Biol. Cybern. 64, 77–82 (1990)

Biological
Cybernetics

A model for neuronal oscillations in the visual cortex

1. Mean-field theory and derivation of the phase equations

H. G. Schuster and P. Wagner

Institut für Theoretische Physik und Sternwarte, Universität Kiel, Olshausenstrasse 40, D-2300 Kiel, Federal Republic of Germany

Received March 27, 1990/Accepted in revised form June 12, 1990

Abstract. We study a neural network consisting of model neurons whose efferent synapses are either excitatory or inhibitory. They are densely interconnected on a local scale, but only sparsely on a larger scale. The local clusters are described by the mean activities of excitatory and inhibitory neurons. The equations for these activities define a neuronal oscillator, which can be switched between an active and a passive state by an external input. Investigating the coupling of two of these oscillators we found their coupling behaviour to be activity-dependent. They are tightly coupled and almost synchronized if both oscillators are active, but weakly coupled if one or both oscillators are passive. This activity-dependent coupling is independent of the underlying connectivities, which are fixed. Finally, for coupled active oscillators we derive a simplified description by disregarding the amplitudes of the oscillators and working with their phases. We use this simplified description in a compagnion article to model the oscillations in the visual cortex.

1 Introduction

Recent studies of the visual cortex of cats and monkeys (Gray and Singer 1989; Gray et al. 1989; Eckhorn et al. 1988; Freeman and van Dijk 1987) found oscillatory responses which are induced by external stimuli. The frequency of these oscillations, which are not stimulus-locked, lies in the range 40–60 Hz. Similar oscillations have long been known for the olfactory bulb of rats and rabbits by investigations of Freeman (Freeman 1975; Freeman et al. 1988). For the oscillations in the visual cortex, which are synchronized over large cortical distances up to 7 mm, there exists some ideas about the generation and the purpose of these oscillations. Recent articles (Kammen et al. 1989; Kammen et al. 1990; Sporns et al. 1989; Finkel and Edelman 1989) suggest that there exist global feedback connections to other parts of the cortex, which synchronize the oscillations in the visual cortex.

It will be shown in the following study that the oscillations in the visual cortex can be understood as an intrinsic phenomenon of a single column. If we assume long range but sparse interactions between columns in one cortical layer we can also explain the experimentally observed synchronization effects.

In this way we avoid the problem of (Kammen et al. 1989, 1990) where the global feedback connections of the so called comparator model tend to synchronize the phases of distributed neural oscillators even if the figure which generates the stimulus is not connected (see below). But we are aware that feedback connections to other areas exist and will be necessary to explain more complicated linking effects.

Our investigation will be reported in two articles. In the first one we describe the emergence of oscillations in a single column which is modelled by subpopulations of excitatory and inhibitory neurons. Furthermore we show that these oscillations can be described by the phases of limit cycle oscillators irrespective of the amplitudes.

In the second article we introduce long range sparse interactions between different columns with the same orientation and velocity preference and show that this leads to a nonlinear interaction.

Our first paper is organized as follows. In Sect. 2, we derive the appropriate macroscopic mean-field equations for a cluster of densily interconnected neurons which model a single column. Two columns are coupled in Sect. 3, and we introduce a reduced phase description of coupled oscillators. We find an activity-dependent coupling between these phase oscillators. The coupling is strong, if the two oscillators are active, and remains weak, if one or both oscillators are passive. Section 4 contains a summary. Appendix A gives a derivation of the mean-field equations, supported by numerical simulations. A derivation of the equations for the phases of the oscillators is given in Appendix B.

2 Model for a single column

We model a single orientation and velocity specific column in the visual cortex (Kandel and Schwarz 1985) by a set of two neuron populations which are distinguished by the fact that their axons end with excitatory or inhibitory synapses, respectively (Dale's law, see for instance (Wilson and Cowan 1972; Shinomoto 1987)).

The description for such groups can be generalized to clusters of neurons, which consist of more than two types of model neurons, and it is related to the concepts of neural assemblies (Gerstein et al. 1989) or to the theory of neuronal groups (Edelman 1978, 1987).

Each neuron can be described by its mean firing rate $e_k(t)$ or $i_l(t)$, where $e_k(t)$ stands for excitatory and $i_l(t)$ for inhibitory neurons and $k = 1, \ldots, N_e$, $l = 1, \ldots, N_i$. If we make the biologically reasonable assumption that within a column each neuron is coupled to all others and denote the couplings as shown in Fig. 1, we arrive at the following set of differential equations for the activities $e_k(t)$ and $i_l(t)$:

$$\mathrm{d}e_k/\mathrm{d}t = -e_k + S(a_e((1/N_e)\sum_{l=1}^{N_e} u_{kl}e_l - (1/N_i)\sum_{l=1}^{N_i} v_{kl}i_l - \theta_k^e + p_k)) \quad k = 1, \ldots, N_e \tag{1a}$$

$$\mathrm{d}i_k/\mathrm{d}t = -i_k + S(a_i((1/N_e)\sum_{l=1}^{N_e} w_{kl}e_l - (1/N_i)\sum_{l=1}^{N_i} z_{kl}i_l - \theta_k^i)) \quad k = 1, \ldots, N_i \tag{1b}$$

