

## Stimulus-Dependent Assembly Formation of Oscillatory Responses: II. Desynchronization

Thomas B. Schillen

Peter König

*Max-Planck-Institut für Hirnforschung, Deutschordenstraße 46,  
6000 Frankfurt 71, Germany*

Recent theoretical and experimental work suggests a temporal structure of neuronal spike activity as a potential mechanism for solving the binding problem in the brain. In particular, recordings from cat visual cortex demonstrate the possibility that stimulus coherency is coded by synchronization of oscillatory neuronal responses. Coding by synchronized oscillatory activity has to avoid bulk synchronization within entire cortical areas. Recent experimental evidence indicates that incoherent stimuli can activate coherently oscillating assemblies of cells that are not synchronized among one another.

In this paper we show that appropriately designed excitatory delay connections can support the desynchronization of two-dimensional layers of delayed nonlinear oscillators. Closely following experimental observations, we then present two examples of stimulus-dependent assembly formation in oscillatory layers that employ both synchronizing and desynchronizing delay connections: First, we demonstrate the segregation of oscillatory responses to two overlapping but incoherently moving stimuli. Second, we show that the coherence of movement and location of two stimulus bar segments can be coded by the correlation of oscillatory activity.

### 1 Introduction

---

As outlined in the preceding paper (König and Schillen 1991), current theories of visual processing lead to the problem of binding distributed feature responses into unique representations for several distinct objects in the visual field (Malsburg 1986; Malsburg and Schneider 1986; Damasio 1989). As a potential solution to this problem it has been proposed that the temporal structure of neuronal activities serves to define cell assemblies that code for particular objects (Malsburg 1981; Abeles 1982; Malsburg and Schneider 1986; Damasio 1989). Meanwhile, this concept of temporal coding has received support by physiological evidence from cat visual cortex (Gray and Singer 1987; Eckhorn *et al.* 1988; Gray and Singer 1989; Gray *et al.* 1989; Engel *et al.* 1990b).

The preceding paper (König and Schillen 1991) addressed the topic of coding stimulus coherency by synchronization of oscillatory activity in two-dimensional layers of delayed nonlinear oscillators. Coding by coupled oscillations requires that synchronization is selective and does not lead to bulk synchronization of entire cortical areas. Utilization of the available phase space requires uncorrelated oscillation of different neuronal assemblies. Assemblies coding for two partially overlapping but distinct objects in the visual field should segregate by engaging in independent oscillatory patterns. These considerations are now also supported by recent experimental observations (Engel *et al.* 1990a).

In order to allow differentiating features, like different velocities, disparities, etc., to segregate assemblies representing different objects, a desynchronizing mechanism must be present. In this paper we describe a second type of excitatory delay connection suitable for this task. Closely following experimental observations, we then present two examples of stimulus-dependent assembly formation in oscillatory layers. The first is a simulation of the experiment by Engel *et al.* (1990a), which demonstrates the segregation of oscillatory responses to two overlapping but incoherently moving stimuli. The second extends the model described in the preceding paper to the experimental condition where synchronization depends on the coherence of movement and location of two collinear stimulus segments (Gray *et al.* 1989).

## 2 Desynchronizing an Oscillatory Layer by Excitatory Delay Connections

---

In order to provide a desynchronizing mechanism within layers of delayed nonlinear oscillators (König and Schillen 1991), we introduce a second type of excitatory delay connection (Fig. 1, dotted lines): Each oscillator's excitatory unit  $u_e$  is coupled to the excitatory units  $u'_e$  of all its next nearest-neighbor oscillators. The coupling weights  $w_{ee}^{(2)}$  are chosen to be isotropic. The delay time  $\tau_{ee}^{(2)}$  is of the order of the oscillator's intrinsic delays ( $\tau_{ee}^{(2)} = 2\tau_{ei} = 8\tau_0$ ), compatible with physiological delay times. [For a description of symbols refer to König and Schillen (1991).] This type of delay coupling tends to establish a nonzero phase relation between coupled oscillators. In particular, with  $\tau_{ee}^{(2)} = \tau_{ei} = 4\tau_0$  one oscillator drives the other into a phase lag of  $\pi/2$ . Within a two-dimensional layer the local solutions cannot all be reconciled with each other simultaneously. This leads to a frustrated system, which in the presence of some noise exhibits quickly varying phase relations of all oscillators.

