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Cortical synchronization suggests neural principles of visual feature grouping

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Review

Abstract. Compositions of visual scenes are related here to neural signals in visual cortex and to cortical circuit models to understand neural mechanisms of perceptual feature grouping. Starting from the hypothesis that synchronization and decoupling of cortical γ-activities (35-90 Hz) define the relations among visual objects, we concentrate on synchronization related to (1) static retinal stimulation during ocular fixation, and (2) transient stimulation by sudden shifts in object position. The synchronization hypothesis has been tested by analyzing signal correlations in visual cortex of monkeys with the following results: Static retinal stimuli induce loosely phase-coupled γ-activities among neurons of an object's cortical representation. Patches of γ-synchronization become decoupled across the representation of an object's contour, and therby can code figure-ground segregation. Transient stimuli evoke synchronized volleys of stimulus-locked activities that are typically non-rhythmic and include low frequency components in addition to those in the γ-range. It is argued that stimulus-induced and stimulus-locked synchronizations may play different roles in perceptual feature grouping.

Key words: visual cortex, synchronization, gamma activity, visual coding, perceptual grouping, figure-ground segregation

INTRODUCTION

Synchronization in visual cortex and feature grouping

It is still not clear how a visual scene is segmented perceptually. How are the local feature detectors, characterized by the receptive field properties of single visual neurons, flexibly combined and grouped such that they are associated into the objects and events actually perceived. It has been proposed that binding of spatially distributed features is based on the synchronization of γ-activities (35-90 Hz) among those neurons belonging to an object's neural representation (Reitboeck 1983, v.d. Malsburg and Schneider 1986). This hypothesis attracted attention when synchronized γ-oscillations were found in the visual cortex of anesthetized cats (Eckhorn et al. 1988, Gray et al. 1989) and awake monkeys (Kreiter and Singer 1992, Frien et al. 1994). Since then a huge number of experimental observations have been made that are supportive for the synchronization hypothesis (reviews in: Eckhorn 1999, Gray 1999). This development continued in recent investigations by other and our groups including our results from monkey striate cortex demonstrating: (1) sharper orientation tuning with γ-oscillations than with lower frequency components of the same recordings (Frien et al. 2000), (2) stronger stimulus dependency for γ-oscillations than for