Here t denotes time, $S(x) = (1 + \exp(-x))^{-1}$ models a sigmoid function and we see that if the couplings u_{kl}, v_{kl}, w_{kl}, z_{kl} and the external stimulus p_k are switched off, all activities simply decay exponentially to zero, provided the thresholds θ_k^e and θ_k^e are large enough. We note that (1) are related to Hopfield's model (Hopfield 1984) by an affine transformation. Hopfield used the input into one neuron, $h_k^e = \Sigma_{l=1}^{N_e} u_{kl}e_l - \Sigma_{l=1}^{N_i} v_{kl}i_l + p_k$ and similar for h_k^i as the variable which describes the state of a neuron. With this transformation (1) becomes equivalent to (5) of (Hopfield 1984). For all to all couplings with means $c_1 = 1/N_e^2\,\Sigma_{k,l}u_{kl}$, $c_2 = 1/(N_eN_i)\Sigma_{k,l}v_{kl}$, $c_3 = 1/(N_eN_i)\Sigma_{k,l}w_{kl}$ and $c_4 = 1/N_i^2\,\Sigma_{k,l}z_{kl}$ the activities of the subpopulations become nonzero and can be described by their means (the mean-fields of our theory):

$$E(t) = (1/N_e)\sum_{l=1}^{N_e} e_l(t) \tag{2a}$$

$$I(t) = (1/N_i)\sum_{l=1}^{N_i} i_l(t) \tag{2b}$$

which in turn obey the differential equations:

$$\dot{E} = -E + S(a_e(c_1E - c_2I - \Theta^e + P)) \tag{3a}$$

$$\dot{I} = -I + S(a_i(c_3E - c_4I - \Theta^i)) \tag{3b}$$

where $\Theta^e = (1/N_e)\Sigma_{k=1}^{N_e}\theta_k^e$, $\Theta^i = 1/N_i\,\Sigma_{k=1}^{Ni}\theta_k^i$ and $P = (1/N_e)\Sigma_{k=1}^{N_e}p_k$.

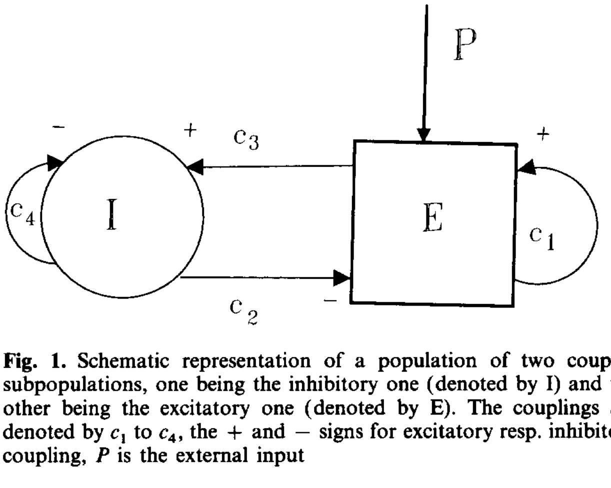

Fig. 1. Schematic representation of a population of two coupled subpopulations, one being the inhibitory one (denoted by I) and the other being the excitatory one (denoted by E). The couplings are denoted by c_1 to c_4, the + and − signs for excitatory resp. inhibitory coupling, P is the external input

Equations (3) are correct to order $1/\sqrt{N_i}$ as shown in Appendix *A*. If we associate with each column about 10^4 neurons, we get $1/\sqrt{N_i} \approx 10^{-2}$. This result shows, that the neural field equations introduced in (Wilson and Cowan 1972), which become equivalent to (3) in the limit $\tau_e = 1$, $\tau_i = 1$ and refractory period $r = 0$ (see (7) and (8) of Wilson and Cowan 1972) can be derived rigorously starting from individual neurons with long range couplings. In contrast to Wilson and Cowan we neglect the refractory period of each neuron, i.e. we set $r = 0$. This is justified by the fact that we are interested in oscillations in the visual cortex which have time scales of about 20 ms which are much larger than the absolute refractory period which is of order 1 ms.