Figure 2 demonstrates this desynchronizing behavior for a  $14 \times 7$  oscillatory layer. Figure 2A 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 initialized in a synchronized

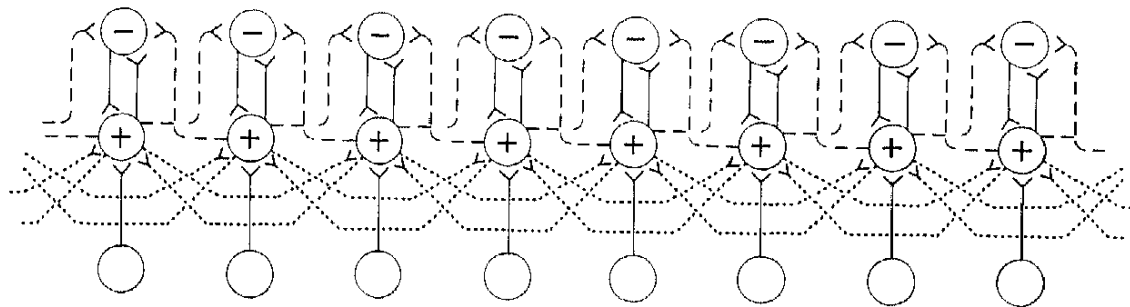


Figure 1: Investigated types of delay coupling within layers of delayed non-linear oscillators. *Dashed*, (short range) synchronizing connections (König and Schillen 1991); *dotted*, (long-range) desynchronizing connections.

state. A small amount of noise is applied to break the symmetry of the system. At  $t = 0$  the  $w_{ee}^{(2)}$  connections are enabled and noise is switched off. For  $t > 0$ , the activity traces show that the layer desynchronizes within a few oscillation cycles. The top of Figure 2B represents the oscillation phases of all oscillators in the layer at  $t = 12T$ . The desynchronization of the layer is shown by the heterogeneity of the distribution of the phases. The bottom part of Figure 2B shows oscillation phases at  $t = 12T$  for a control simulation in which the desynchronizing connections were not enabled.

This simulation demonstrates that suitably chosen connections between excitatory units are able to desynchronize different "neuronal" oscillators. We verified that this desynchronization does not critically depend on the exact value of the coupling delay.

### 3 Stimulus-Dependent Segregation of Oscillatory Responses

We now want to demonstrate the stimulus-dependent segregation of oscillators into different "neuronal" assemblies, as suggested by experimental evidence (Engel *et al.* 1990a).

For this purpose we use a one-dimensional chain of 8 oscillators, which is now coupled by both synchronizing (König and Schillen 1991) and desynchronizing delay connections as shown in Figure 1. The coupling length of the desynchronizing connections (next nearest neighbor) is chosen to be larger than that of the synchronizing ones (nearest neighbor). The desynchronizing coupling weights  $w_{ee}^{(2)}$  are set to about half the