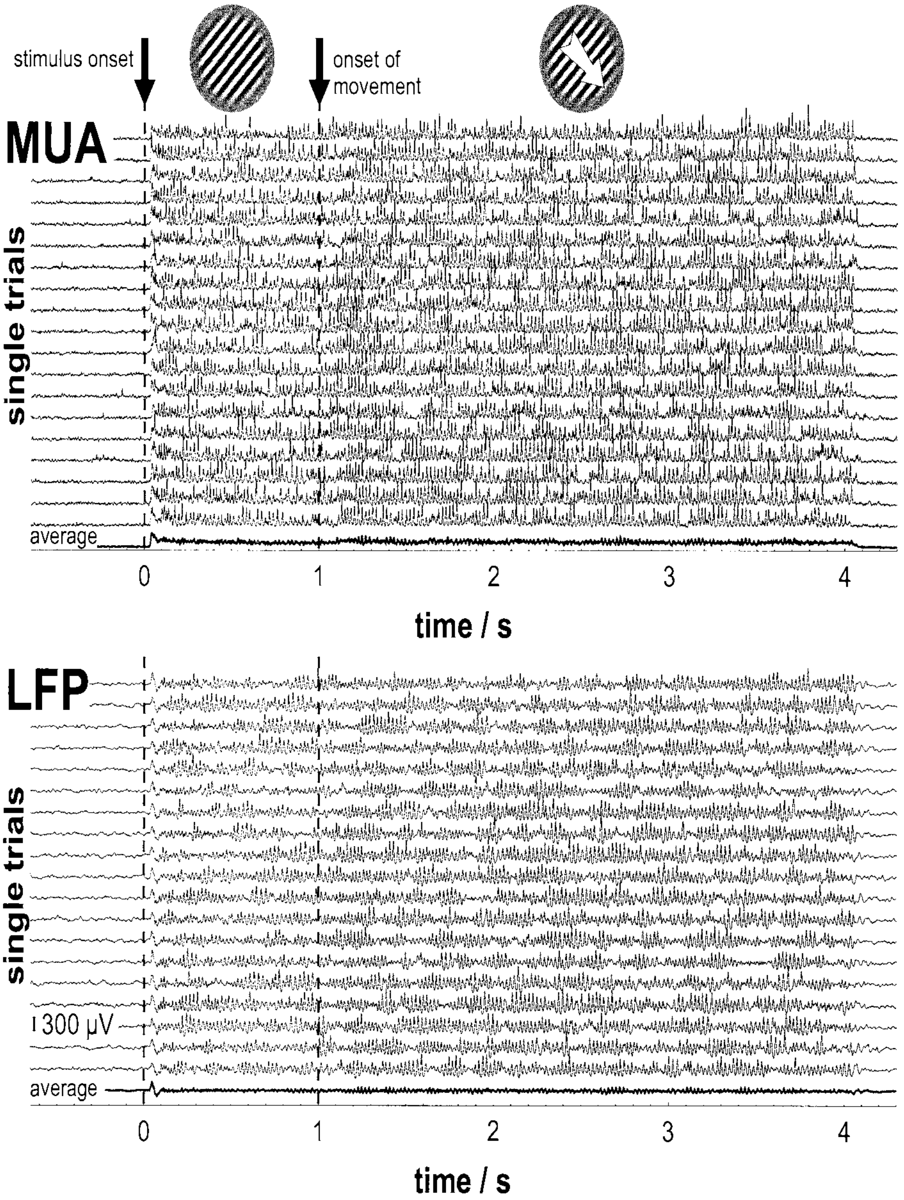

Fig. 1. Original multi unit (MUA) and local field potential (LFP) traces recorded in response to 19 identical stimulus repetitions in V1 of fixating monkey. Stimulation by a static grating patch (1st s), and slow drift of the grating in the (2nd to 4th s). Arrows indicate stimulus appearance and onset of stimulus movement. Lowermost trace: averaged time course of above traces at the same amplitude scale. Note the appearance of γ-oscillations during the presentation of the stimulus in the original traces and its absence after ensemble averaging, because oscillation phases are not locked to stimulus-onset. However, the first response transient, locked to stimulus onset, survives averaging (lowermost traces). Figure modified from (Frien et al. 2000).

lower frequency components (Frien and Eckhorn 2000), (3) loose phase-coupling of γ-oscillations across the total representation of an object so that object continuity may be coded by phase continuity (instead of synchronization at zero phase) (Eckhorn and Gabriel 1999), (4) decoupling of γ-activity across the contour of a texture representation in monkey striate cortex (Gail et al. 2000), and (5) lateral conduction velocity determining the spatial range of synchronization in visual cortex, which in turn determines receptive field size at the next level of processing (the latter is a model result (Saam and Eckhorn 2000).

Stimulus-locked and stimulus-induced synchrony may support feature grouping

Induced γ-activities (typically not phase-locked to stimulus events) would be inappropriate for the fast segmentation of a fast changing scene as they occur with relatively long latencies in the visual cortex (50 ms to 100 ms; Fig. 1). However, fast changing stimuli do elicit fast transient cortical responses (stimulus-locked activities) and they occur with shorter latency (down to 30 ms) than stimulus-induced oscillations (Juergens et al.1999). In addition, stimulus-locked responses gradually reduce present γ-oscillations (Fig. 2) (Kruse and Eckhorn 1996). This suggests that during sudden stimulus changes, stimulus-locked activation may take over segmentation coding from non-phase-locked γ-activities, because transient stimuli also evoke coherent volleys of discharges. If segmentation in such situations is carried out by stimulus-locked responses they should suppress ongoing oscillations of recent more static scenes in order to avoid confusion in fresh segmentations. This is an assumption for which experimental evidence is still lacking.

