

Stimulus-Dependent Assembly Formation of Oscillatory Responses: I. Synchronization

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Current concepts in neurobiology of vision assume that local object features are represented by distributed neuronal populations in the brain. Such representations can lead to ambiguities if several distinct objects are simultaneously present in the visual field. Temporal characteristics of the neuronal activity have been proposed as a possible solution to this problem and have been found in various cortical areas.

In this paper we introduce a delayed nonlinear oscillator to investigate temporal coding in neuronal networks. We show synchronization within two-dimensional layers consisting of oscillatory elements coupled by excitatory delay connections. The observed correlation length is large compared to coupling length. Following the experimental situation, we then demonstrate the response of such layers to two short stimulus bars of varying gap distance. Coherency of stimuli is reflected by the temporal correlation of the responses, which closely resembles the experimental observations.

1 Introduction

Current theories of visual processing assume as a first step the extraction of local object features like color, velocity, disparity, etc. (Treisman and Gelade 1980; Julesz 1981; Marr 1982; Ballard *et al.* 1983; Malsburg and Singer 1988). This processing is considered to occur in parallel through corresponding feature detectors involving spatially separated populations of neurons in the brain. Simultaneous processing of several objects in a natural scene will then elicit superposed responses in each of the detectors. This leads to the problem of uniquely binding responding cells into the correct assemblies that code for the different objects in the visual field (Malsburg 1986; Damasio 1989). A solution to this problem by conjunction of all possible feature constellations to dedicated cardinal neurons is prohibited by the ensuing combinatorial explosion. As a consequence, it has been suggested that temporal structure of neuronal activity would allow the unique definition of assemblies. In particular,

temporal correlation of responses to the same object would provide a solution to the binding problem (Malsburg 1981; Abeles 1982; Crick 1984; Malsburg 1986; Damasio 1989).

Stimulus-driven oscillations of neuronal activity have been found in various cortical areas (Freeman 1975; Gray and Singer 1987; Eckhorn *et al.* 1988; Gray and Singer 1989). Furthermore, stimulus-dependent synchronization and assembly formation of these oscillations have recently been demonstrated in cat visual cortex (Gray *et al.* 1989; Engel *et al.* 1990).

As a consequence, first attempts have been made to include oscillatory behavior into models of visual processing (Malsburg and Schneider 1986; Sporns *et al.* 1989; Reitboeck *et al.* 1989; Wilson and Bower 1990; Hartmann and Drüe 1990; Sompolinsky *et al.* 1990; Kammen *et al.* 1990).

In this paper, we investigate the temporal structure of responses in two-dimensional layers of delayed nonlinear oscillators. We demonstrate the use of excitatory delay connections for the synchronization of oscillatory responses. Closely following experimental observations, we show that the coherence of stimuli can be coded by synchronizing the oscillatory responses of spatially distributed cell assemblies.

2 Simulation of Delayed Nonlinear Oscillators

In order to investigate temporal coding in neuronal activity, we have implemented a delayed nonlinear oscillator as a basic oscillatory element (Fig. 1A).

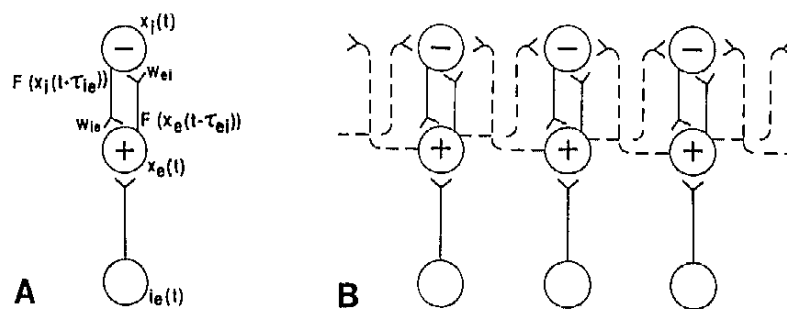


Figure 1: (A) Basic oscillatory element implemented by coupling an excitatory unit (\oplus) with an inhibitory unit (\ominus) using delay connections. An additional unit (\circ) allows for external input of a stimulus. t , time; $x(t)$, unit activity; $F(x)$, output function; w , coupling constant; τ , delay time; $i_e(t)$, external input. Subscripts: e , excitatory unit; i , inhibitory unit. For details see text. (B) Synchronization between oscillators is achieved by coupling the excitatory unit of one oscillator to the inhibitory unit of another (dashed lines). The coupling delay is chosen to be of the order of the oscillator's intrinsic delays.