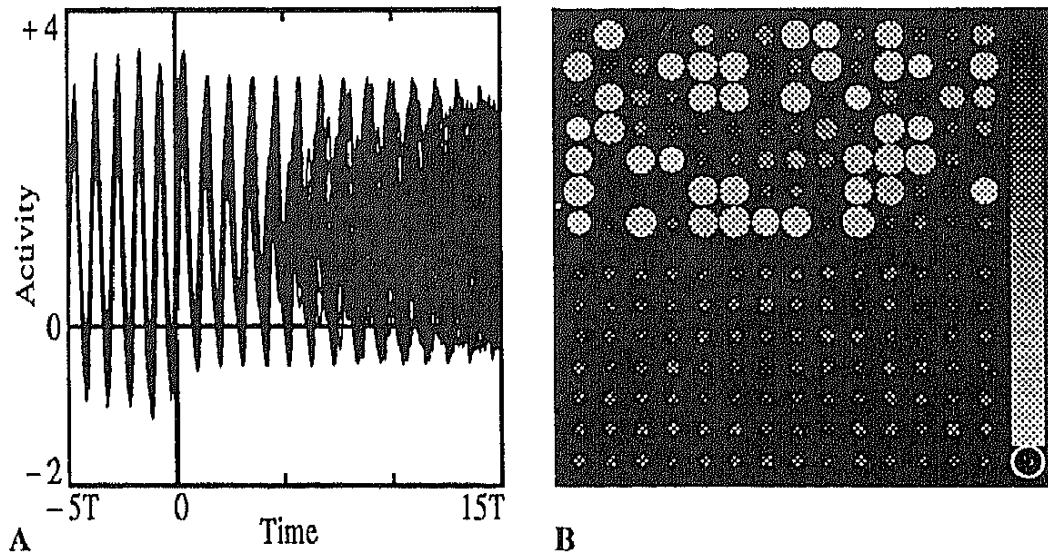


Figure 2: Desynchronizing an oscillatory layer by excitatory delay connections. (A) Activity traces of 20 excitatory units arbitrarily selected from a layer of  $14 \times 7$  delayed nonlinear oscillators (König and Schillen 1991).  $t < 0$ , isolated oscillators initialized in a synchronized state at low noise level for symmetry breaking.  $t > 0$ , desynchronizing the entire layer by enabling next nearest-neighbor excitatory delay connections ( $w_{ee}^{(2)}$ ). No noise. Cyclic boundary conditions.  $T$ , period length of isolated oscillator. (B, top) Activity-phase map of all oscillators at  $t = 12T$ . Each circle represents a single oscillator. Activity is coded by circle radius, oscillation phase by shading ( $0 \cdots 2\pi$ ). (B, bottom) Activity-phase map at  $t = 12T$  from a control simulation that did not enable  $w_{ee}^{(2)}$  connections. Parameters:  $t < 0$ , standard set (cf. König and Schillen 1991) and  $\beta = 0.2 \tau_0^{-1/2}$ ;  $t > 0$ , standard set and  $w_{ee}^{(2)} = 0.01$ ,  $\tau_{ee}^{(2)} = 8 \tau_0$ ,  $\beta = 0 \tau_0^{-1/2}$ .

synchronizing weights  $w_{ei}^{(1)}$  and delay times are  $\tau_{ee}^{(2)} = 2 \tau_{ei}^{(1)} = 0.2 T$ . To allow for fluctuations in neuronal activity some level of noise is maintained throughout the simulation.

Each of the oscillators is meant to represent a receptive field (RF) of a different preferred orientation at identical "retinal" location. For this simulation we assume a continuous sequence of 8 orientations in steps of  $22.5^\circ$  (Fig. 3A). All RFs are considered to exhibit a gaussian orientation tuning.

As in the experiment (Engel *et al.* 1990a), we “record” from two oscillators, whose preferred orientations differ by  $45^\circ$  ( $112.5^\circ$ ,  $157.5^\circ$ ) (Fig. 3A, hatched). We present two distinct stimulus paradigms: (1) a single stimulus bar of intermediate orientation ( $135^\circ$ ) (Fig. 3B–E, left column) and (2) two superimposed stimuli oriented at  $0^\circ$  and  $90^\circ$  (Fig. 3B–E, right column). Panels (C) depict the corresponding external inputs to the oscillator chain in accordance with the assumed orientation tuning. Input to the two monitored oscillators is identical for both stimulus conditions. Panels (D) show the resulting activity traces. In the case of the single stimulus both oscillators are well synchronized and thus belong to the same oscillatory assembly. With the superimposed stimuli each of the monitored oscillators couples to one of the two assemblies representing the two presented stimulus orientations. Because of the desynchronizing connections these assemblies are driven out of phase, while the amplitudes of the oscillators’ activities remain unchanged as compared to the corresponding single stimulus conditions. The phase relationship between the two monitored oscillators is indicated by the cross correlograms in panels (E).

The simulation shows that two oscillators can couple to different “neuronal” assemblies in a stimulus-dependent manner, as demonstrated by physiological experiments (Engel *et al.* 1990a). The synchronizing connections enable an oscillator to couple also to assemblies representing suboptimal orientation preferences, again consistent with experimental evidence (Gray *et al.* 1989). The inclusion of desynchronizing connections with a coupling length greater than that of the synchronizing ones establishes stimulus-dependent correlation lengths. Thus, the correlation length of an assembly activated by a single stimulus is larger than that found in one of the ensembles coding for the two superimposed stimuli. This is the origin of the decoupling in the case of the two conflicting stimuli. Without desynchronizing connections every sufficiently overlapping input configuration would readily synchronize completely. In particular, as predicted, the oscillatory responses to the two superimposed stimuli (Fig. 3D, right) become synchronized if the desynchronizing connections are eliminated (data not shown). Note that the stimulus-specific variation of correlation length cannot be achieved by simply choosing an appropriate noise level in a system containing only synchronizing connections. Note also that with the superimposed stimuli the desynchronizing excitatory connections affect only the phase relation not the activity amplitudes of the monitored oscillators, as compared to the single stimulus condition.