However, our experiments in which stimulus-induced and -locked synchronization were generated simultaneously provide clues that synchronization, independent of its type and source, may be appropriate to support segmentation processes (Kruse and Eckhorn 1996). This seems convincing, because neurons in higher visual areas will respond more strongly to synchronized than to temporally unrelated inputs, independent of the stimulus locked or non-locked nature of the response. Another hint in the same direction is the observed inverse relationship between the amplitudes of stimulus-induced oscillatory and stimulus-locked response components (Fig. 2). It suggests that the amount of cortical synchronization is kept at a constant level for the different stimulus conditions used in our experiments. We found with strong transient stimuli, that the afferent stimulus-locked input dominates the cortical synchronization. On the other hand, if stimuli do not provide strong temporal modulation of the cortical input, γ-oscillations are induced in the cortical network that are not phase-locked to external events (Kruse and Eckhorn 1996).

NEW EXPERIMENTAL RESULTS ON CORTICAL γ-SYNCHRONIZATION

Orientation tuning of γ-oscillations is sharper than of lower frequencies

Do γ-oscillations play a special role in visual coding? As the main coding property of striate cortex is orientation coding of contours, we investigated whether this

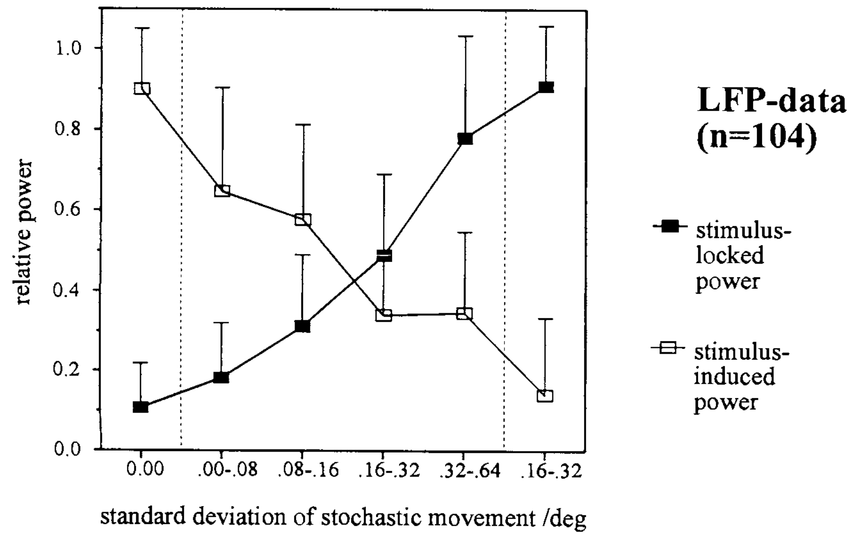

Fig. 2. Perturbation of stimulus-induced γ-synchronization by stimulus-locked signals. Intracortical recordings of local field potential (LFP) by microelectrodes from cat primary visual cortex. Stimulus: grating, moving with a random component superimposed on a constant slow velocity (0.8/s). Open symbols: average normalized response power of γ-oscillations. Filled symbols: normalized power of the stimulus-locked components. Figure modified from (Kruse and Eckhorn 1996).

property is represented more precisely by (1) γ-oscillations, (2) slower signal components, or (3) broad-band signals of the same recordings (Frien et al. 2000). As γ-oscillations are probably of cortical origin this test may further clarify whether cortical network mechanisms are substantially involved in generating orientation selectivity. We tested these questions by recording multi-unit spike activities (MUA) and lower frequency components (LFP) by the same μ-electrodes from upper layers of macaque striate cortex during visual stimulation with grating textures of different orientations. These calculations revealed that the sharpness of orientation tuning, quantified by an orientation index, is significantly higher with γ-oscillations than with signal components of the lower frequency ranges and the initial broad band transient responses (Fig. 3). Thus, our main result is the sharper orientation tuning of γ-oscillations in the spike trains of local populations compared with the slower components of the same broad-band recordings (Frien et al. 2000). As γ-oscillations occur synchronized in the awake monkey's striate cortex we assume that they have enhanced probability of activating successive stages of visual processing, and hence, contribute to the perception of orientation.

