Neural mechanisms of visual associative processing

Reinhard Eckhorn, Alexander Gail, Andreas Bruns, Andreas Gabriel, Basim Al-Shaikhli and **Mirko Saam**

Physics Department, Neurophysics Group, Philipps-University, Renthof 7, D-35032 Marburg, Germany

Minireview

Abstract. This is a review of our work on multiple microelectrode recordings from the visual cortex of monkeys and subdural recordings from humans - related to the potential underlying neural mechanisms. The former hypothesis of object representation by synchronization in visual cortex (or more generally: of flexible associative processing) has been supported by our recent experiments in monkeys. They demonstrated local synchrony among rhythmic or stochastic γ-activities (30-90 Hz) and perceptual modulation, according to the rules of figure-ground segregation. However, γ-synchrony in primary visual cortex is restricted to few millimeters, challenging the synchronization hypothesis for larger cortical object representations. We found that the spatial restriction is due to γ-waves, traveling in random directions across the object representations. It will be argued that phase continuity of these waves can support the coding of object continuity. Based on models with spiking neurons, potentially underlying neural mechanisms are proposed: (i) Fast inhibitory feedback loops can generate locally synchronized γ-activities; (ii) Hebbian learning of lateral and feed forward connections with distance-dependent delays can explain the stabilization of cortical retinotopy, the limited size of synchronization, the occurrence of γ-waves, and the larger receptive fields at successive levels; (iii) slow inhibitory feedback can support figure-ground segregation; (iv) temporal dispersion in far projections destroys coherence of fast signals but preserves slow amplitude modulations. In conclusion, it is proposed that the hypothesis of flexible associative processing by γ-synchronization, including coherent representations of visual objects, has to be extended to more general forms of signal coupling.

The correspondence should be addressed to R. Eckhorn, Email: Reinhard.Eckhorn@Physik.Uni-Marburg.de

DYNAMIC ASSOCIATIVE PROCESSING BY DIFFERENT TYPES OF SIGNAL COUPLING IN THE VISUAL CORTEX

In the proposed view of the visual system, temporal coding is intimately linked to the neural mechanisms of dynamic cortical cooperativity and flexible associative processing, including the largely unknown mechanisms of perceptual feature binding. How are local features flexibly grouped into actually perceived objects and events, and how do their current representations interact with visual memory and other higher-order processes? It has been proposed that binding of spatially distributed features and inter-areal cooperation are supported by the temporal code of fast synchronization among neurons involved in a common task, for example, the coding of a visual object (Reitboeck 1983, von der Malsburg and Schneider 1986). This hypothesis attracted attention when synchronized γ-oscillations (30-90 Hz) were found in the primary visual cortex (V1) of anesthetized cats (Eckhorn 1994, Eckhorn et al. 1988, Gray et al. 1989) and awake monkeys (Frien et al. 1994, Kreiter and Singer 1992). Many subsequent experiments were supportive, some challenging with respect to binding of local features by γ-synchronization (for reviews see Eckhorn 1999, Gray 1999). For example, synchronization of signals in the γ-range was found to be restricted to few millimeters in primary visual cortex, even with large coherent stimuli (Eckhorn 1994, Frien and Eckhorn 2000). According to a strict interpretation of the original synchronization hypothesis, this should result in locally restricted perceptual feature binding. But this is in contradiction to the capability of perceiving local features of large objects as coherently bound. However, the capability of long-range feature binding across the surface of a large visual object is probably due to a continuous binding among overlapping regions of locally restricted feature binding (as demonstrated by the perceptual laws of Gestalt psychology; e.g., Wertheimer 1923). This view is supported by our observation of γ-waves that propagate across the surface of the representation of visual objects in the primary visual cortex of awake monkeys. Accordingly, we suggest that the phase continuity of such γ-waves (by which we mean a continuum of overlapping near-synchronized patches as opposed to strict long-range synchrony), may be a basis of spatial feature binding across entire objects. Such (locally synchronous) long-range phase coupling has been found to cover larger cortical areas than γ-synchrony as it is measured with spectral coherence (Gabriel and Eckhorn 2003), and we will argue why it can fill the entire surface representation of visual objects in primary visual cortex.

Such continuity may not be available between separate topographical maps (different visual cortical areas). However, γ-synchronization has been found between neural groups with overlapping receptive fields in adjacent visual cortical areas V1 and V2 in cats (Eckhorn 1994, Eckhorn et al. 1988) and monkeys (Frien et al. 1994). It is probable that such synchrony is also present among other visual areas when feed-forward-backward delays are short (e.g., as between V1 and MT (Nowak and Bullier 1997)). In contrast, when cortical areas are far apart, long conduction delays may cause cooperativity to be reflected in other forms of signal coupling which are less sensitive to any spatio-temporal restriction of synchronization. Taking into account the time-varying amplitude (amplitude envelope) of γ-signals seems to be a particularly promising approach (Bruns and Eckhorn 2004).

For our present work different types of neural signals have been recorded, and different forms of temporal coding have been investigated by means of various coupling measures. We will demonstrate dynamic coupling of cortical signals in the form of local intra-areal phase synchrony, and medium-range phase continuity of γ-waves. Our examples show that neural-signal measures correlate with sensory events, and with perceptual and behavioral outputs in monkeys. In essence, we argue that the temporal coding hypothesis of binding-by-synchronization, initially restricted to γ-synchrony of oscillatory signals, has to be extended to more general forms of temporal coding, including non-linear signal coupling across the entire frequency range of cortical activity with phase- and amplitude-coupling among transient and stochastic (non-rhythmic) signals. On the basis of neural models with locally coupled spiking neurons we will discuss most of the physiological results and suggest potential neural mechanisms underlying the presented types of flexible temporal coding.

EXPERIMENTAL EVIDENCE

γ-activity in monkey primary visual cortex is phase-coupled within representations of scene segments and decoupled across their contours

The binding-by-synchronization hypothesis suggests coupling among γ-activities representing the same ob-

ject, or more generally, the same scene segment. Accordingly, neural groups representing different scene segments should decouple their γ-activities. Both predictions have been tested by investigating the effect of a static figure-ground stimulus on local field potentials (LFPs) (see Appendix) in primary visual cortex (V1) of