The interpretation of the described oscillator chain as orientation-selective cells only serves to demonstrate a principle. The above results extend canonically to other stimulus modalities. The oscillator chain could, for example, be equally well interpreted as a sequence of RFs having different velocity preferences but identical preferred orientation.

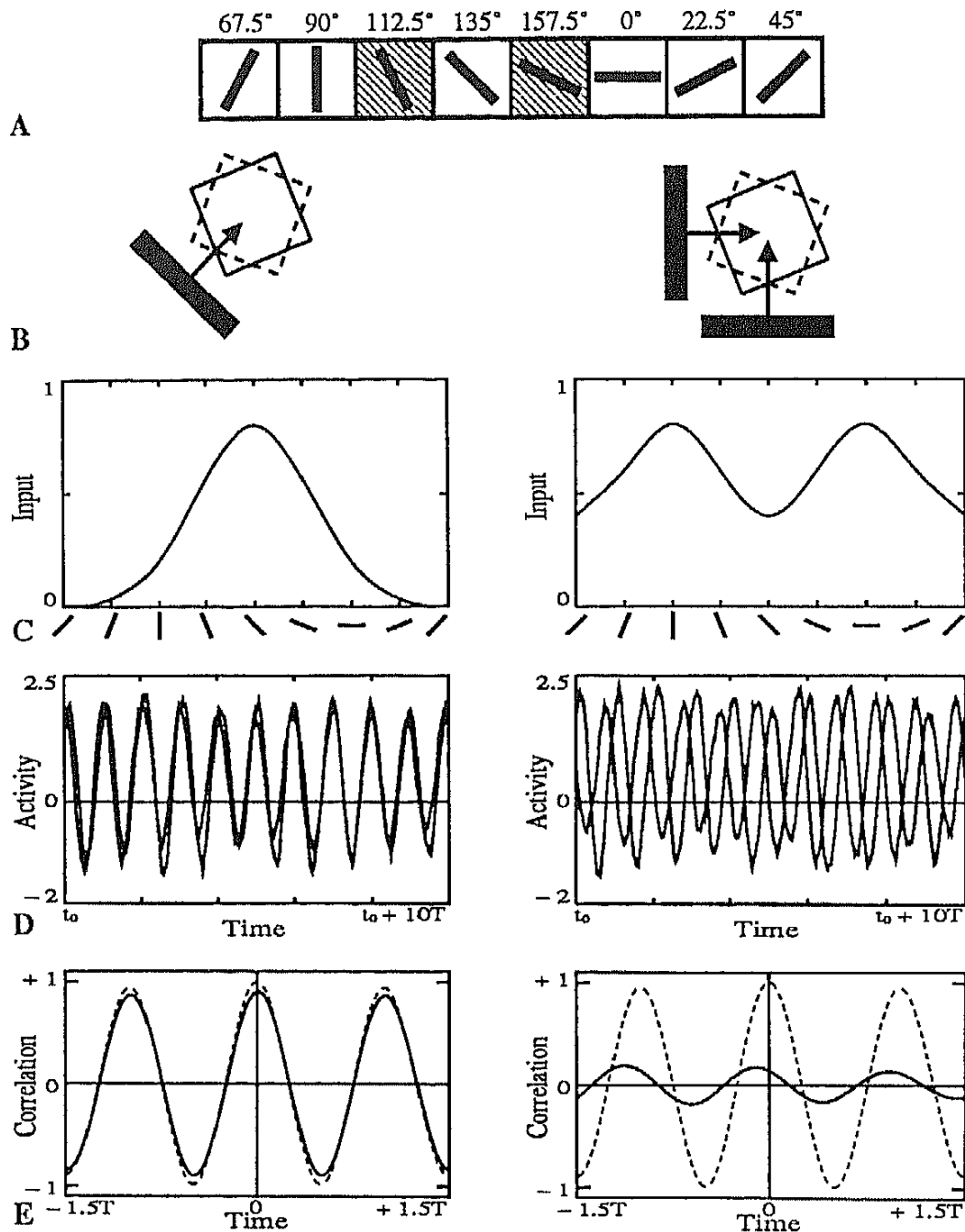


Figure 3: Stimulus-dependent assembly formation in a one-dimensional chain of delayed nonlinear oscillators. (A) Eight oscillators representing orientation-selective cells with identical receptive field location. (B) Stimulus conditions of one (left) and two (right) light bars. The corresponding stimulus input to the oscillators is shown in (C). (D) Activity traces from the 112.5° and 157.5° unit [(A), hatched]. (E) Mean normalized auto (dashed) and cross (solid) correlations of the units shown in (D). Mean of 20 epochs of  $20T$ . Normalization by geometric mean of the two auto correlations. Parameters: standard set and  $i_e(t)$  as specified in (C),  $w_{ei}^{(1)} = 0.1$ ,  $w_{ee}^{(2)} = 0.04$ ,  $\tau_{ei}^{(1)} = 4\tau_0$ ,  $\tau_{ee}^{(2)} = 8\tau_0$ ,  $\beta = 0.2\tau_0^{-1/2}$ .

#### 4 Coding Stimulus-Coherency in Oscillatory Multilayers

Using the concepts of the previous section we now extend our model of temporal coding (König and Schillen 1991) to include the direction of stimulus movement (Gray *et al.* 1989).

Three two-dimensional layers of delayed nonlinear oscillators are used to represent "neuronal" populations having different preferences with respect to direction of stimulus movement (Fig. 4A): two layers with forward and backward direction selectivity (forward layer, backward layer) and one layer lacking direction preference (neutral layer). Each layer is of the type described in Section 4 of König and Schillen (1991, Fig. 4). Accordingly, all three layers are again interpreted as retinotopic representations of RFs, where corresponding RFs are taken to represent matched "retinal" locations. The RFs of all three layers are assumed to have the same orientation preferences.