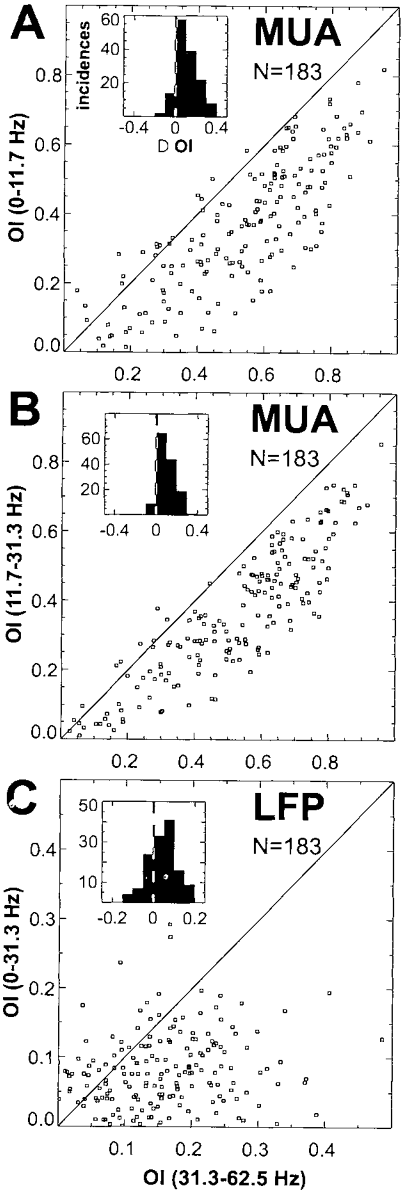

Fig. 3. Orientation tuning is sharpest for γ-oscillations (31.3 Hz to 62.5 Hz). Comparison of the orientation index OI from different frequency ranges for multi unit (MUA) and local field potential (LFP). A, low frequency MUA (0 to 11.7 Hz); B, medium frequency (11.7 Hz to 31.3 Hz MUA; C, low and medium frequency LFP (0 to 31.3 Hz). Insets show the distributions of differences in OI. Positive values correspond to sharper orientation tuning of γ-oscillations. Figure modified from (Frien et al. 2000).

Synchronization of γ-oscillations depends stronger on visual stimulation than lower frequency components

During visual stimulation by a grating texture we studied functional synchronization by calculating spectral coherence among pairs of signals recorded in striate cortex of awake monkeys (Frien and Eckhorn 2000). In responses to appropriate stimuli we found spectral coherence dominated by γ-oscillations and often by additional low frequency components (0 Hz to 12 Hz). Synchronization among separate cortical sites is more stimulus specific for spike activities (MUA) than for slow wave field potentials (LFPs) recorded simultaneously *via* the same electrodes (Fig. 4): MUA coherence at high and low frequencies depends highly significant (1) on the similarity of the preferred orientations at the two sites - the more similar the higher the coherence, (2) on the orientation of the stimulus grating - with highest coherence at half angle between the preferred orientations at the two sites, (3) on cortical distance - coherence decreases to noise levels at about 3 mm (MUA) and 6 mm (LFP). (4) Coherence of γ-oscillations does not depend on the degree of coaxiality of the orientation sensitive receptive fields, whereas low frequencies show significant dependency. This indicates that different frequency components may engage different coupling networks in striate cortex: one for object con-