An excitatory unit u_e is coupled with delay τ_{ei} to an inhibitory unit u_i , which in turn projects back to unit u_e with delay τ_{ie} . An additional unit allows for external input of a stimulus.

The dynamics of the system is determined by the following delay differential equations:

$$\begin{aligned}\tau_0 \dot{x}_e(t) &= -\alpha_e x_e(t) - w_{ie} F[x_i(t - \tau_{ie})] + i_e(t) + \eta_e(t) \\ \tau_0 \dot{x}_i(t) &= -\alpha_i x_i(t) + w_{ei} F[x_e(t - \tau_{ei})] + \eta_i(t)\end{aligned}$$

where t is time, $x(t)$ is unit activity, α is a damping constant, w is the coupling strength ($w > 0$), τ is delay time, $i_e(t)$ is external stimulus input, and

$$F[x(t)] = \frac{1}{e^{\sigma [\Theta - x(t)]} + 1}$$

is a Fermi function output nonlinearity with slope σ and threshold Θ . Here, $\tau_0 \approx 0.5$ msec corresponds to our unit of time, and with our standard set of parameters, $\tau_0 \ll T \approx 20$ msec, where T is the oscillation period length. $\eta(t)$ introduces white noise with variance $V[\eta(t)] = 1/12 \beta^2 \tau_0$, where β is a measure of the noise level. These differential equations evolve naturally from the description of a simple harmonic oscillator by the introduction of a nonlinear and delayed coupling. Aspects of a related system have been analyzed by Wilson and Cowan (1973).

Assuming that not single neurons but rather ensembles of neurons are the essential elements of cortical information processing, this formulation represents "neuronal" activity as a real-valued function. In this context, we therefore interpret each of our units u_e and u_i to represent a neuronal population with a combined firing probability reflected by the output nonlinearity.

The inclusion of transmission delays into the system's dynamic description is motivated by two reasons: (1) Delays are naturally present in biological networks through synaptic transmission and finite conduction velocity, and (2) in two-dimensional layers of coupled delayed oscillators, delays have a profound influence on the phase relations within the layer.

The effect of varying delay time τ on the oscillatory behavior of the two coupled units is shown in Figure 2A. With no or too little delay the system relaxes to a stable fixed point determined by coupling parameters and external input. Increasing delay time sufficiently transfers the system to a stable limit cycle. Note that with the specified parameter set the minimum delay time necessary to facilitate oscillation is of the order of 0.1 of the oscillation period length, well compatible with physiological data (Gray and Singer 1989).

A similar dependence of oscillatory behavior as for delay also holds for input amplitude $i_e(t)$ (Fig. 2B). Depending on the level of input