awake monkeys, recorded simultaneously from inside and outside a figure's representational area (Fig. 1A) (Gail et al. 2000). Time-resolved analysis of phase coupling by means of spectral coherence revealed: (i) γ-coherence between neurons representing the same scene segment (figure or ground) is higher than for a homoge-
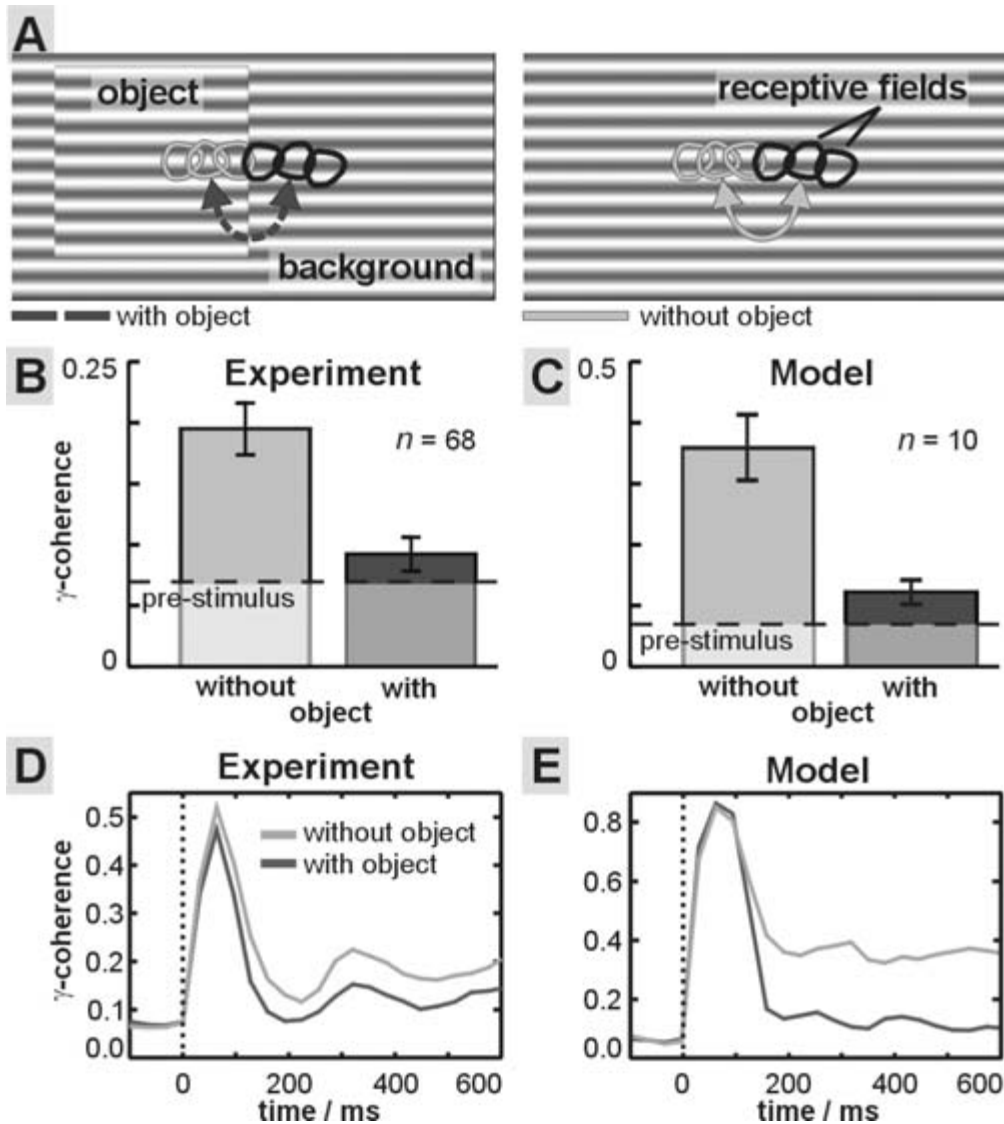

Fig. 1. Coherence of γ-activity is reduced across the representation of an object's contour. (A) Figure-ground stimulus and schematic positions of receptive fields. Stimuli were arranged in such a way that some of the receptive fields from the simultaneously recorded sites were located on the "object" (only present in the left condition), the others on the "background". (B) A grating without object (right condition in (A)) induced a substantial increase in γ-coherence among local field potentials (LFPs) (light gray) compared to a blank screen condition (pre-stimulus: dashed line). Introduction of the object (left condition in (A)) reduced LFP γ-coherence between object and background representations almost to pre-stimulus level (dark gray) (Gail et al. 2000). Coherence within each segment (object or background) remained high (data not shown). (C) A network model (Fig. 11) shows equivalent results. (D), (E) Time courses of coherence in the no-object condition (light gray) and across the object-background contour (dark) in the experiment and the model. Note that decoupling across the contour emerges about 100 ms after stimulus-onset. Data in (B) is taken from the time intervals with maximal decoupling for each monkey. (Modified from Gail et al. 2000, Eckhorn et al 2001)

neous gray background of the same average luminance (Fig. 1B,D); (ii) stimulus-specific γ-coherence is strongly reduced across the representation of the figure-ground contour compared to a spatially continuous stimulus (Fig. 1B,D); (iii) decoupling across the contour emerges with a latency of about 100 ms, and is absent in the earliest neuronal response transients (Fig. 1D); (iv) coherence of low-frequency components does not show a difference between the figure-ground and the continuous condition (not shown). We propose that the increased γ-coherence between neurons representing the same scene segment and the decoupling of γ-activity at a contour representation are crucial for figure-ground segregation, in agreement with the initial binding-by-synchronization hypothesis.

γ-phase coupling in monkey extra-striate cortex correlates with perceptual grouping

Are such synchronization effects correlated with perceptual feature grouping and figure-ground segregation? This was tested in a difficult figure-ground task in which a monkey indicated whether he perceived a figure composed of blobs among identical distractor blobs serving as background (Woelbern et al. 2002) (Fig. 2). This task was sufficiently difficult such that about 25 % of responses were incorrect (failed figure detection). Pairs of local populations of figure-activated neurons in visual area V2 showed increased synchronization within the γ-range in correct compared to incorrect responses during a short period before the monkey's behavioral response (Fig. 2). Other signal measures were unrelated to perception. These were the first indications that γ-synchronization in V2 may not only represent physical stimulus properties but also supports perceptual grouping.

Phase continuity but not synchrony of γ-waves is present across medium cortical distances in monkey primary visual cortex