Within each layer synchronizing connections ( $w_{ei}^{(1)}$ ,  $w_{ei}^{(2)}$ ,  $w_{ei}^{(3)}$ ) are implemented as described before (König and Schillen 1991). The connections between layers generalize the concepts of the previous section into three dimensions (cf. Fig. 4A): A particular layer is coupled to its nearest-neighbor layer by synchronizing connections and to its next nearest-neighbor layer by desynchronizing ones. Because of computational limitations and without loss of generality, we have simulated only an appropriate subset of this coupling. In particular, the forward and backward layers synchronize the neutral layer by  $w_{ei}^{(0)}$ ,  $w_{ei}^{(1)}$ , and  $w_{ei}^{(2)}$  connections and mutually desynchronize each other by means of  $w_{ee}^{(3)}$ ,  $w_{ee}^{(4)}$ , and  $w_{ee}^{(5)}$  couplings. As with the single oscillatory layer,  $w^{(r)}$  denotes the coupling strength of an oscillator to its  $r$ -nearest-neighbor oscillators, being as before specified by retinotopic coordinates. All connection weights within and between layers are chosen to be isotropic with respect to retinotopy.

In correspondence to the experiment, the input to the three layers emulates the different stimulus conditions of forward and backward moving light bars (Fig. 4B). Within each layer input is applied as described in König and Schillen (1991).

As in the experiment, we "record" from the population lacking direction selectivity. We compute cross correlations within and between stimulus segments, again as detailed in König and Schillen (1991). The resulting cross correlograms are shown in Figure 4C: Within each stimulus segment all oscillators are synchronized with zero-phase lag independent of stimulus condition (Fig. 4C, dashed). This defines the oscillatory assemblies that code for each particular stimulus bar. Coupling between the two assemblies representing the two bar segments depends on the direction of movement of and the gap distance between the stimuli (Fig. 4C, solid).