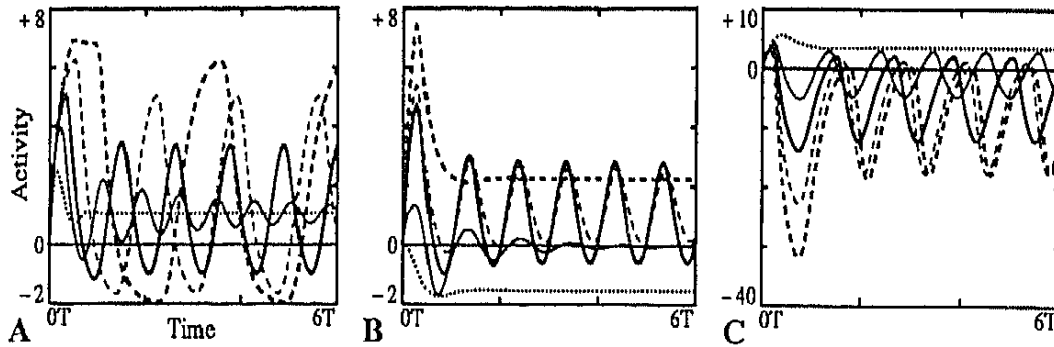


Figure 2: Dependence of a single oscillator's activity $x_e(t)$ on delay time τ , input level i_e , and coupling strength w . Our standard set of parameters is $\alpha \equiv \alpha_e = \alpha_i = 0.1$, $w \equiv w_{ei} = w_{ie} = 1.0$, $\tau \equiv \tau_{ei} = \tau_{ie} = 4\tau_0$, $i_e(t) = 0.8$, $\sigma = 1.0$, $\Theta = 2.0$. $\beta = 0\tau_0^{-1/2}$, with exceptions where noted. $T \approx 40\tau_0$ is the period length of an oscillator with standard parameters. (A) Effect of varying delay time $\tau \equiv \tau_{ei} = \tau_{ie}$. Dotted, $\tau = 0\tau_0$; solid thin, $\tau = 2.5\tau_0$; solid thick, $\tau = 5\tau_0$; dashed thin, $\tau = 10\tau_0$; dashed thick, $\tau = 20\tau_0$. (B) Effect of varying input level $i_e \equiv i_e(t) = \text{const}$. Dotted, $i_e = 0.0$; solid thin, $i_e = 0.3$; solid thick, $i_e = 0.6$; dashed thin, $i_e = 0.9$; dashed thick, $i_e = 1.2$. (C) Effect of varying coupling strength $w \equiv w_{ei} = w_{ie}$. Dotted $w = 0.5$; solid thin, $w = 1.5$; solid thick, $w = 2.5$; dashed thin, $w = 3.5$; dashed thick, $w = 4.5$.

activity the system is located at a fixed point or exhibits a limit cycle oscillation. Increasing input amplitude from zero increases the amplitude of the oscillation, while leaving the frequency fairly constant. Note that the input activity is stationary and, thus, is not driving the oscillator by itself. This input dependence, therefore, allows a stimulus-dependent transition of units between a nonoscillatory and an oscillatory state. It also avoids problems of frequency coding of stimulus intensity as in Kammen *et al.* (1989), which interferes with the synchronization between coupled oscillators.

Figure 2C demonstrates the influence of varying coupling strength w . As can be seen, the oscillation frequency depends only modestly on the exact value of w . This is physiologically reasonable if synchronization of oscillatory activity is to be employed for information processing. The brain's synaptic efficacy will vary by biological variance and modifications through learning. If oscillation frequency were sensitively

dependent on synaptic coupling strength, learning might easily destroy the very synchronization that was the cause of the learned synaptic modification. The restriction to a limited frequency band thus renders synchronization less sensitive to exact biological parameters.

3 Synchronizing an Oscillatory Layer by Excitatory Delay Connections

As a next step, we investigate the behavior of two-dimensional layers of coupled oscillators of the described type.

Aiming at synchronization of oscillatory activities within the layer, we introduce a coupling of the following type (Fig. 1B, dashed lines): Each oscillator's excitatory unit u_e is coupled to the inhibitory units u_i of all its nearest-neighbor oscillators. The coupling weights $w_{ei}^{(1)}$ are chosen to be isotropic. The delay time $\tau_{ei}^{(1)}$ is of the order of the oscillator's intrinsic delays. With this type of delay coupling every oscillator will excite all its neighboring inhibitory units simultaneously to its own. By this arrangement every oscillator is promoting synchronized oscillations of its neighboring oscillators with zero phase lag, as required by experimental evidence (Gray *et al.* 1989).

Figure 3 demonstrates synchronization within a 14×7 oscillatory layer. Figure 3A shows activity traces of 20 units arbitrarily selected from the layer. Throughout the simulation all oscillators receive identical constant input $i_e(t)$ corresponding to a limit cycle oscillation. For $t < 0$ all the oscillators are isolated and desynchronized by a high noise level. For $t \geq 0$ the $w_{ei}^{(1)}$ -connections are enabled, which are able to rapidly synchronize the layer within very few oscillation cycles. The top part of Figure 3B represents the oscillation phases of all oscillators in the layer at $t = 8T$. The apparent homogeneity reflects the layer's synchronized state. The bottom of Figure 3B shows oscillation phases at $t = 8T$ for a control simulation, in which the synchronizing connections were not enabled.