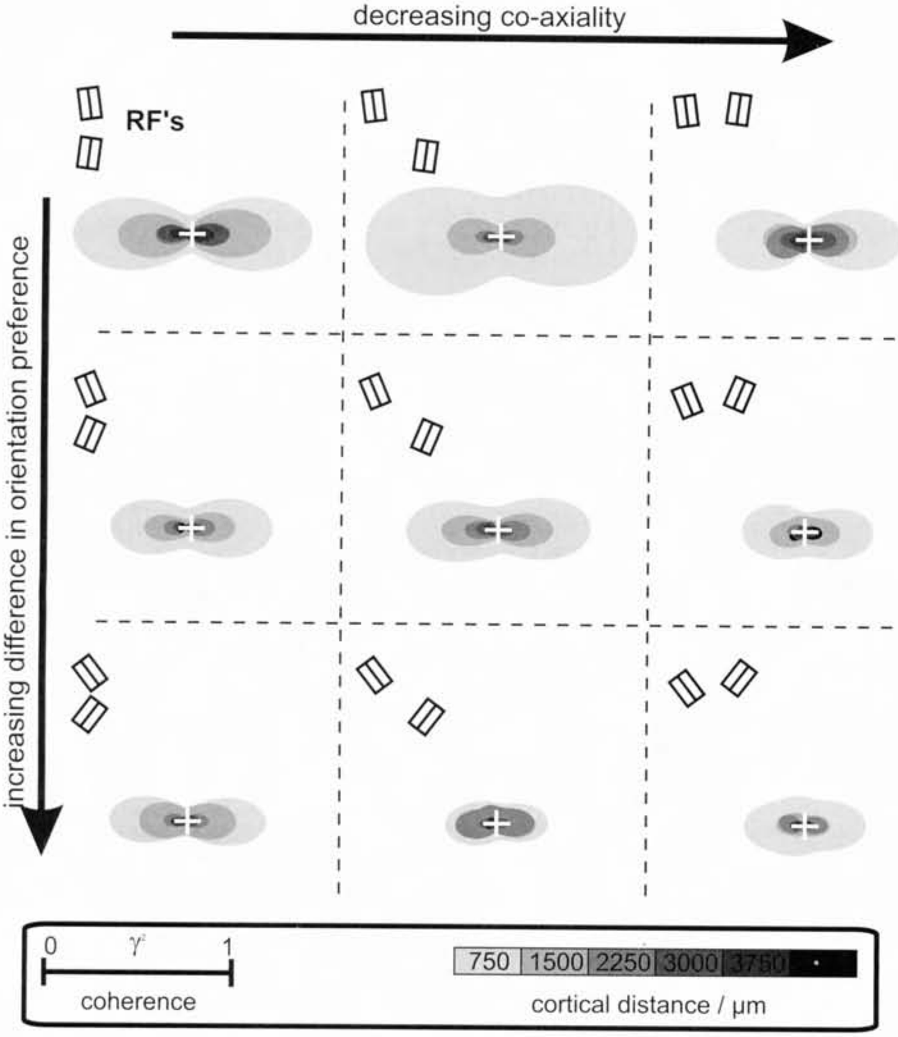

Fig. 4. Coupling among γ-oscillations at separate cortical sites depends on stimulus orientation, on the coaxiality, and on the difference in preferred orientations of the receptive fields at the two sites. Multi unit activity (MUA) recorded simultaneously in V1 of fixating monkey. Polar tunings of dominant components for three classes of receptive field coaxiality (columns) and three classes of difference in preferred orientation (rows). Cortical distance is encoded by gray value (scale bar at lower right). Coupling strength is measured by the coherence values given by the radius (scale at lower left). Figure modified from (Frien and Eckhorn 2000).

tour, the other for object surface coding. (5) Changes in average oscillation frequency with stimulus orientation are highly significant for γ-oscillations while there was no dependency for low frequencies. (6) Finally, stimulus related spectral power and coherence of γ-oscillations are considerably higher than of low frequency components. γ-oscillations may therefore contribute more to feature binding and coding of object continuity than low frequency components, at least for texture surfaces as analyzed here (Frien and Eckhorn 2000).