With no gap distance (Fig. 4, right column) the two segments form one long stimulus bar, responses to which are completely synchronized without phase lag within its entire area. If the two stimulus bars move

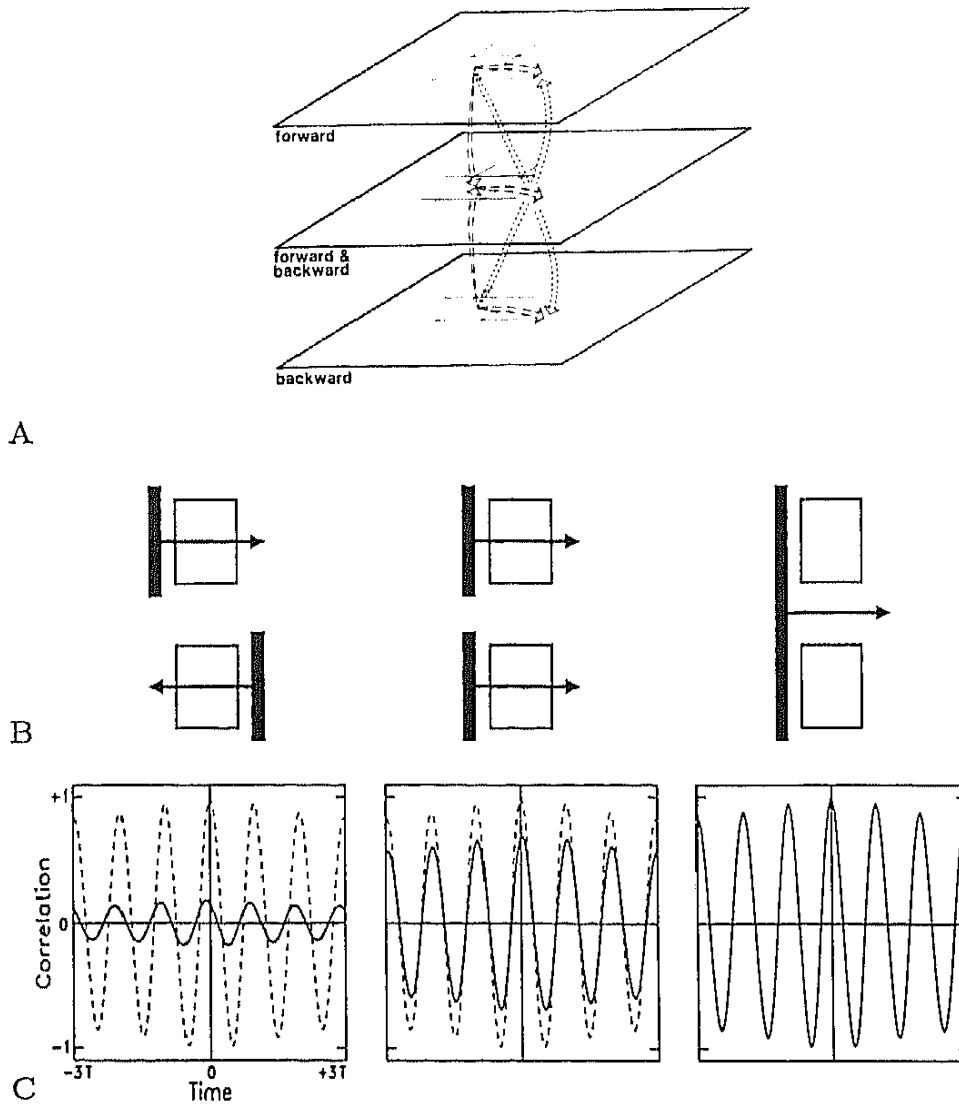


Figure 4: Temporal coding of stimulus coherency with respect to direction of movement and location of stimuli. (A) Three oscillatory layers for the representation of "neuronal" populations with different preferences for the direction of stimulus movement: selectivity for forward (top) and backward (bottom) direction and no direction preference (middle layer). Coupling by synchronizing (dashed) and desynchronizing (dotted) delay connections as described in the text. (B) Stimulus conditions: two short light bars moving in opposite directions, two short light bars moving in the same direction, and one continuous long bar. (C) Mean normalized cross correlations within (dashed) and between (solid) stimulus bar segments, computed for the middle layer. Mean of 20 epochs of  $20T$ . For correlation details see König and Schillen (1991, Fig. 4). Cross correlations between stimulus segments reflect stimulus coherency, in agreement with experimental observations (Gray *et al.* 1989). Parameters: within each layer: parameter set and input as with König and Schillen (1991, Fig. 4). Input applied to layers according to stimulus condition; from top to middle layer:  $w_{ei}^{(0)} = 0.05$ ,  $w_{ei}^{(1)} = 0.05$ ,  $w_{ei}^{(2)} = 0.035$ ,  $w_{ee} = 0.01$ ,  $w_{ee}^{(4)} = 0.01$ ,  $w_{ee}^{(5)} = 0.01$ ,  $\tau_{ei}^{(0)} = \tau_{ei}^{(1)} = \tau_{ei}^{(2)} = 4\tau_0$ ,  $\tau_{ee}^{(3)} = \tau_{ee}^{(4)} = \tau_{ee}^{(5)} = 8\tau_0$ ; from bottom to middle layer: correspondingly;  $\beta = 0.1\tau_0^{-1/2}$ .