In the following we choose for the averaged couplings the values $c_1 = 10$, $c_2 = 6$, $c_3 = 10$, $c_4 = 1$, for the

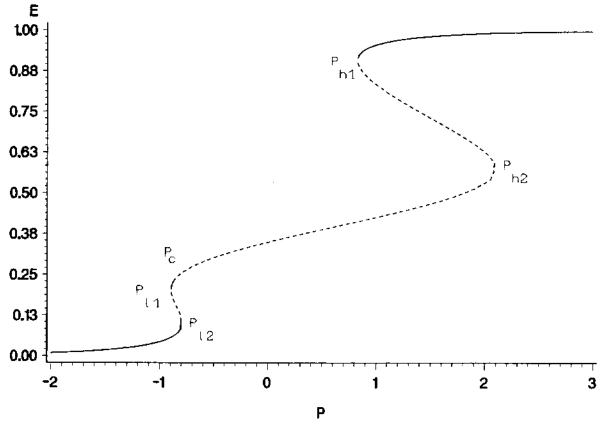

Fig. 2. The bifurcation diagram. Shown is – as function of the input P – the value E_0 of the fixed points. Solid lines indicate stable fixed points, broken lines instable fixed points. For low values of P there is a stable fixed point only, at P_{l1} an additional pair of fixed points arises, one of them a saddle, the other a stable fixed point with complex conjugate eigenvalues, but negative realpart. Increasing P further, the fixed point with the complex conjugate eigenvalues undergoes (at P_c) a Hopf bifurcation, i.e. its two eigenvalues cross the imaginary axis, so creating the limit cycle of the system. At P_{l2}, the stable fixed point meets the saddle point and disappears, leaving only the unstable fixed point with its limit cycle. At P_{h1}, a new pair of fixed points arises, a stable one and a saddle. The limit cycle becomes semi-stable, i.e. it is attracting to all points that lie inside it, and repelling to the points outside. If one increases P further, ultimately (*at* P_{h2}) the saddle and the unstable fixed point met and disappear

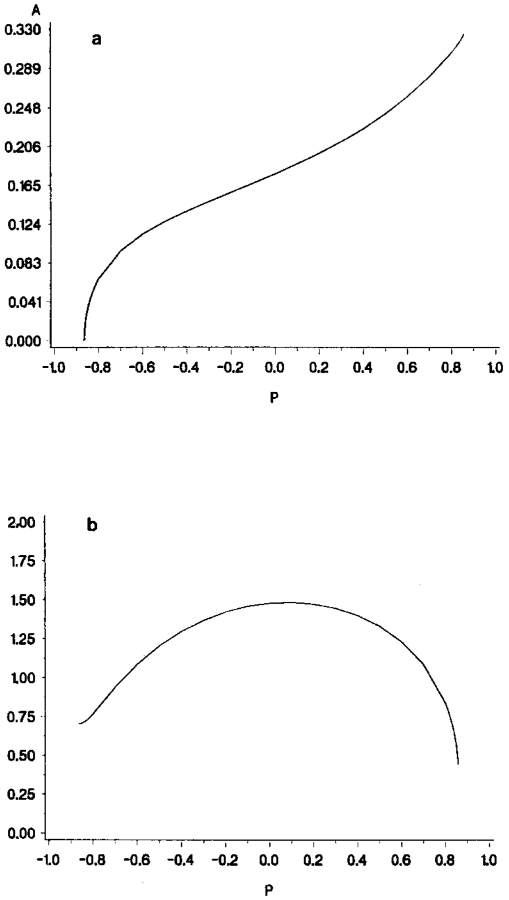

Fig. 3. Amplitude A (**a**) and frequency ω(**b**) of the limit cycle as function of the input P. The results are obtained by numerical integration of (3)

prefactors $a_e = 1.2$, $a_i = 2$ and $\Theta^e = 2$ and $\Theta^i = 3.5$ for the thresholds, similar to the values reported by Wilson and Cowan.

The dynamical behaviour of the solutions of (3) as a function of the input stimulus P is summarized in the bifurcation diagram shown in Fig. 2. Our main conclusion is that for small stimuli $P \leqslant -0.9$ the mean activities of both populations are time independent i.e. we have a stable fixed point $E(t) = E_0, I(t) = I_0$, whereas for higher stimuli $-0.9 \leqslant P \leqslant 0.9$ there occurs a transition to oscillatory behaviour via a Hopf bifurcation, which has also been seen in (Baird 1986; Wilson and Cowan 1972). The amplitude of the excitatory activity, given as $A(P) = (1/2)(\max\{E(t)\} - \min\{E(t)\})$ and the frequency $\omega(P)$ of the corresponding limit cycle as obtained by numerical integration of (3) are shown in Fig. 3. This suggests that the oscillations which have been observed experimentally in the orientation specific columns in the visual cortex of cats could result from a dynamical competition between two macroscopically coupled subpopulations of neurons within each column. In the following we make explicit use of the fact that in our model this oscillation can be switched on and off via the external stimulus (as shown in Fig. 3b).