Previous work demonstrated that the synchronization range of γ-activity in primary visual cortex is limited to about 5 mm (Frien and Eckhorn 2000, Steriade et al. 1996) (Fig. 4A). Hence, objects with larger cortical representations can not solely be coded by γ-synchrony
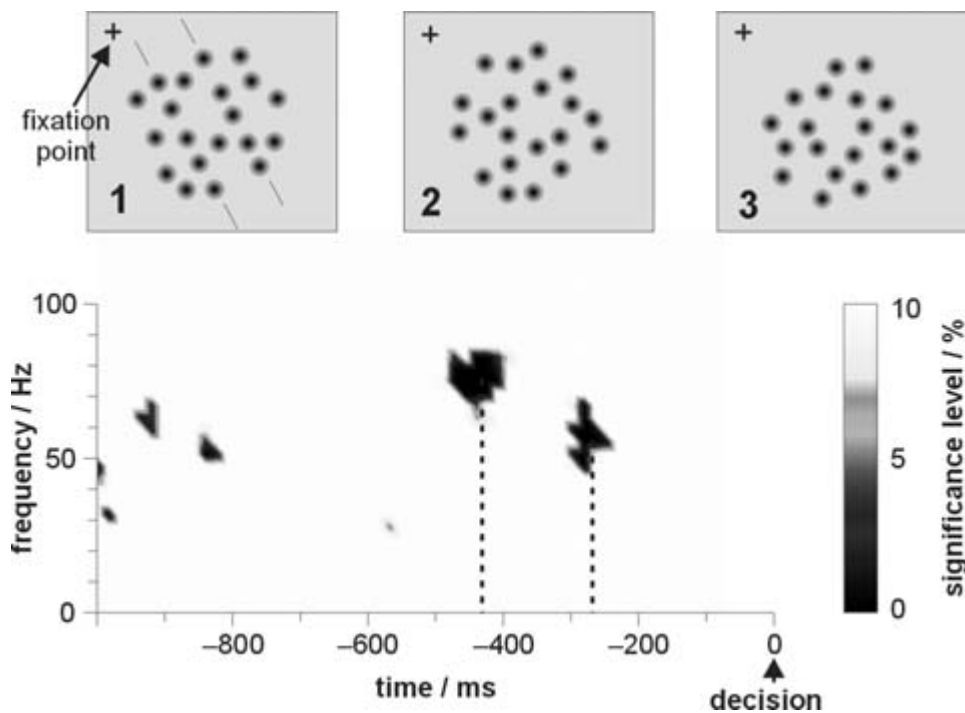

Fig. 2. A monkey's correct perception of the orientation of a dual-inline row of dots within a set of distractors (stimuli 1 and 2) caused a short increase in coherence at about 80 Hz and 60 Hz in visual area V2, shortly before the monkey reported his perception (*t*=0 ms). The time-frequency map indicates the significance of increase in LFP coherence in trials with correct vs. failed detection of the figure. Three figure-ground stimuli are shown above, with dot rows being left-tilted (1; thin lines were not shown), right-tilted (2) or absent (3). (Modified from Woelbern et al. 2002)

within their representational area. One explanation for the limited synchronization range lies in the spatio-temporal characteristics of γ-activity. In fact, wave-like phenomena defined by spatially continuous phase-fronts (γ-*waves*) do extend farther than 5 mm, but phase differences between any two sites change randomly already within 100 ms and also increase with cortical distance (Fig. 3A) (Gail et al. 2000). Conventional pairwise coupling measures (cross-correlation, coherence) do not capture such non-trivial phase relationships across medium-range cortical distances, which explains the findings of restricted synchronization ranges. To quantify those waves a new method has been developed in our group (Gabriel and Eckhorn 2003). It revealed that γ-waves travel at variable velocities and

directions. Fig. 3C shows the velocity distribution measured with a 4 × 4 microelectrode array in monkey primary visual cortex during retinally static visual stimulation. Note that this distribution is rather similar to the distribution of spike velocities of horizontal connections in this area (V1) (Nowak and Bullier 1997). We suggest that continuity of γ-waves supports the coding of object continuity, in which case their extent over object representations in visual area V1 and the related visual fields should be much larger than that covered by γ-synchronization. We have indeed found that the cortical span of γ-wave fronts is much larger than the span of γ-synchronization (Fig. 4A,B) and that y-waves are cut-off (damped down) at the cortical representation of object contours.
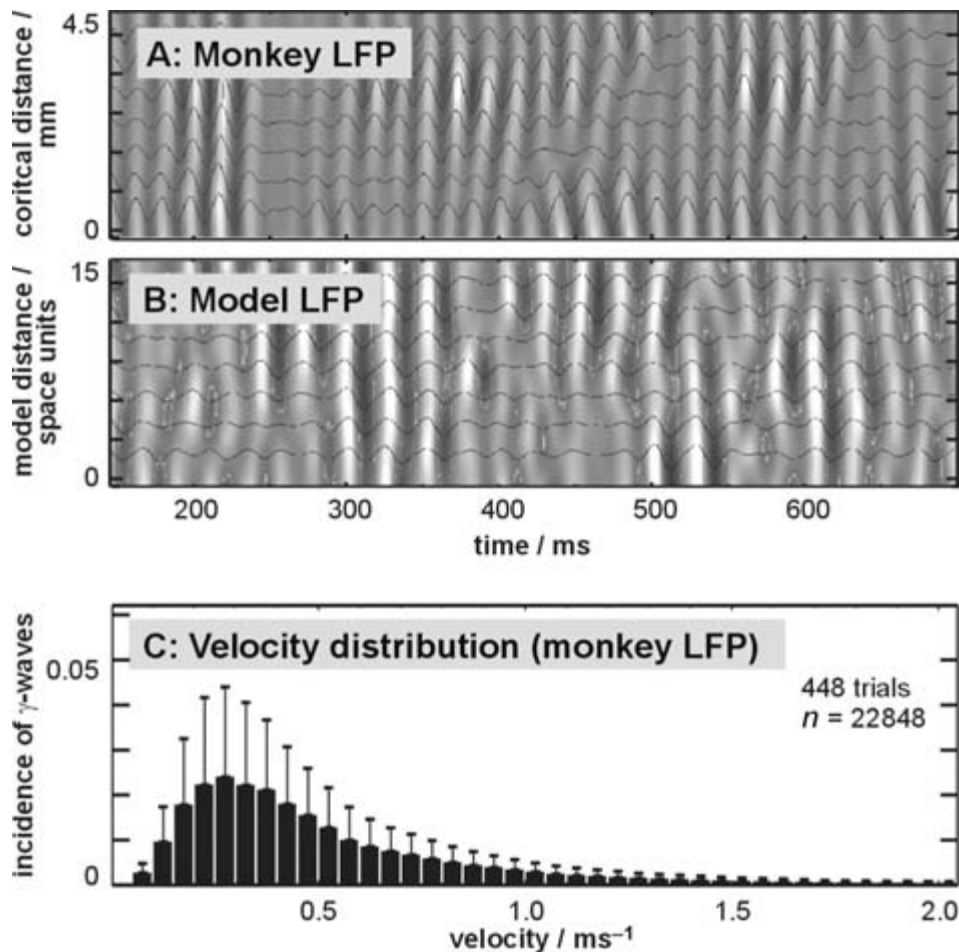

