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Feed-forward synchronization: propagation of temporal patterns along the retinothalamocortical pathway

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Visual responses in the cortex and lateral geniculate nucleus (LGN) are often associated with synchronous oscillatory patterning. In this short review, we examine the possible relationships between subcortical and cortical synchronization mechanisms. Our results obtained from simultaneous multi-unit recordings show strong synchronization of oscillatory responses between retina, LGN and cortex, indicating that cortical neurons can be synchronized by oscillatory activity relayed through the LGN. This feed-forward synchronization mechanism operating in the 60 to 120 Hz frequency range was observed mostly for static stimuli. In response to moving stimuli, by contrast, cortical synchronization was independent of oscillatory inputs from the LGN, with oscillation frequency in the range of 30 to 60 Hz. The functional implications of synchronization of activity from parallel channels are discussed, in particular its significance for signal transmission and cortical integration processes.

Keywords: visual cortex; thalamus; retina; synchronization; oscillation

1. INTRODUCTION

Evidence increases that neurons are sensitive to the precise temporal relations in the discharge patterns of input connections. This provides the option to encode information about stimulus features, not only in the discharge rate of individual neurons, but also in the temporal relations between discharge patterns (Singer 1999). These relational codes can only be studied by recording the responses of several neurons simultaneously and by investigating stimulus-related changes in the temporal relations of the respective discharge patterns. In this short review, we present the results obtained with simultaneous recordings of neuronal responses in the retina, the LGN and the visual cortex. One goal of these studies was to elucidate the relationship between subcortical and cortical synchronization mechanisms.

2. FEATURE-RELATED SYNCHRONIZATION IN THE LATERAL GENICULATE NUCLEUS

Multielectrode recordings in the LGN revealed that responses to stationary and moving light stimuli often exhibit an oscillatory patterning that is associated with precise synchronization of the discharge sequences in parallel channels (Neuenschwander & Singer 1996). As shown in figure 1, the centre peaks in the correlograms computed from simultaneously recorded responses are typically a few milliseconds wide, indicating precise synchronization of individual discharges and phase locking of the oscillatory responses. Oscillatory response patterns have been reported in a number of earlier studies in cats and monkeys (Doty & Kimura 1963; Bishop *et al.* 1964; Laufer & Verzeano 1967; Arnett 1975). Our investigations revealed that the occurrence and the regularity of these oscillatory response patterns, as well as their synchronization, depend, critically, on the size of the stimulus. Small stimuli placed in the centre of the RFs elicit weak oscillations while large stimuli extending across the centre–surround region of the RFs induce strong oscillatory responses.

Synchronization of oscillatory responses was observed only among LGN cells that received their input from the same eye, whereby it did not matter whether the cells were located in the same LGN or in the LGNs of the two hemispheres. Cells driven by the same eye had their responses synchronized even when their RFs were separated by as much as 15° and there was no evidence for a distance-dependent decay of synchronization. By contrast, cells connected to different eyes never exhibited correlations between their oscillatory responses, even if oscillation frequencies were similar.

For such long-range synchronization to occur, the responses had to be elicited with a spatially continuous stimulus (see figure 1). Two contiguous stimuli extending across the spatially segregated RFs of two LGN cells led to strong synchronization of the oscillatory responses. However, when the very same stimuli were shifted apart, leaving a small gap between them, synchronization disappeared without a decrease in oscillation strength of the individual responses. These results suggested the existence

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One contribution of 22 to a Discussion Meeting Issue 'The essential role of the thalamus in cortical functioning'.