3 Coupled columns and phase description

In the following we couple two units according to Fig. 4. This leads to the following equations of motion:

$$\dot{E}_k = -E_k + S(A^e_k + \eta a_e U_l), \quad k,l = 1,2\; k \neq l \tag{4a}$$

$$\dot{I}_k = -I_k + S(A^i_k + \eta a_i V_l), \quad k,l = 1,2\; k \neq l \tag{4b}$$

where:

$$U_l = a_1 E_l - a_2 I_l$$

$$V_l = a_3 E_l - a_4 I_l$$

$$A^e_k = a_e(c_1 E_k - c_2 I_k - \Theta^e + P_k)$$

$$A^i_k = a_i(c_3 E_k - c_4 I_k - \Theta^i)$$

By expanding (4) to first order in the coupling strength η, which can be done if the coupling is weak $\eta \ll \max\{c_j\}_{j=1,\ldots,4}$, and introducing the deviations $x_k := E_k - E_{k0} \propto r_k \cos\phi_k$, $y_k := I_k - I_{k0} \propto r_k \sin\phi_k$ from the unstable fixed points (E_{k0}, I_{k0}), we obtain analytically, as shown in Appendix *B*, the following equations for the phases $\phi_{1,2}$ of the limit cycle oscillators (Kuramoto 1984; Winfree 1980) which describe two coupled columns in the active state:

$$\dot{\phi}_1 = \omega_1 - K_{12}\sin(\phi_1 - \phi_2) \tag{5a}$$

$$\dot{\phi}_2 = \omega_2 - K_{21}\sin(\phi_2 - \phi_1) \tag{5b}$$

where $\omega_{1,2}$ are the frequencies of the oscillators, and the couplings K_{kl} (with $K_{kl} \neq K_{lk}$ in general) are proportional to η. The expansion (4) with respect to η, i.e. $\dot{E}_k = -E_k + S(A^e_k) + \eta a_e S'(A^e_k)U_l$ and similar for $\dot{I}_k$, leads to the coupling terms $L^e_{kl} = \eta a_e S'(A^e_k)U_l$ and $L^i_{kl} = \eta a_i S'(A^i_k)V_l$ respectively. They depend strongly on the inputs into the two oscillators, which is shown in

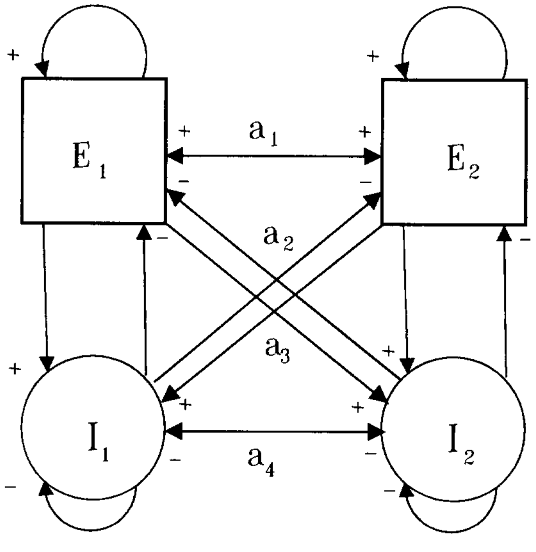

Fig. 4. Model of the couplings of two neuronal oscillators. Each oscillator is connected to the other one by coupling a_1 and a_4. Again the "+" and "−" and signs stand for excitatory respective inhibitory couplings. We have omitted the designation of the intrinsic couplings c_1 to c_4

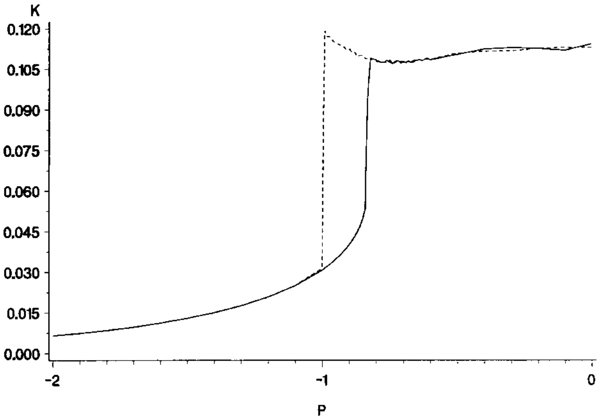

Fig. 5. The activity dependent coupling $K = a_e \eta S'(A^e)$ of the passive oscillator as a function of the input into this oscillator, while the input into the active oscillator is fixed. Note the steep step in the coupling constant, and the hysteresis in the switching-on process. The solid line is for increasing the input into the passive oscillator, while the dashed line stands for decreasing input. This figure is obtained by numerical integration of two coupled oscillators, the plotted coupling constant is the long time average $(1/T)\int_0^T K(t)\mathrm{d}t$

Fig. 5 for the prefactor of L^e_{kl}, $K = \eta a_e S'(A^e_k)$. Figure 5 is obtained by increasing the input into oscillator k while holding the input into oscillator l on a constant value where a selfsustained oscillation occurs. It is seen that the coupling is weak if one or both oscillators are passive, and it is enhanced by nearly one order of magnitude if both oscillators are active.