Fig. 3. γ-waves occur with fast and random changes of spatial phase relations in monkey primary visual cortex. (A) Time-space maps of simultaneously recorded single-trial time courses of local field potentials (LFPs) from a linear array of 7 recording positions during sustained static visual stimulation. Gray scales give the instantaneous electrical potentials at the electrodes (in arbitrary units). (B) Model-LFPs during presentation of an equivalent stimulus (cf. Section III-B) (Modified from Eckhorn et al. 2001). (C) Velocity distribution of traveling waves of γ-activity measured with 4×4 microelectrode arrays in monkey primary visual cortex.
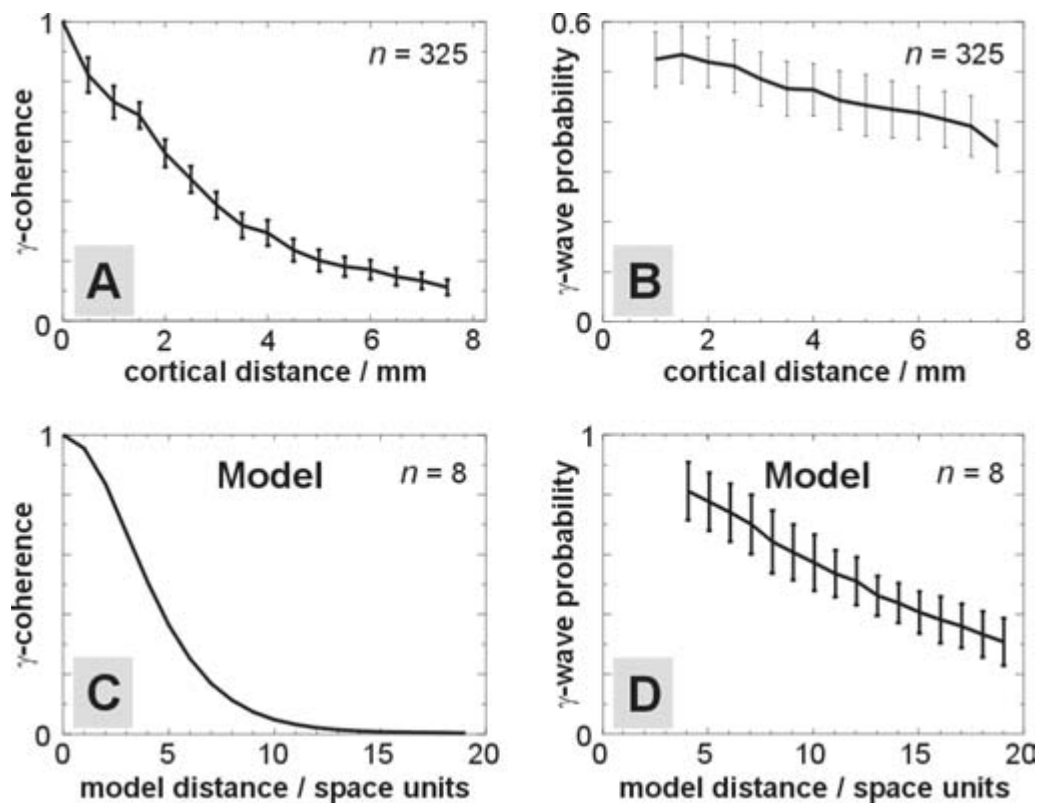
Fig. 4. The spatial range of γ-waves is larger than that of γ-coherence. (A) Coherence of local field potentials in monkey primary visual cortex is restricted to few millimeters (half-height decline 2.2 mm). (B) The probability of occurrence of continuous γ-waves remains high across larger distances (estimated half-height decline: 9.5 mm). (C), (D) The model (cf. Section III-B) shows equivalent dependencies (4.1 vs. 12.8 space units). (Modified from Eckhorn et al. 2001)

POTENTIAL NEURAL MECHANISMS OF FLEXIBLE SIGNAL COUPLING

At present it is not possible to identify directly from experimental measurements the neural mechanisms underlying the above mentioned experimental observations of spatio-temporal processing in cortical sensory structures. We therefore use largely reduced model networks with spike-coding neurons to discuss potential mechanisms.

γ-oscillations and synchrony of spike densities in local populations, generated by feedback inhibition and local lateral coupling

How can the cortex generate γ-oscillations in local neural groups, as observed in LFP- and MUA-recordings? We argue (see Fig. 5) that membrane potentials of local populations of excitatory neurons are simultaneously modulated by inhibition exerted *via* a common feedback loop (physiology (Bosking et al. 2002,

Jefferys et al. 1996, McGuire et al. 1991), models (Bush and Sejnowski 1996, Chang and Freeman 1996, Freeman 1996, van Vreeswijk et al. 1994, Wennekers and Palm 2000), discussion in Eckhorn 2000). This loop can quickly reduce transient activations, whereas sustained input will lead to repetitive inhibition of the population in the γ-frequency range (Fig. 5). In both modes– transient and rhythmic chopping– the common modulation of the neurons' membrane potentials causes their spike trains to become partially synchronized, even if they fire at very different rates. The stronger a neuron is activated and depolarized, the earlier it will discharge its first spike during the common repolarization phase, whereby such a population burst will be dominated by the most strongly activated neurons. As local cortical populations generally project to common targets (Braitenberg and Schüz 1991), synchronized spike densities (population spike packages) will have stronger impact there than uncorrelated spike densities of equal average amplitudes, because they: (i) appear quasi-simultaneously; and (ii) mainly comprise spikes of
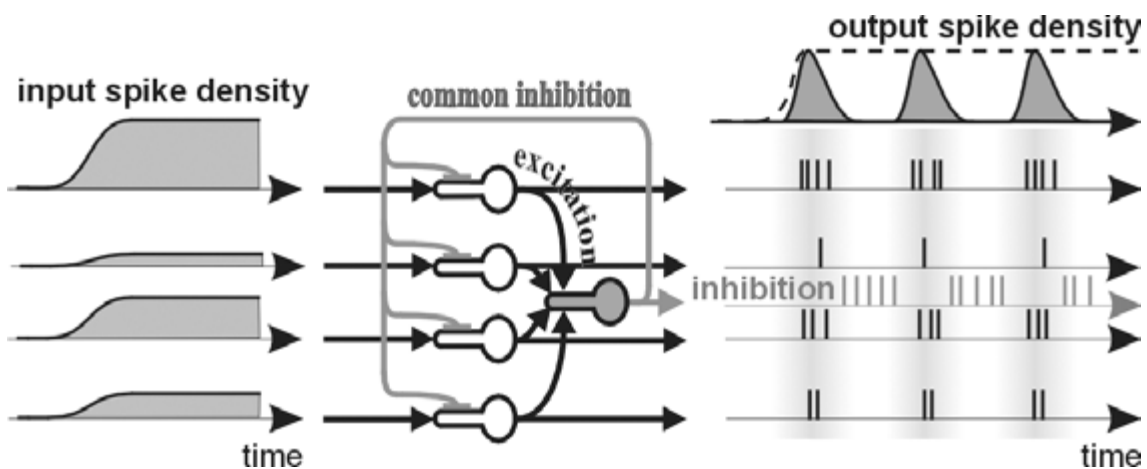
Fig. 5. Basic model of common spike density modulation in a local population of excitatory neurons by a common inhibitory feedback neuron. Note that first-spike latencies in each modulation cycle at the outputs (right) are roughly inversely proportional to the input spike densities (profiles at left), whereas the output spike rates are proportional to it (details in text).

strongly activated neurons, which represent the stimulus at a better signal-to-noise ratio than the neurons that were less activated by the same stimulus. In addition to partial local synchronization by inhibitory feedback, the most relevant mechanism for explaining synchronization in our models are lateral, activity-dependent, facilitatory connections. Local (instead of global) lateral connections are critically important for models of visual feature-binding by synchronization when pattern segmentation (desynchronization) is an important task (Eckhorn et al. 1990, König and Schillen 1991, Wang 1995). While Wang used lateral excitatory connections that were modulated in their efficacy by scene properties (in some respect similar to the facilitatory connections in our models (Eckhorn et al. 1990)), others used lateral connections from excitatory to inhibitory neurons for synchronization (Bush and Sejnowski 1996, König and Schillen 1991). It is likely that a mixture of these local mechanisms is operative in the generation of rhythmic spiking activities and their partial synchronization. Future experiments have to answer this question.