Note that with the specified coupling, the layer's correlation length is much larger than the implemented coupling length. This is achieved without the use of a mean field comparator as proposed to be necessary by Kammen *et al.* (1990).

Note also that the coupling delay $\tau_{ei}^{(1)} = 0.1T$ is small compared to the oscillation period length, in correspondence to physiological observations (Gray and Singer 1989). The synchronization of the layer does not critically depend on the exact value of the coupling delay, in agreement with the observations for a system of two oscillators reported by Schuster and Wagner (1989). In particular, synchronization was verified for this model for uniform coupling delays $\tau_{ei}^{(1)} = 0.1T, \dots, 0.5T$ as well as for a rectangular delay distribution $\tau_{ei}^{(1)} \in [0.1T, 0.5T]$. In order not to

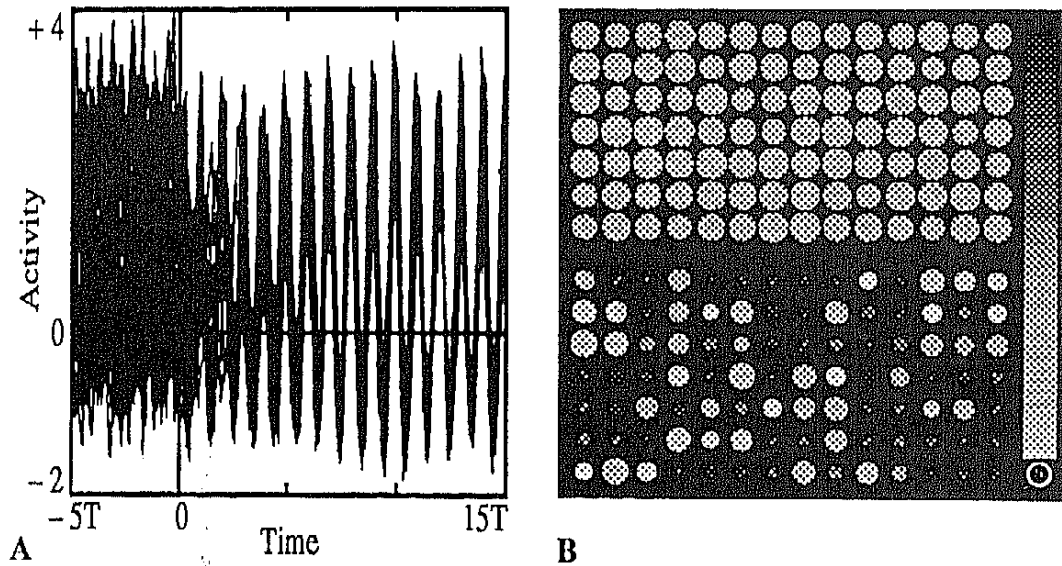


Figure 3: Synchronizing an oscillatory layer by excitatory delay connections. (A) Activity traces of 20 excitatory units arbitrarily selected from a layer of 14×7 delayed nonlinear oscillators. $t < 0$, isolated oscillators desynchronized by high noise level. $t > 0$, synchronizing the entire layer by enabling nearest-neighbor excitatory delay connections ($w_{ei}^{(1)}$). High noise level maintained throughout. Cyclic boundary conditions. T , period length of isolated oscillator. *Notation:* Throughout this paper, $w^{(r)}$ denotes the (isotropic) coupling weights, with which an oscillator is coupled to its $8r$ neighboring oscillators located on the surrounding square of edge length $2r + 1$ oscillators (r -nearest-neighbor coupling). (B, top) Activity-phase map of all oscillators at $t = 8T$. Each circle represents a single oscillator. Activity is coded by circle radius, oscillation phase by shading ($0 \dots 2\pi$). (B, bottom) Activity-phase map at $t = 8T$ from a control simulation that did not enable $w_{ei}^{(1)}$ -connections. Parameters: $t < 0$, standard set; $t > 0$, standard set and $w_{ei}^{(1)} = 0.08$, $w_{ei} = 0.8$, $w_{ie} = 1.0$, $\tau_{ei}^{(1)} = \tau_{ei} = \tau_{ie} = 4\tau_0$; $\beta = 0.4\tau_0^{-1/2} \forall t$.

increase the number of parameters in the model unnecessarily we use in the following only a single uniform coupling delay.