4 Discussion

We have introduced a mean-field theory for the dynamical behaviour of neuronal groups of densely interconnected model neurons. The theory reduces drastically the number of variables involved in a description of such a group, and therefore it is possible to economize computer power in large scale integration of model neurons, such as in Sporns et al. (1989) and Finkel and Edelman (1989).

In cases, where such clusters behave oscillatory, we have shown that it is possible to reduce the set of variables once more: It is sufficient to use the phase of such an oscillator as the only remaining variable, if the radius of the limit cycle is robust against weak perturbations.

In our system, we found that the coupling of such neuronal groups leads to a novel feature, i.e. the coupling strength depends on the activity of the two coupled clusters. It is enhanced nearly one order of magnitude, if the two coupled columns are active.

The advantage of this reduction is, that it gives a transparent description of the synchronization behaviour of such nonlinear oscillators and eventually makes it possible to get analytical results. In a compagnion article we will use the results of this reduction to model the experimentally observed synchronization of oscillations in the visual cortex.

Acknowledgements. It is a pleasure to thank W. Singer for most fruitful discussion and the Sonderforschungsbereich 185 Frankfurt/Darmstadt for financial support.

Appendix A: derivation of the mean field equations and numerical simulations

Summation in (1) over k yields:

$$\dot{E} = -E + (1/N_e) \sum_{k=1}^{N_e} S(a^e_k) \tag{6a}$$

$$\dot{I} = -I + (1/N_i) \sum_{k=1}^{N_i} S(a^i_k) \tag{6b}$$

where a^e_k and a^i_k are abbreviations for the arguments of the sigmoidfunctions (see (1)). We decompose each term, i.e. the couplings $u_{kl} = c_1 + \delta u_{kl}$ etc. and the activities $e_k = E + \delta e_k$ and $i_k = I + \delta i_k$ in its mean value plus a fluctuation $a^{e,i}_k = A^{e,i} + \delta a^{e,i}_k$, where $A^{e,i} = 1/N_{e,i} \Sigma_{l=1}^{N_{e,i}} a^{e,i}_l$ and expand (6) as:

$$\dot{E} = -E + (1/N_e) \sum_{k=1}^{Ne} (S(A^e) + S'(A^e)\delta a^e_k$$
$$+ (1/2)S''(A^e)(\delta a^e_k)^2 + \cdots)$$

$$\dot{I} = -I + (1/N_i) \sum_{k=1}^{N_i} (S(A^i) + S'(A^i)\delta a^i_k$$
$$+ (1/2)S''(A^i)(\delta a^i_k)^2 + \cdots)$$

The lowest order terms contain no fluctuations and yield the mean field approximation eqns (3). All first order terms cancel, because the fluctuations have mean zero by construction. Terms of the form $(1/N)\, \Sigma_{l=1}^{N} \delta u_{kl} \delta e_l$ can be estimated as follows. If we assume, that all δu_{kl} have probability distributions $p(\delta u_{kl})$ which are independent of k and l, then the central limit theorem guarantees, that $(1/N)\, \Sigma_{k=1}^{N} \delta u_{kl}$ obeys a gaussian probability distribution with mean zero and standard deviation $1/\sqrt{N}$. Therefore $(1/N)\, \Sigma_{k=1}^{N} \delta u_{kl} = \mathcal{O}(1/\sqrt{N})$ and $(1/N)\Sigma_{k=1}^{N}(1/N)\ \Sigma_{l=1}^{N} \delta u_{kl} \delta e_l = \mathcal{O}(1/\sqrt{N})(1/N)\sum_{l=1}^{N} \delta e_l = \mathcal{O}(1/\sqrt{N})$.

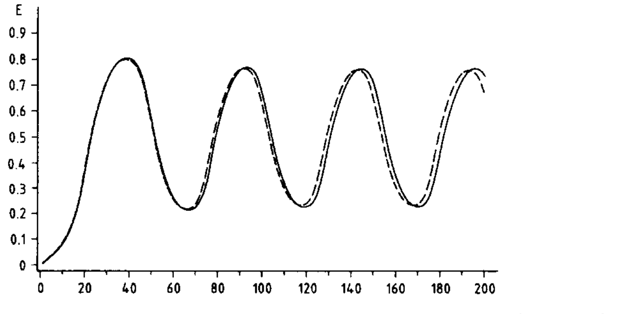

Fig. 6. Comparison between numerical simulation of (1) (microscopic description – broken line) and numerical integration of (3) (macroscopic description – solid line). Plotted is the activity E of the excitatory population as function of time t. The system size is $N_e = N_i = 400$. Only small deviation are seen, which scale approximately as $1/\sqrt{N}$, were we used as an error parameter the phase difference per period between the two oscillations