The continuity of an object's cortical representation may be coded by phase continuity

γ-oscillations have been reported as synchronized in different cortical and subcortical visual structures and it was proposed that they support the coding of object continuity (Eckhorn et al. 1988, Gray et al. 1989, reviews in: Eckhorn 1999, Gray 1999). Correlation analysis revealed average phase differences of γ-oscillations narrowly distributed around zero, but coherence vanished within 3–5 mm cortical distance in V1 and V2 (Frien and Eckhorn 2000). However, cortical object representations are often larger so that zero–delay phase relations seem not suitable for coding feature associations across entire objects. In order to search for alternative codes that define an object's continuity we developed a new signal correlation method utilizing single–response multiple-channel recordings (Eckhorn and Gabriel 1999).

For this, neural signals were recorded in primary visual cortex of awake fixating monkeys by a linear array of µ-electrodes during visual stimulation by whole-field sinusoidal gratings. We evaluated phase correlations of single response γ-oscillations simultaneously for the array of recordings resolved in space and time which gave

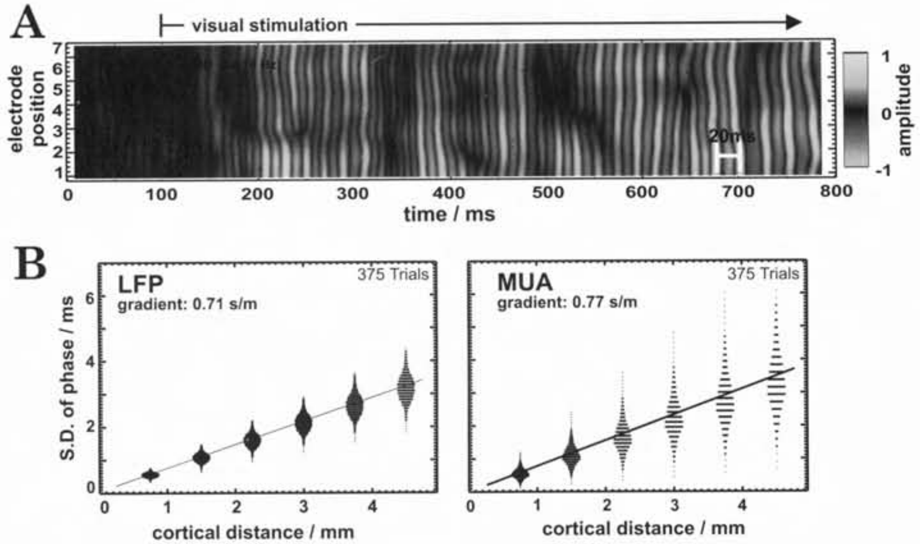

Fig. 5. Loosely coupled γ-waves with fast and random changes in relative phase (from phase-lead to -lag and vice versa). A, time course of wavefronts of local field potentials (LFPs) recorded by a linear coaxial array of microelectrodes in V1 of an awake monkey (single response epoch); B, phase-jitter (ordinate) increases with cortical distance (abscissa). Figure modified from (Eckhorn and Gabriel 1999).

two dimensional correlograms of delay and cortical distance.

We found that wave fronts of γ-oscillations have generally continuous phases across the recording positions and appear in response to specific visual stimulation (Fig. 5A). Wave fronts are generated in paricular when the stimulus grating is parallel to the row of the linearly arranged receptive fields (Eckhorn and Gabriel 1999). These waves appear not synchroneously across the cortex but show relative correlation delays among γ-oscillations from neighboring neural populations that change continuously and randomly from phase lead over synchronization to phase lag and they reverse within few 100 ms. This phase variance increases on average linearly with cortical distance (Fig. 5B).