4 Coherency Detection by Coupled Oscillators

We now demonstrate the response of a two-dimensional layer of delayed nonlinear oscillators to stimulus bar segments.

A 10×20 layer of oscillators is configured with nearest, next nearest, and double next nearest-neighbor coupling of the described type ($w_{ei}^{(1)}$, $w_{ei}^{(2)}$, $w_{ei}^{(3)}$). Coupling weights are again isotropic and represent a gaussian distribution of synaptic connectivity. Some level of noise is maintained to represent fluctuations in oscillatory activity and to allow symmetry breaking.

Each oscillator in the layer is interpreted to represent an entire retinal receptive field (RF). In this example, we restrict ourselves to cells that show no direction selectivity and that are all of identical orientation preference. With this interpretation an oscillator's external input $i_e(t)$ reflects the presence of an appropriate light bar stimulus moving across the pertaining RF. Correspondingly, movement of a light bar on the retina will provide a stimulus to the covering map of RFs and their pertaining oscillators.

Following the experimental situation (Gray *et al.* 1989, Fig. 3), Figure 4 depicts the simulated response of the layer to two short light bars separated by varying gap distances (4, 2, and 0 oscillator positions). Each single bar segment provides homogeneous input $i_e(t)$ to an area of 2×5 oscillators. The data for each stimulus condition are presented in separate columns of the figure.

Figure 4A shows the distribution of external input to the layer. The oscillators analyzed for the cross correlograms of activities shown in (B) and (C) are marked by numbered white dots. Panel (B) depicts cross correlations (2–3) between stimulus segments for 20 epochs of 20 cycles each. The average of these correlations as compared to cross correlations within stimulus segments (1–2, 3–4) is shown in (C).

As demonstrated in the previous section, oscillators within every single bar segment are tightly coupled and cross correlations show zero phase lag. In the case of no gap distance (Fig. 4, right column) the two bar segments form a continuous long bar, which then is completely coupled without phase lag across its entire area. Cross correlation (2–3) coincides with correlations (1–2) and (2–4). In the other extreme, with the gap distance exceeding the range of synchronizing connections (left column), coupling is restricted to each bar segment's area. Between segments, the oscillators' activities relative to each other shift through all phases resulting in a minimum cross correlation (2–3). With an intermediate gap distance (middle column) coupling between bar segments is still established but is less stringent. Phase differences between segments vary somewhat around zero leading to a reduced amplitude in the cross correlogram. Note, however, that as in the case of the continuous long bar there is no phase lag between the oscillatory responses induced by the two segments, as required by experimental evidence (Gray *et al.* 1989; Engel *et al.* 1990).