To check the validity of our mean-field approximation we performed numerical simulations of (1). The values for the matrices u_{kl}, v_{kl}, w_{kl} and z_{kl} have been chosen at random between zero and the twice of their mean values. All the inputs p_k were set to the same value, and so were the thresholds. We used a fourth order Runge-Kutta integration routine and investigated systems of four different sizes, $N = 50$, $N = 100$, $N = 200$ and $N = 400$, where we have chosen the numbers of the neurons of the two subpopulations to be equal, $N = N_e = N_i$. This can be done without loss of generality, because the mean values of the couplings are the only relevant variables. Our results differed from those obtained by direct integration of (3) only by finite size effects which are of order $\mathcal{O}(1/\sqrt{N})$, see Fig. 6 for comparison.

Appendix B: derivation of the phase equations

We introduce in (4) the deviations $x_k := E_k - E_{k0}$ and $y_k := I_k - I_{k0}$ from the unstable fixed points E_{k0}, I_{k0} and expand the sigmoid functions into a Taylorseries up to third order:

$$\dot{x}_k = -x_k + \sum_{v=1}^{3} (1/v!) a_e^v S^{(v)}(A_{k0}^e)(\delta A_k^e + \eta U_l)^v + \mathcal{O}((\delta A_k^e + \eta U_l)^4) \tag{7a}$$

$$\dot{y}_k = -y_k + \sum_{v=1}^{3} (1/v!) a_i^v S^{(v)}(A_{k0}^i)(\delta A_k^i + \eta V_l)^v + \mathcal{O}((\delta A_k^i + \eta V_l)^4) \tag{7b}$$

with $k, l = 1, 2$ and $k \neq l$

where the terms of zero order in $\delta A_k^{e,i}$ cancelled, and with $\delta A_k^e = c_1 x_k - c_2 y_k$ and $\delta A_k^i = c_3 x_k - c_4 y_k$. Equations (7) become:

$$\dot{x}_k = -x_k + \sum_{v=1}^{3} (1/v!) a_e^v S^{(v)}(A_{k0}^e)(\delta A_k^e)^v + \mathcal{O}((\delta A_k^e)^4) + \eta U_l \sum_{v=0}^{2} (1/v!) a_e^{v+1} S^{(v+1)}(\delta A_{k0}^e)^v + \mathcal{O}(\eta^2) \tag{8a}$$

$$\dot{x}_k = -x_k + \sum_{v=1}^{3} (1/v!) a_i^v S^{(v)}(A_{k0}^i)(\delta A_k^i)^v + \mathcal{O}((\delta A_k^i)^4) + \eta V_l \sum_{v=0}^{2} (1/v!) a_i^{v+1} S^{(v+1)}(\delta A_{k0}^i)^v + \mathcal{O}(\eta^2) \tag{8b}$$

This expansion is the starting point for the derivation of the normal form of the Hopf bifurcation (Guckenheimer and Holmes 1983; Hassard and Wan 1978) and for the derivation of the phase equations. First we consider only the uncoupled situation $\eta = 0$. We transform (8) to new coordinates $\tilde{x}$, $\tilde{y}$ (Hirsch and Smale 1974) via:

$$x_k = \Omega_k \tilde{x}_k + (\mu_k - a_{22}^k)\tilde{y}_k \tag{9a}$$

$$y_k = a_{21}^k \tilde{y}_k \tag{9b}$$

with $a_{11}^k = -1 + a_e c_1 S'(A_k^e)$, $a_{12}^k = -a_e c_2 S'(A_k^e)$, $a_{21}^k = a_i c_3 S'(A_k^i)$, $a_{22}^k = -1 - a_i c_4 S'(A_k^i)$, $\mu_k = (a_{11}^k + a_{22}^k)/2$ and $\Omega_k = (-a_{12}^k a_{21}^k - (a_{11}^k - a_{22}^k)^2/4)^{1/2}$. This diagonalizes the linear part of (8):

$$\dot{\tilde{x}}_k = \mu_k \tilde{x}_k - \Omega_k \tilde{y}_k + \mathcal{O}(\tilde{x}_k^2, \tilde{y}_k^2) \tag{9c}$$

$$\dot{\tilde{y}}_k = \Omega_k \tilde{x}_k + \mu_k \tilde{y}_k + \mathcal{O}(\tilde{x}_k^2, \tilde{y}_k^2) \tag{9d}$$