Our results imply that the previously reported zero–delay correlations among γ-oscillations are phase averaging effects of wave phenomena with large but symmetric phase variations. However, as smooth phase continuity in V1 is present along representations of contours and texture surface, including neurons of different orientation preference, we propose that continuity coding of object representations in visual cortex may be supported by phase continuity of γ-oscillations (Eckhorn and Gabriel 1999).

Figure-ground-coding by decoupled γ-activities

Previous work on figure-ground coding in monkey V1 revealed synchronization of γ-oscillations in object and background regions (Eckhorn et al. 1988, Gray et al. 1989, Kreiter and Singer 1992, Frien et al. 1994, 2000, Frien and Eckhorn 2000), but no decrease in signal correlation across the representation of a contour (Lamme and Spekreijse 1998). The latter observation contradicts previous statements on the role of synchronization for scene segmentation. We therefore re-examined these findings and looked in addition for a potential role of low frequencies in coding figure-ground segregation in monkey primary visual cortex area V1 (Fig. 6) by a grating in which an object was defined by a shifted rectangle. In contradiction to previous work we demonstrate (Gail et al. 2000) that coherence of stimulus induced γ-activity is strongly reduced across the contour's representation. Reduction is almost absent for stimulus-locked components at all frequencies and for unlocked low frequency components.

As surface- and contour-specific modulations of spike rates and coherence reduction of γ-activity differ in time course and stimulus dependence in V1 they probably reflect complementary mechanisms of figure-ground coding.

NEW MODELS OF CORTICAL SYNCHRONIZATION

From lower- to higher-order receptive fields *via* synchroniation and Hebbian learning

The size of classical receptive fields (CRFs) in mammalian visual systems increases systematically from retina to higher cortical areas. We asked for the neural mechanisms and possible functional roles of this CRF-increase and tested the hypothesis that the visual space, covered by the CRFs of synchronized cortical neurons

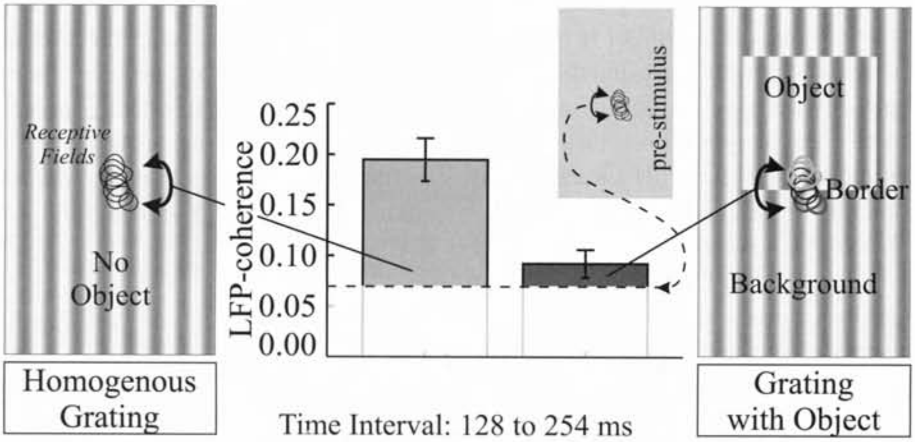

Fig. 6. Coherence is interrupted by a contour. Changes in γ-coherence for different relative positions of the receptive fields to a square figure-ground contour normalized to the homogeneous grating stimulation. The bar hights represent the median ratio of γ-coherence for the figure-ground stimulus and the homogeneous grating (the response epoch 100 ms to 250 ms post-stimulus was taken for calculation). Due to the introduction of the figure-ground contour, within-segment situations (background-background and object-object) have slightly reduced coherences (about -20%, not shown here), while across-contour situations (background-object) show strong reductions in coherence (80%; right bar). Figure modified from (Gail et al. 2000).

(which has been termed the association field, AF, (Eckhorn et al. 1990)), determines the CRF-size at the subsequent level under conditions of Hebbian learning without visual experience.