in the same direction but are separated by a small gap (middle column), a somewhat reduced cross correlation between the two corresponding assemblies results. If, with the same gap distance, the two bar segments now move in opposite directions (left column) the resulting oscillatory activities become decoupled, as indicated by only a residual cross correlation.

The model is thus capable of evaluating direction of stimulus movement as an additional coherency criterion besides stimulus location. Accordingly, the model desynchronizes oscillatory responses to stimulus bars moving in opposite directions, while synchronizing responses to coherently moving stimuli if they are located sufficiently close to each other. This coding of stimulus coherency closely resembles the experimental observations (Gray *et al.* 1989).

## 5 Conclusions

---

The simulations presented in this paper show that an appropriate choice of excitatory delay connections ( $w_{ee}^{(r)}$ ) can provide desynchronization in layers of delayed nonlinear oscillators. This desynchronization does not critically depend on the exact value of the coupling delay. Desynchronization by excitatory connections is particularly interesting with respect to the preponderance of non-GABAergic neurons in cortex (Beaulieu and Somogy 1990).

In the following we want to discuss some aspects of the different delay connections employed in our model (Fig. 4).

**Connections within a Layer:** Each layer corresponds to a retinotopic map of a neuronal population having identical feature preferences. The synchronizing connections within a layer couple oscillatory responses to extended stimuli having the appropriate features. All oscillatory activity at neighboring "retinal" locations is recruited into the same assembly defined by zero-phase-lag synchronization. The local character of the coupling allows responses to sufficiently separated stimuli to engage into different oscillatory patterns, the correlation of which reflects the separation of the stimuli. In this case, noise is the cause for the segregation of distinct assemblies within a layer.

**Connections between Layers:** At each "retinal" location, the oscillators of the different layers form an oscillatory column similar to the chain of oscillators shown in Figure 3. If we visualize the multilayer arrangement of oscillators as a three-dimensional oscillatory module then the dimension of the column corresponds to the module's spectrum of preferred features (e.g., preferred orientations, directions) while the other two dimensions represent the retinotopic map. Within the column, presentation of a single stimulus will elicit oscillatory responses of neighboring oscillators in accordance with the oscillator's feature tuning (cf. Fig. 3). These responses are coupled by short-range synchronizing connections into an

assembly coding for the single stimulus. Long-range desynchronizing connections provide segregation of responses to partially overlapping but distinct stimuli into independently oscillating ensembles.

The properties of the desynchronizing connections go beyond desynchronization by noise. Desynchronizing connections actively dephase different neighboring oscillatory assemblies while noise impairs only the synchronizing interaction between such assemblies. Furthermore, desynchronizing connections affect stimulus responses in a specific way as opposed to the effects of noise. It would also be possible, for example, to achieve the segregation of assemblies shown in Figure 3 by a suitable choice of noise level. However, increasing intensity or overlap of the two stimuli at other locations of the module would render this choice inappropriate. As a consequence, the noise level would have to be increased, but this would then pose the problem of synchronizing responses to low intensity stimuli. In contrast, desynchronization by delay connections is based on the oscillatory activity itself and therefore scales with increased activity. Furthermore, a system containing both long-range desynchronizing and short-range synchronizing connections exhibits stimulus-dependent variations of correlation lengths: the size of an assembly synchronized by a single stimulus will be reduced if a second overlapping stimulus is presented. This facilitates segregation of the two pertaining assemblies further.