A subsequent nonlinear transformation (Hassard and Wan 1978), $u_k = \tilde{x}_k + \Sigma_{2 \leqslant i+j \leqslant 3} f_{ij}^{(k)} \tilde{x}_k^i \tilde{y}_k^j$ and $v_k = \tilde{y}_k + \Sigma_{2 \leqslant i+j \leqslant 3} g_{ij}^{(k)} \tilde{x}_k^i \tilde{y}_k^j$, removes the terms of second order from (8), and finally yields the Hopf normal form in polar coordinates $u_k = r_k \cos \phi_k$, $v_k = r_k \sin \phi_k$:

$$\dot{r}_k = \mu_k r_k + a_k r_k^3 + \mathcal{O}(r_k^5) \tag{10a}$$

$$\dot{\phi}_k = \Omega_k + b_k r_k^2 + \mathcal{O}(r_k^4) \tag{10b}$$

where a_k and b_k depend on the coefficients of the second and third order terms of the Taylor series (8). Thereby one can identify the parameters, which leads to the amplitude $r_{0k} = \sqrt{-\mu_k / a_k}$ and the frequency $\omega_k = \Omega_k - \mu_k b_k / a_k$ of the limit cycle.

We now discuss two coupled oscillators. By keeping in (8) only the leading term to order η, i.e. $a_e S'(A_{k0}^e) U_l$ and transforming the equations for each oscillator to their Hopf normal form (see also (Baird 1986)), we obtain in rectangular coordinates:

$$\dot{u}_k = u_k u_k - \Omega_k v_k + (a_k u_k - b_k v_k)(u_k^2 + v_k^2) + \eta K_u U_l(u_l, v_l) + \eta \mathcal{O}(u_k^2 + v_k^2) \tag{11a}$$

$$\dot{v}_k = \Omega_k u_k + \mu_k v_k + (a_k v_k + b_k u_k)(u_k^2 + v_k^2) \tag{11b}$$

$$K_u = a_e S'(A_{k0}^e) / \Omega_k \tag{11c}$$

$$U_l(u_l, v_l) = a_1 \Omega_l u_l + (a_1(\mu_l - a_{22}^l) - a_2 a_{21}^l) v_l \tag{11d}$$

with $k, l = 1, 2$ and $k \neq l$

where we have chosen $V_l = 0$ for simplicity. According to (Kuramoto 1984) we can reduce (11) to equations for the phases alone by application of the theory of phase description, which yields:

$$\dot{\phi}_k = \omega_k + \Gamma_{kl}(\phi_k, \phi_l), \quad k, l = 1, 2 \text{ and } k \neq l \tag{12}$$

where

$$\Gamma_{kl}(\phi_k, \phi_l) = \eta K_u Z(\phi_k) U_l(u_l(\phi_l), v_l(\phi_l))$$

$$Z(\phi_k) = -(1/(a_k r_{0k}))(b_k \cos \phi_k + a_k \sin \phi_k)$$

$Z(\phi_k)$ is the first component of the phase-dependent sensitivity, which measures the influence of an external perturbation on the limit cycle (see (3.2.9) in Kuramoto 1984). The term U_l has to be evaluated along the unperturbed limit cycle, which is the solution $\dot{r}_k = 0$ of (10) and is parametrized as $u_k = r_{0k} \cos \phi_k$ and $v_k = r_{0k} \sin \phi_k$.

The coupling $\Gamma_{kl}(\phi_k, \phi_l)$ between the phases consists of two parts involving different time scales. It can be split into a term proportional to $\sin(\phi_k + \phi_l + \tilde{\alpha}_{kl})$, which undergoes a fast motion with frequency $\bar{\omega}$ where $\bar{\omega} = \omega_1 + \omega_2$, and a term $\sin(\phi_k - \phi_l - \alpha_{kl})$, which varies on a longer time scale. We make these different time scales more explicit by introducing into (12) new variables $\phi_k := (1/2)\bar{\omega}t + \psi_k$ to obtain:

$$\begin{aligned}\dot{\psi}_k &= \Delta\omega_k - K_{kl}\sin(\psi_k - \psi_l - \alpha_{kl})\\ &\quad - \tilde{K}_{kl}\sin(\tilde{\omega}t + \psi_k + \psi_l + \tilde{\alpha}_{kl}),\\ &\quad k, l = 1, 2 \text{ and } k \neq l \end{aligned} \tag{13}$$

with

$$K_{kl} = \eta(a_e S'(A^e_{k0})r_{0l})/(\Omega_k a_k r_{0k})\sqrt{A^2 + B^2}$$

$$\tan\alpha_{kl} = A/B$$

$$A = b_k a_1 \Omega_l + a_k(a_1(\mu_l - a^l_{22}) - a_2 a^l_{21})$$

$$B = b_k(a_1(\mu_l - a^l_{22}) - a_2 a^l_{21})) - a_k a_1 \Omega_l$$

$$\Delta\omega_k = \omega_k - \bar{\omega}$$

We have omitted the explicit expressions for $\tilde{K}_{kl}$ and $\tilde{\alpha}_{kl}$, because this terms will be averaged out as shown below. Equation (13) shows, that $\dot{\psi}_k$ hardly changes during a period $T = 4\pi/\bar{\omega}$, because $K_{kl} \propto \eta$ and $\Delta\omega_k/\bar{\omega} \ll 1$ are small. Averaging (13) over one period T by integrating each term over the interval $[0, T]$, the explicitly t-dependent term cancels (Kuramoto 1984; Nayfeh and Mook 1979):