For this we modelled a largely simplified version of visual cortex (Saam and Eckhorn 2000) by networks of pulse coding neurons arranged in two retinotopically organized cortical levels (e.g. V1 and V2). Level-1 neurons have overlapping concentric CRF profiles and lateral nonlinear coupling with spatially declining strength. A special property of this model are the lateral axonal connections transmitting spikes at constant velocity, i.e. spike delay increases with distance. Level-1 neurons are driven by random pattern (Poisson) spike trains of equal and constant rate that are loosely correlated by simultaneously occurring wave packets. The temporal correlation among each pair of inputs is identical, which means that there is no spatial correlation in the inputs.

Before learning, all level-1 to –2 feed forward connections are completely connected *via* excitatory synapses of low and randomly distributed strength. During learning, first the weights of lateral level-1 connections, and then the level-1 to -2 projections are modified by a Hebbian rule. This rule consists of a temporal function of consecutive epochs of learning and unlearning.

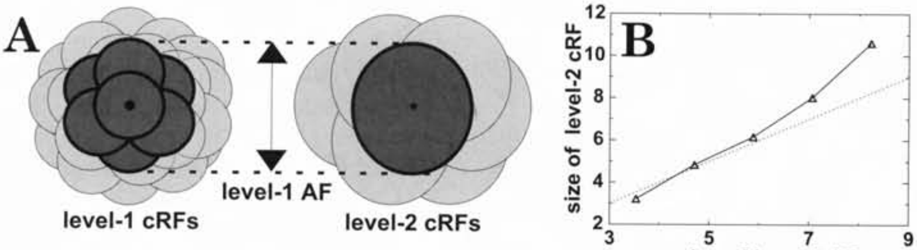

Fig. 7. Size of cortical synchronization field (and of the respective association field, AF) at one level of processing (level-1) determines the size of the classical receptive field (CRF) at the consecutive level of processing (level-2). Note that this dependence emerges during Hebbian learning exclusively from lateral conduction delays that increase with cortical distance – without visual experience. AFs and CRFs increase with increasing lateral spike conduction velocity. Figure modified from (Saam and Eckhorn 2000).

Three properties emerged after learning in this network (Fig. 7). (1) The output spiketrains of level-1 are correlated at an average delay around zero and the lateral connections have spatially decaying coupling strengths over a range defining a cortical synchronization field at level-1 (and correspondingly an AF). (2) Level-2 neurons form retinotopically organized and spatially restricted CRFs. (3) Level-2 CRF-size is linearly related with level-2 AF-size due to interactions among input correlations and lateral transmission delays.

In conclusion, this model implies that the range of feature grouping at a lower level of visual processing, characterized by the cortical synchronization field, can define the CRF-size at the consecutive level, if Hebbian learning is operative. This is achieved by lateral spike transmission delays and stochastic external input that mimicks development before visual experience. Applied to observations in monkey V1 these results suggest, that the lateral conduction velocities and the cortical range of coherent γ-oscillations (determining the AF-size) may therefore significantly influence the CRF size of V2 neurons. Thus, our results support a new hypothesis of the functional role of γ-synchronization in visual cortex and other brain structures (Saam and Eckhorn 2000).

CONCLUSIONS

Two types of signal correlations are proposed as candidate codes for feature grouping and scene segmentation. (1) Synchronization due to stimulus-locking, evoked by transient retinal stimulation as it occurs in response to sudden object movements: it is typically fast, of short latency (30 ms to 100 ms), and has a broad-band spectral composition (5 Hz to 100 Hz). Because of its quick appearance stimulus-locked synchronization seems especially suited for grouping in vision-for-action. (2) Synchronized γ-activities (including γ-oscillations, 35-90 Hz), induced by sustained stimuli during ocular fixation of objects, occur at longer latencies (100 ms to 200 ms), are not locked in their phases to stimulus events and are restricted to the γ-band. As stimulus-induced γ-synchronization appears at the long latencies corresponding to those of object recognition, it may particularly support feature grouping in this task.

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