We can apply the discussed schemes to the primary visual cortex, where local neural clusters represent similar feature values (e.g., receptive field position, contour orientation, etc.). According to the synchronization hypothesis, partial synchronization of spike densities by a common inhibitory feedback means that currently present local combinations of visual feature values are systematically selected by their strength of activation and tagged as belonging together, which is reflected in single or repetitive population discharges.

Other models of visual feature binding use local oscillators, consisting of excitatory and inhibitory units with mutual feedback that generate local oscillations depending on a driving input (König and Schillen 1991, Li 1998, Wang 1995). In these models, the oscillatory signal of a local element stands for the spike density of a local group of partially synchronized spike-coding neurons. Thus, local inhibition in these models implicitly represents the synchrony of local populations of spike-coding neurons with similar receptive field properties, as has been explicitly modeled in our and other simulations (Bush and Sejnowski 1996, van Vreeswijk et al. 1994).

Lateral conduction delays can limit γ-synchrony to few millimeters in cortex, produce wave-like phenomena, stabilize cortical topography, and lead to larger receptive fields at successive levels of processing

The synchronization effect of fast orientation-specific inhibitory neurons is probably restricted to an area smaller than a single hypercolumn in primary visual cortex (Braitenberg and Schüz 1991). The most relevant mechanism for explaining flexible synchronization across several millimeters in the cortex in our (Eckhorn et al. 1990) and Wang's (1995) model are the activity-dependent facilitatory connections. They are also highly useful for enabling fast desynchronization as is required for scene segmentation. Their putative physiological substrate in the primary visual cortex are the dense horizontal connections: they cannot directly ex-

cite their target neurons, but modulate their activities evoked from their classical receptive fields. The lateral connections project monosynaptically over a range of several hypercolumns (Bosking et al. 1997, 2002, Gilbert 1993, McGuire et al. 1991) and models have shown that this type of connectivity is capable of synchronizing neural populations across larger distances (Eckhorn et al 1990, Wang 1995). Another type of local lateral connectivity enabling transient synchronization over larger distances was proposed in the model of König and Schillen (1991). They connected their oscillators by coupling the excitatory units *via* delay lines to the neighboring inhibitory units. However, it is difficult to show experimentally which mechanisms are operative in the visual cortex for synchronization across several hypercolumns.

In visual processing for example, one could suppose that neural populations representing the entire surface of a visual object might synchronize their spike packages *via* horizontal connections. However, γ-synchrony is restricted to about 5 mm of cortical distance in area V1 of awake monkeys (corresponding to 5 hypercolumns), even if the cortical representation of a visual object is much larger (Eckhorn 1994, Frien and Eckhorn 2000). Hence, feature binding based on γ-synchrony would also be restricted to visual objects being not larger in their cortical representations. In the following we will develop a concept of how distance-dependent spike conduction delays can explain this restricted range of γ-synchrony and the occurrence of wave-like phenomena in a network of spiking neurons. In addition, we will show that Hebbian learning combined with distance-dependent spike conduction delays leads to spatially restricted lateral connectivity within the same layer and restricted feed-forward divergence between different layers. Therefore, such a mechanism is also suitable to explain the emergence of larger receptive fields at suc-

cessive levels of processing while preserving a topographical mapping. Note that these conditions are also present in topographically organized cortical areas of other sensory modalities, including auditory and somatosensory.

HEBBIAN-LEARNING MODEL WITH FINITE CONDUCTION VELOCITIES

The local generation of γ-oscillations and their spatial synchronization are two separate mechanisms. For the sake of simplicity, the following model solely investigates synchronization effects, thereby neglecting any inhibition and the generation of oscillations. The model (Saam and Eckhorn 2000) consists of spike-coding neurons (as in Fig. 11B) at two successive, 2-dimensional retinotopic visual processing stages named level-1 (representing visual cortical area V1) and level-2 (V2) (Fig. 6). Learning of lateral weights and level-1-to-level-2 weights is implemented using a Hebbian spike correlation rule (Kempter et al. 1999). Feed-forward connections are additive excitatory and determine the properties of the classical receptive fields. Lateral connections are multiplicatory (with a factor ≥1, i.e., facilitatory), which means they cannot directly evoke spikes in a target neuron (as exitatory synapses can do), but require quasi-simultaneous feed-forward input to that neuron (model (Eckhorn et al. 1990), physiology (Fox and Daw 1992)). Spikes evoked by quasi-simultaneous feeding input to neighboring neurons can synchronize *via* their mutual lateral facilitatory connections because these spikes will often occur within the so-called capture range of the spike encoder's dynamic threshold (Eckhorn et al. 1990, Johnson 1993, 1994). The lateral connections have constant conduction velocities, i.e., conduction delays become proportionally larger with distance. This reduces the probability of
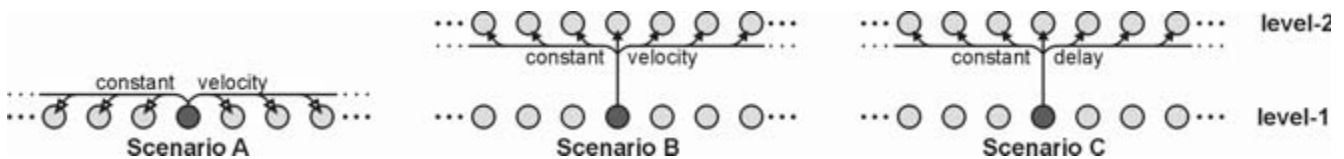