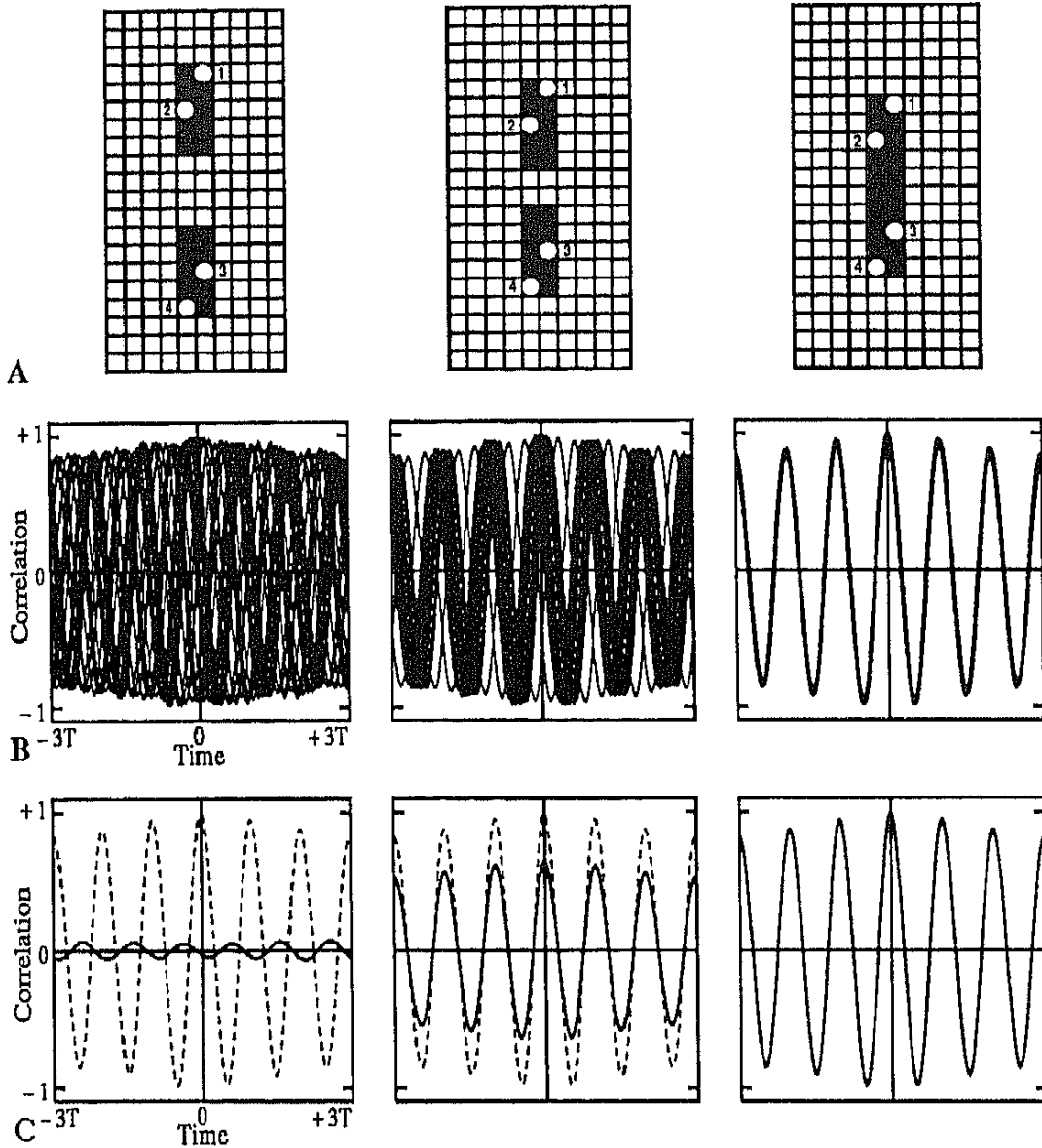


Figure 4: Effect of stimulus-coherency on cross correlations in a two-dimensional layer of delayed nonlinear oscillators: (A) Stimulus configurations for two short light bars with gap distances of 4 and 2 RFs, and one continuous long bar. The oscillators analyzed for cross correlations of activities are marked by numbered white dots. (B) Normalized cross correlations (2-3) between stimulus bar segments for 20 epochs of $20T$. Normalization by geometric mean of the two auto correlations. (C) Mean normalized cross correlations within (1-2, 3-4) (dashed) and between (2-3) (solid) stimulus bar segments. Mean of 20 epochs of $20T$. Cross correlations (2-3) between stimulus segments correspond to stimulus-coherency in agreement with experimental observations (Gray *et al.* 1989). Parameters: standard set and $i_e(t) = 0.8$ where depicted (black boxes), $i_e(t) = 0$ elsewhere, $w_{ei}^{(1)} = 0.05$, $w_{ei}^{(2)} = 0.035$, $w_{ei}^{(3)} = 0.01$, $\tau_{ei}^{(1)} = \tau_{ei}^{(2)} = \tau_{ei}^{(3)} = 4\tau_0$, $\beta = 0.1\tau_0^{-1/2}$.