$$\dot{\psi}_k = \Delta\omega_k - K_{kl}\sin(\psi_k - \psi_l - \alpha_{kl}) \quad k, l = 1, 2 \text{ and } k \neq l \tag{14}$$

which is (5). Note, that the phases ψ_k are time coarse grained variables. Their use can be motivated further by the fact, that the experimentally measured phases are time coarse grained, too, because they have been obtained from filtered signals, and we recall that a low pass filter just performs an integration in time, which eliminates high frequencies.

Finally we assume that the phase α_{kl} can be neglected without changing our results. This is justified by the following facts: First we observed numerically that α_{kl} depends only weakly on P_k and P_l, and second it is found in (Sakaguchi and Kuramoto 1986) that the additional phase makes synchronization difficult, but still possible.

References

Baird B (1986) Nonlinear dynamics of pattern formation and pattern recognition in the rabbit olfactory bulb. Physica 22D:150–175

Eckhorn R, Bauer R, Jordan W, Brosch M, Kruse W, Munk M, Reitboeck HJ (1988) Coherent oscillations: a mechanism of feature linking in the visual cortex. Biol Cybern 60:121–130

Edelman GM (1978) In: Edelman GM, Mountcastle VB (eds) The mindful brain. MIT Press, Cambridge, Mass, pp 51–100

Edelman GM (1987) Neural Darwinism. The theory of neuronal group selection. Basic Books, New York

Finkel LH, Edelman GM (1989) Integration of distributed cortical systems by reentry: a computer simulation of interactive functionally segregated visual areas. J Neurosci 9:3188–3208

Freeman WJ (1975) Mass action in the nervous system. Academic Press, New York

Freeman WJ, van Dijk BW (1987) Spatial patterns of visual cortical fast EEG during conditioned reflex in a rhesus monkey. Brain Res 422:267–276

Freeman WJ, Yao Y, Burke B (1988) Central pattern generating in olfactory bulb: A correlation learning rule. Neural Networks 1:277–288.

Gerstein GL, Bedenbaugh P, Aertsen AMHJ (1989) Neuronal assemblies. IEEE Trans Biomed Eng 36:4–14

Gray CM, Singer W (1989) Neuronal oscillations in orientation columns of cat visual cortex. Proc Natl Acad Sci USA 86:1698–1702

Gray CM, König P, Engel AK, Singer W (1989) Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. Nature 338:334–337

Guckenheimer J, Holmes P (1983) Nonlinear oscillations, dynamical systems, and bifurcations of vector fields. Springer, Berlin Heidelberg New York

Hassard B, Wan YH (1978) Bifurcation formulae derived from center manifold theory. J Math Anal Appl 63:297–312.

Hirsch MW, Smale S (1974) Differential equations, dynamical systems and linear algebra. Academic Press, New York

Hopfield JJ (1984) Neurons with graded response have collective properties like those of two-state neurons. Proc Natl Acad Sci USA 81:3088–3092

Kammen DM, Holmes PJ, Koch C (1989) Cortical architecture and oscillations in neuronal networks: feedback versus local coupling. In: Cotterill RMJ (ed) Models of brain function. University Press, Cambridge

Kammen DM, Holmes PJ, Koch C (1990) Origin of synchronized oscillations in visual cortex: global feedback versus local coupling. Proc Natl Acad Sci USA (submitted for publication)

Kandel ER, Schwarz JH (eds) (1985) Principles of neural science 2nd edn. Elsevier, New York Amsterdam Oxford

Kuramoto Y (1984) Chemical oscillations, waves, and turbulence. Springer, Berlin Heidelberg New York

Nayfeh AL, Mook DT (1979) Nonlinear oscillations. Wiley, New York

Sakaguchi H, Kuramoto Y (1986) A soluble active rotator model showing phase transitions via mutual entrainment. Prog Theor Phys 76:576–581

Shinomoto S (1987) A cognitive and associative memory. Biol Cybern 57:197–206

Sporns O, Gally JA, Reeke GN, Edelman GM (1989) Reentrant signaling among simulated neuronal groups leads to coherency in their oscillatory activity. Proc Natl Acad Sci USA 86:7265–7269

Wilson HR, Cowan JD (1972) Excitatory and inhibitory interactions in localized populations of model neurons. Biophys J 12:1–24

Winfree AT (1980) The geometry of biological time. Springer, New York Berlin Heidelberg

Prof. Dr. H. G. Schuster
Institut für Theoretische Physik und Sternwarte
Universität Kiel
Olshausenstrasse 40
D-2300 Kiel
Federal Republic of Germany