Fig. 6. One-dimensional sketch of the initial connectivity in the Hebbian learning model with distance-dependent lateral conduction delays. For a given level-1 neuron (dark), the scheme shows lateral modulatory (facilitatory) connections (scenario A), and feed-forward connections with either distance-dependent (scenario B) or constant (scenario C) conduction delays. (Modified from Saam and Eckhorn 2000)
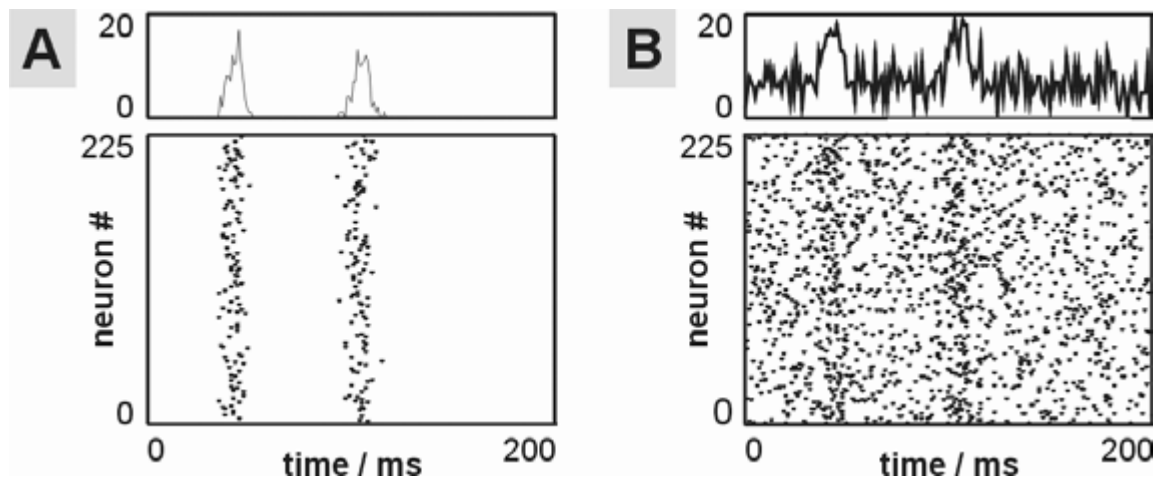
Fig. 7. Spatio-temporal properties of level-1 output activity in the Hebbian learning model. (A) Two events of spatially homogeneous, transient spike-rate enhancement (upper panel: total population spike density; lower panel: single spike traces). (B) As in (A), but with additional independent Gaussian white noise at the inputs. Note that the activity is spatially homogeneous in the sense that any two spike trains have the same weakly correlated temporal statistics. (Modified from Saam and Eckhorn 2000)

neurons becoming quasi-synchronized because constructive superposition of locally evoked and laterally conducted activities gets less probable for increasing delay. Hence, synchrony is laterally restricted to a spatial range which is proportional to the conduction velocity of the lateral connections.

SPATIO-TEMPORAL STRUCTURING OF LATERAL CONNECTIVITY WITH HEBBIAN LEARNING

The relation between conduction velocity and synchronization range suggests an influence of temporal neighborhood (defined by the distance-dependent delays) on the ontogenetic, possibly prenatal formation of

functionally relevant structures from an initially unstructured system (Crair et al. 1998, Ruthazer and Stryker 1996, Trachtenberg and Stryker 2001). This effect can be simulated with our model. In the beginning, neurons are fully interconnected within level-1 (Fig. 6, scenario A). Feed-forward input spike trains have spatially homogeneous random patterns and are given a temporally confined, weak co-modulation, mimicking activity before visual experience. This type of spike pattern appears, slightly modified by the connections, at the output of the level-1 neurons (Fig. 7) and hence, is used for Hebbian learning. The only topography in the network is given by the distance-dependent time delays of the lateral connections. During a first learning period,
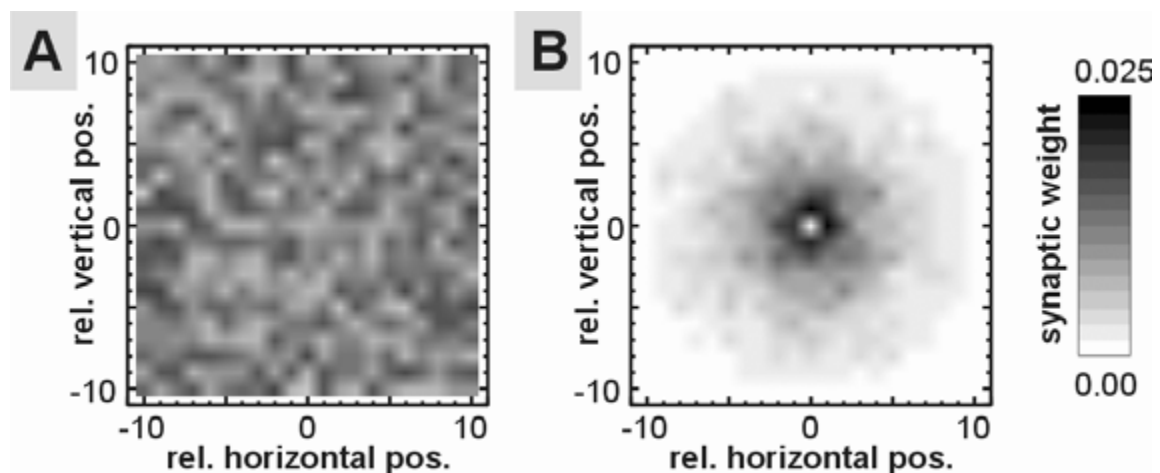

Fig. 8. Spatial coupling profile between a single level-1 neuron (center position) and its neighbors. (A) Before learning weights are randomly initialized; (B) after learning synaptic strength decays with increasing distance. (Modified from Saam and Eckhorn 2000)
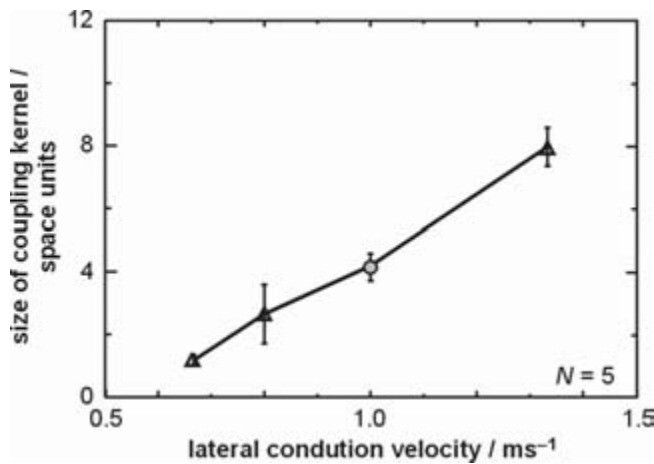
Fig. 9. As a result of Hebbian learning, the size of the synaptic weight profile (coupling kernel) of lateral linking connections within level-1 becomes directly proportional to the lateral conduction velocity. (Modified from Saam and Eckhorn 2000)
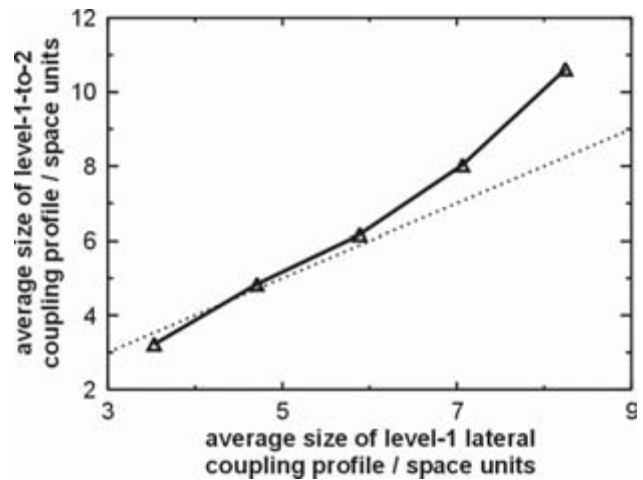