5 Conclusions

The results presented in this paper demonstrate that neighbor coupling by the described excitatory delay connections ($w_{ei}^{(r)}$) is well suited to establish zero phase lag synchronization within two-dimensional oscillatory layers (Fig. 3). This synchronization exhibits a correlation length that is large compared to the employed coupling length. Synchronization does not critically depend on the exact value of the coupling delay and it is robust against noise. The finding that synchronization by neighbor coupling necessarily leads to phase lags (Kammen *et al.* 1990) cannot be confirmed within our system.

In the formulation of our model, each oscillator is meant to represent an entire neuronal population and the oscillator's activity is, therefore, specified as a continuous function. In this context, the oscillator's output function reflects the combined firing probability of all the neurons in the ensemble. This approach follows from the assumption that not single neurons but rather ensembles of neurons are essential for information processing in the brain. A conversion of the present model into one using a detailed spike description should pose no major problems. That essential characteristics of the oscillatory neuronal behavior can be formulated in a continuous model is shown by the results of our simulations.

The inclusion of delays into the analysis of temporal coding by oscillatory activity extends the approaches presented by others (Sporns *et al.* 1989; Reitboeck *et al.* 1989; Sompolinsky *et al.* 1990; Kammen *et al.* 1990). Considering a synaptic delay of 1 msec, an intracortical conduction velocity of the order of 1 mm msec⁻¹ (Luhmann *et al.* 1990), and an oscillation period in cat visual cortex of about 20 msec (Gray and Singer 1989), intracortical transmission delays amount to approximately 0.1 of the oscillation period length. Delays may therefore have a substantial influence on the temporal characteristics of oscillatory activity in the brain. The results reported in this and the following paper (Schillen and König 1991) demonstrate the effects coupling delays can have on the temporal structure of oscillatory responses in layers of delayed nonlinear oscillators. In particular, the simulations presented in this paper show synchronization in layers of this type by an appropriate choice of excitatory delay connections ($w_{ei}^{(r)}$). We verified that synchronization occurs for a wide range of coupling delays as well as for a distribution of coupling delays within the same layer. At this stage, we did not want to increase the model's number of parameters unnecessarily. Therefore, we used only one delay for all connections within a layer for the current simulations.

The inverse of our damping constant α was chosen to be compatible with ranges of physiological membrane time constants ($\alpha^{-1} = 10 \cdot \tau_0 = 5$ msec) (Connors *et al.* 1982; McCormick *et al.* 1985). We also checked our results for a parameter set using $\alpha^{-1} = 10$ msec. For the current study we did not further extend the range of investigated values of α .

The described model represents stimulus intensity by oscillation amplitude and codes for stimulus coherence by the phase of the oscillation. This avoids the problems of frequency coding of stimulus intensity as it is used by Kammen *et al.* (1990). In particular, the layer exhibits oscillatory activity only at locations where a stimulus is applied and the stimulus response, therefore, need not be segregated from background oscillations. This agrees with experimental evidence, which demonstrates the nonoscillatory character of spontaneous neuronal activity.

Furthermore, the model qualitatively shows the same temporal coherence relations in response to stimulus bar segments (Fig. 4) as the physiological data (Gray *et al.* 1989). This includes also the observed residual coupling between responses to two coherently moving stimuli separated by a small gap. This residual correlation approaches more closely the experimental observations (Gray *et al.* 1989) improving on the behavior exhibited by the model by Sporns *et al.* (1989). In addition, the local structure of the employed coupling allows sufficiently separated stimuli of identical intensity to generate independent oscillatory patterns. This agrees with experimental data and contrasts with the effect of a global mean field comparator as proposed by Kammen *et al.* (1990).

With the restriction to cells without direction selectivity, the current simulation cannot show the loss of synchronicity in response to stimulus bars moving in opposite directions (Gray *et al.* 1989). What is also missing so far is the interaction of cells of different orientation preferences. These issues will be addressed in the following paper (Schillen and König 1991).

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