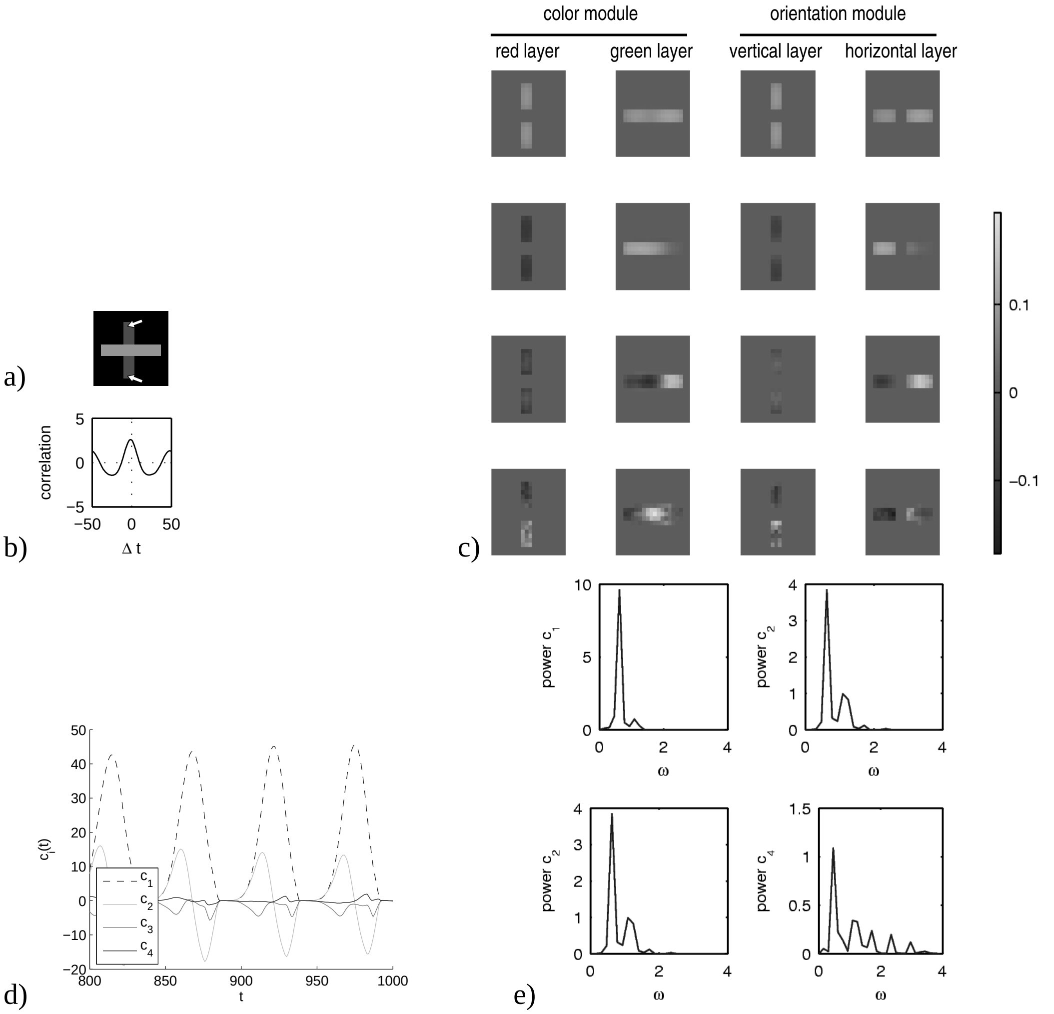

Figure 2. **a)** A stimulus showing a red vertical and a green horizontal (visualized by different shades of gray). **b)** The cross-correlogram shows zero phase-lag synchronization between the two oscillators at the position marked by white arrows in a). **c)** Four largest eigenmodes (from top to bottom) generated by the mean-field model. **d)** Characteristic functions associated with the eigenmodes. **e)** Fourier spectrum of the characteristic functions. Note the different scales on the y-axis.

Projecting the network activity into the eigenmode space yields the characteristic functions $c_i(t)$ (Fig. 2d). While eigenmodes depict the spatial distribution of activity, the as-