Another argument in favor of desynchronizing connections involves the specificity of active desynchronization. Sompolinsky *et al.* (1990) present a study of a network of coupled oscillators applying mean field theory to a continuous phase model. In their description of the direction-selective stimulus response by use of synchronizing connections, these authors have to exclude synchronization within the layer of neutral direction selectivity. This is necessary as otherwise the oppositely moving stimulus bars would also elicit synchronized responses in the neutral layer. This implies exclusion of an entire population of cells from cooperative interactions, which is physiologically implausible. This concept appears as contrainuitive also with respect to learning. Cells lacking direction selectivity are particularly likely to respond simultaneously, and this should facilitate the development of connections within this population. Furthermore, without specific desynchronizing connections, synchronizing mechanisms will, in general, have to be avoided unless they are selective with respect to a particular feature dimension. However, implementing only feature selective synchronizing connections becomes more and more difficult as the number of feature dimensions increases. This would lead to just the combinatorial problems, which we want to solve by the introduction of temporal coding.

These considerations suggest that active desynchronization might also occur in natural cortical networks. If this is indeed the case we would expect stimulus-dependent variations of correlation length to be found in physiological experiments.

Extending these concepts to several feature dimensions, we propose (1) synchronizing connections for the formation of assemblies corresponding to coherent features and (2) desynchronizing connections for the segregation of responses to differentiating features of an object.

### Acknowledgments

---

We would like to thank the same people that helped us with the preceding paper: Wolf Singer for discussions of the physiological background, H. Sompolinsky and D. Kleinfeld for useful discussions, Jan C. Vorbrüggen for his support on computer operation, Wolf Singer, Jan C. Vorbrüggen, and Julia Delius for comments on the first draft of this paper, and Renate Ruhl for her excellent graphical assistance.

### References

---

- Abeles, M. 1982. *Local Cortical Circuits. An Electrophysiological Study*. Springer-Verlag, Berlin.
- Beaulieu, C., and Somogy, P. 1990. Targets and quantitative distribution of GABAergic synapses in the visual cortex of the cat. *Eur. J. Neurosci.* **2**(4), 296–303.
- Damasio, A. R. 1989. The brain binds entities and events by multiregional activation from convergence zones. *Neural Comp.* **1**, 123–132.
- Eckhorn, R., Bauer, R., Jordan, W., Brosch, M., Kruse, W., Munk, M., and Reitboeck, H. J. 1988. Coherent oscillations: A mechanism of feature linking in the visual cortex? *Biol. Cybern.* **60**, 121–130.
- Engel, A. K., König, P., Gray, C. M., and Singer, W. 1990. Synchronization of oscillatory responses: A mechanism for stimulus-dependent assembly formation in cat visual cortex. In *Parallel Processing in Neural Systems and Computers*, R. Eckmiller, ed., pp. 105–108. Elsevier, Amsterdam.
- Engel, A. K., König, P., Gray, C. M., and Singer, W. 1990. Stimulus-dependent neuronal oscillations in cat visual cortex: Inter-columnar interaction as determined by cross-correlation analysis. *Eur. J. Neurosci.* **2**, 588–606.
- Gray, C. M., König, P., Engel, A. K., and Singer, W. 1989. Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature (London)* **338**, 334–337.
- Gray, C. M., and Singer, W. 1987. Stimulus-specific neuronal oscillations in the cat visual cortex: A cortical functional unit. *Soc. Neurosci. Abstr.* **13**(404.3).
- Gray, C. M., and Singer, W. 1989. Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex. *Proc. Natl. Acad. Sci. U.S.A.* **86**, 1698–1702.
- König, P., and Schillen, T. B. 1991. Stimulus-dependent assembly formation of oscillatory responses: I. Synchronization. *Neural Comp.* **3**, 155–166.
- Sompolinsky, H., Golomb, D., and Kleinfeld, D. 1990. Global processing of visual stimuli in a neural network of coupled oscillators. *Proc. Natl. Acad. Sci. U.S.A.* **87**, 7200–7204.

- von der Malsburg, C. 1981. The correlation theory of brain function. Internal Report 81-2, Max-Planck-Institute for Biophysical Chemistry, Göttingen, Germany.
- von der Malsburg, C. 1986. Am I Thinking Assemblies? In *Brain Theory*, G. Palm and A. Aertsen, eds., pp. 161–176. Springer-Verlag, Berlin.
- von der Malsburg, C. and Schneider, W. 1986. A neural cocktail-party processor. *Biol. Cybern.* **54**, 29–40.

---

Received 6 July 1990; accepted 12 November 1990.