Fig. 10. The size of level-1 synchronization fields determines the size of receptive fields of level-2 neurons. Synaptic weight profiles of level-1-to-2 feeding connections evolve correspondingly to synaptic weight profiles of level-1 lateral linking connections. (Modified from Saam and Eckhorn 2000)

the homogeneous coupling within layer-1 shrinks to a spatially limited coupling profile for each neuron, with a steep decline of coupling strength with increasing distance (Fig. 8). The diameter of the resulting coupling profile for each neuron is near the lateral synchronization range, and hence directly proportional to the lateral conduction velocity (Fig. 9).

SPATIO-TEMPORAL STRUCTURING OF INTER-LEVEL CONNECTIVITY

In a second learning period following the learning period within level-1, the excitatory level-1-to-level-2 connections are adapted, also starting from full connectivity (Fig. 6, scenario B). Again, as a result of Hebbian correlation learning (Kempter et al. 1999), the feed-forward divergence retracts to a limited spatial range which is given by the size of the level-1 synchronization fields, i.e., excitatory forward connections from neurons within a level-1 synchronization field (sending near-synchronized spike packages) converge onto one level-2 neuron (Fig. 10). This convergent projection pattern even emerges if the feed-forward connections and the level-2 lateral connections are modeled with distance-independent constant delays (Fig. 6, scenario C). The physiological interpretation of this result is that the size of level-1 synchronization fields (in visual area V1) can determine the size of level-2 receptive fields (in area V2). Indeed, synchronization fields in V1 and classical receptive fields in V2 of the monkey do have similar

sizes. Since equivalent considerations should hold for projections from the retina to V1, the model accounts for the emergence not only of a spatially regular, but also of a retinotopically organized connectivity.

TRAVELING γ-WAVES WITH ALTERING PHASE RELATIONS

After the learning period, we wanted to investigate the network dynamics. To compare the results with experimental data, we added local inhibitory feedback neurons and provided a sustained spatially homogeneous input to level-1 neurons. This inhibition did not invalidate the previous results, because its dynamics rarely overlap with the learning process. This model reproduces the phenomenon of waves with jittering phase relations, traveling in random directions, just as it was observed in the primary visual cortex (Fig. 3) (Eckhorn et al. 2001, Gabriel and Eckhorn 2003). Traveling waves of γ-activity, though concentrically expanding, have already been described in different cortical areas of different animal species (Freeman and Barrie 2000). The varying phase relations in our model as well as the more rapid spatial decline of γ-coherence (compared to γ-wave probability) are consistent with the experimental data (Figs. 4A,B and 5). Formation of γ-waves in the model results from the locally restricted inhibition, the lateral conduction velocity, and the steep spatial decline of coupling strength (Saam and Eckhorn 2000). It seems probable that cortical γ-waves are also strongly depend-

ing on the lateral conduction velocities, because the distribution of γ-wave velocities (Fig. 3C) is similar to the distribution of spike conduction velocities of lateral connections in primary visual cortex. These velocities have been estimated in different preparations, including rat slices and *in vivo* recordings from cats and monkeys, to range between 0.1 and 1.0 m/s (for review see Nowak and Bullier 1997).

In conclusion, the lateral conduction velocities in primary visual cortex, combined with Hebbian correlation learning, can explain the restricted spatial range of γ-synchrony and the occurrence of traveling γ-waves with random phase relations. They can also account for the larger receptive fields at higher processing levels and for the emergence and stability of topographic visual (and other sensory) representations without the need for visual (sensory) experience. During visual experience, of course, similar influences on synchronization-field and receptive-field size and on topographic stability are probably operative at successive levels of processing, including other parts of the visual system. As the traveling waves can cover the entire representation of an object's surface in the primary visual area, we propose that phase continuity of γ-waves may constitute a mechanism that supports the coding of object continuity in visual cortex (Gabriel and Eckhorn 2003).

Model explaining figure-ground segregation and induced modulations at lower frequencies by slower and more globally acting feedback circuit

In a further approach the above model of the visual cortex has been expanded by using orientation-selective excitatory neurons and two types of inhibitory neurons with different spatio-temporal properties. However, the lateral connections among the excitatory neurons were modeled without delay and learning has been excluded in order to keep the complexity of the network within limits in order to understand its processing. Fig. 11A shows a simplified wiring diagram of this model. The spiking neurons (Fig. 11B) have linearly and nonlinearly acting synapses and are retinotopically arranged in two primary layers with receptive fields at perpendicular orientation preferences. Additionally to the fast inhibitory feedback loop, serving neurons with similar orientation preference and generating local γ-rhythms (see above and Fig. 5), a slow shunting inhibition is added in this model that forms a feedback circuit among neurons with overlapping receptive fields and receive

input from, as well as feed output to, excitatory neurons of all orientation preferences.

DECOUPLING OF γ-SIGNALS ACROSS FIGURE-GROUND CONTOUR

In the figure-ground experiment, representations of different scene segments in primary visual cortex (area V1) were decoupled in their γ-activities (Fig. 1B,D), while the same sites showed substantial γ-coupling when representing one coherent scene segment. Analogous results are obtained with the model (Fig. 1C,E). It explains the reduced γ-coherence as a blockade of lateral coupling at the position of the contour representation due to several effects. First, neurons responding preferentially to the horizontal grating are only weakly activated by the vertical contour. Second, their activity is even more reduced by the orientation-independent slow shunting inhibition that is evoked by the strongly activated vertically tuned neurons at the contour. As a consequence, neurons activated by the horizontal grating near both sides of the contour can not mutually interact, because the orientation-selective lateral coupling is interrupted by the inhibited horizontally tuned neurons at the contour representation. The resulting decoupling of inside and outside representations is not present during the first neural response transient after stimulus onset (Fig. 1D,E) since the sharp, simultaneous response onset common to both orientation layers denotes a highly coherent broad-band signal which dominates internal dynamics. Note that orientation-selectivity was implemented for the sake of comparability with the experimental data. This does not limit the general validity of this model, since any object border constitutes a discontinuity in at least one visual feature dimension, and therefore an analogous argumentation always holds for other local visual features.