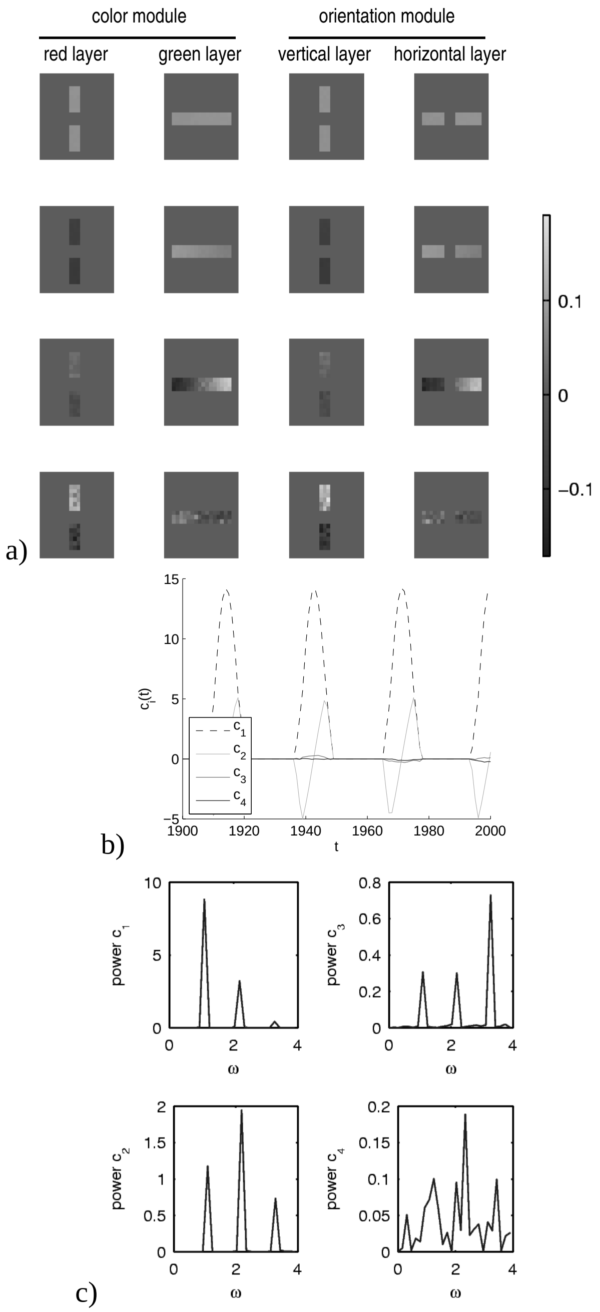

Figure 3. Eigenmode analysis of the dynamics of the phase model. **a)** eigenmodes, **b)** characteristic functions, **c)** Fourier spectrum of the characteristic functions. Note the different scales on the y-axis. Parameters: $\omega = h_i = 1$, $s_{ij} = 0.625/-0.125/0.125$ for synchronizing connections within a layer / desynchronizing connections to neighboring layers / synchronizing connections to other feature module, $r = 1$, $\eta = 0.2$

sociated characteristic functions show the contribution of each eigenmode to the network activity over time. From Figures 2d and 3b it can be seen that the characteristic function for the first eigenmode constitutes an envelope for the function of the second eigenmode. This result suggests a mechanism for the definition of hierarchical relations between different interpretations of the stimulus. The network dynamics is the representational basis of these interpretations and eigenmode analysis is just one way to extract a pictorial version. Selection of an interpretation would be possible by synchronization with network states which are dominated by the respective eigenmode, i.e. by synchronization with the corresponding characteristic function. In an accompanying article (see article by Werning and Maye in this issue) we show how characteristic functions can indeed serve as object representations.

A Fourier transform has been used to analyze the spectral components of the characteristic functions (Fig. 2e). It shows that subordinate hierarchy levels are associated with increasing frequencies. The hypothesis that different frequency bands are involved in stimulus processing at different spatial scales is supported by experiments (Frien & Eckhorn, 2000). We tested if this effect is depending on the noise level in the network. Doubling the noise ($\eta = 0.4$) did not change the results qualitatively.

Exactly the same analyses were applied to the dynamics generated by the phase model. The results are shown in Figure 3.

5. Conclusion

The results demonstrate that eigenmodes can represent different binding solutions and, therefore, different interpretations of the stimulus. This capability is prerequisite for a hierarchical binding mechanism which allows recognition of an object as a single entity as well as distinguishing its parts. Our results predict that this binding mechanism employs synchronization of neural activity in different frequency bands.

A comparison of the two modeling approaches shows that, qualitatively, the results are model independent. It is known that nonlinear oscillators interacting through amplitude coupling can be reduced to a phase model in the condition of weak coupling (Kuramoto, 1984). Since amplitude interactions between oscillators were eliminated in the phase model we conclude that phase interactions are sufficient to generate the observed results. This leaves amplitude interactions with the possibility for another functional role which will be the focus of future investigations.

Our results suggest that understanding the function of neuronal synchrony is likely to involve the analysis of temporal correlations between a large number of neurons. Application of our analysis to experimental data is limited by the low spatial resolution of current experimental techniques. The most advanced method in this respect uses voltage sensitive dyes in conjuction with optical imaging (Leznik et al., 2002; Jancke et al., 2004). It allows analyzing the activity of larger cortical patches with high temporal and spatial resolution. Together with the eigenmode analysis presented here, this might be a promising approach for studying the functional role of neuronal oscillations.

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