Spatial and temporal aspects of object representations

We have seen that within an object's representation in primary visual cortex (V1), locally synchronized γ-activations emerge that overlap in space and time and thereby support the formation of γ-waves traveling across the object's surface representation with random phase relations. When waves of γ-activity travel across V1, this is paralleled by quasi-synchronous activity of those neurons in area V2 having corresponding recep-
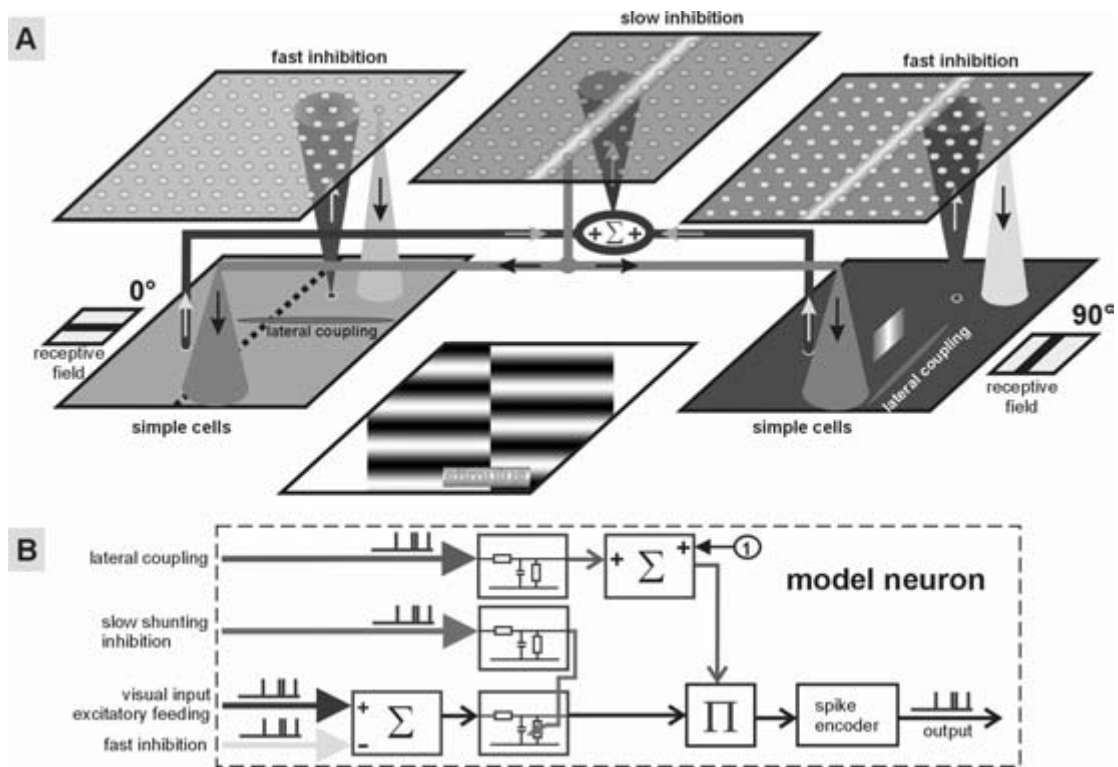
Fig. 11. (A) Simplified model of primary visual cortex with two retinotopic layers (left and right) of orthogonal orientation detectors. Each layer consists of an excitatory (simple cells at 0° and 90°) and an inhibitory sublayer forming fast, local feedback loops preferring the γ-frequency range (Fig. 7). The cones between layers indicate direction and width of divergent projections of each single neuron. Modulatory (facilitatory) lateral coupling is confined to excitatory neurons of the same orientation preference with coaxially aligned receptive fields. Both orientation maps share an additional sublayer (middle) mediating slow, local shunting inhibition. To account for stochastic input from brain regions excluded from the model, all neurons receive independent broad-band noise. (B) The spike-coding model neuron with dynamic threshold (Eckhorn et al 2000) is extended by inputs exerting shunting inhibition on the feeding pathway. Synapses are modeled by leaky RC-filters, lateral modulatory input is offset by +1 (Σ) and then coupled to the feeding pathway by multiplication (Π).

tive field positions (Eckhorn 1994, Eckhorn et al. 1988, Frien et al. 1994), i.e., those receiving input from, and sending γ-feedback to, corresponding V1 neurons. Thus, adjacent V2 neurons, driven simultaneously by adjacent parts of a traveling wave, will also form a traveling wave of γ-activity (with similar extent, velocity and direction if projected to visual space). We expect such an argumentation to hold for subsequent stages of processing, provided that they are retinotopically arranged, are activated by bottom-up input, and have fast inter-areal feedback (compared to a half-cycle of a γ-wave). Accordingly, quasi-synchrony should generally be present among neurons with overlapping receptive field positions across cortical levels connected *via* fast feed-forward-backward loops (e.g., as among V1-V2 and V1-MT (Girard et al. 2001, Nowak and Bullier 1997)). As the traveling waves are γ-activities

and we observed γ-decoupling across the cortical representation of a figure-ground contour (explained in our model by the slow inhibition of neurons at the contour), we assume that the waves do not pass object contour representations with any figure-ground feature contrast. Object continuity across the entire surface may thus be coded by phase continuity of traveling γ-waves.

CONCLUSIONS

We investigated neural mechanisms of associative processing by considering a variety of flexible forms of signal coupling. In particular, we were interested in associations of local visual features into perceptually coherent visual objects by transient synchronization. In our recent experiments in monkeys, we have shown that local synchrony among γ-activities correlates with per-

ceptual modulation, which supports the hypothesis of object representation by synchronization in the visual cortex. The synchronization hypothesis for larger cortical object representations, however, has been challenged by our experimental finding that γ-synchrony in primary visual cortex (V1) already drops to noise levels across few (4-6) millimeters of cortex. We can explain this restriction by the randomly changing phase relations among locally synchronized patches, which, however, form continuous waves of γ-activity, traveling across object representations. Extending the initial synchronization hypothesis, we propose that phase continuity of these waves may support the coding of object continuity across intermediate and longer ranges within V1.

We have discussed the different types and ranges of experimentally observed signal coupling on the basis of visual cortex models with locally coupled, spike-coding neurons. In these models, the lateral, activity-dependent facilitatory connections with distance-dependent delays are the most important feature for explaining synchronous activity. They can account for local and medium-range γ-synchronization, the occurrence of γ-waves and the limited extent of γ-synchrony. Hebbian learning of these connections can explain the stabilization of cortical retinotopy and the larger receptive fields at successive levels of visual cortical processing. Fast local feedback inhibition in our models can generate local γ-oscillations and support local synchrony, while slow shunting-inhibitory feedback supports figure--ground segregation by decoupling activities within neighboring cortical representations of figure and background. In conclusion, we propose that the hypothesis of associative processing by γ-synchronization be extended to more general forms of signal coupling.

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