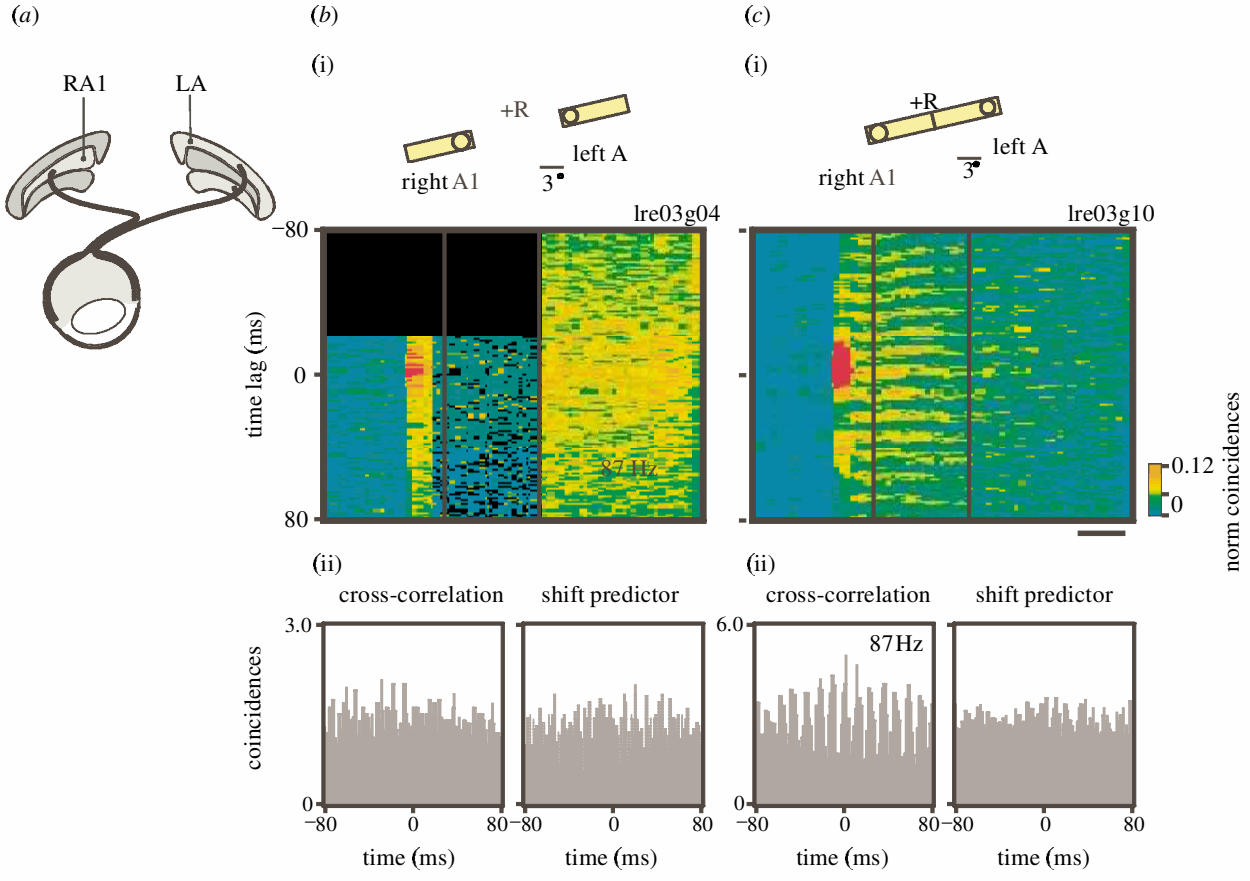

Figure 1. Synchronization of oscillatory responses in the LGN depends on stimulus continuity. (*a*) Multi-unit activity was recorded from lamina A1 of the right LGN, and a single ON-cell from lamina A of the left LGN, with receptive fields separated by 15° across the vertical meridian. Thus, cells at both sites were driven from the right eye. The cells were activated by rectangular light stimuli of constant size that were either separated by a gap or were contiguous and covered the area between the receptive fields. (*b*) When the stimuli were separated, they elicited responses that oscillated with similar frequency (*ca*. 87 Hz) at both sites but showed no synchrony. (*c*) When the stimuli were spatially contiguous, the oscillatory responses in the LGN became highly correlated. (i) Series of cross-correlation functions obtained with a moving-window analysis (step 50 ms, analysis window 200 ms; amplitude normalized by the number of spikes in each window). Scale bar, 500 ms. (ii) Cross-correlation functions and corresponding shift predictor controls computed within a 1 s window as shown by the boxes in the moving-window analysis. The fact that the control cross-correlograms were flat indicates that the oscillatory responses were not phase locked to the onset of the stimulus.

of a synchronization mechanism that is associated with an oscillatory patterning of the responses, operates over large distances and depends critically on the spatial configuration of the stimulus. It is important to mention at this point that in all the experiments from which those results are derived, shift predictors (correlograms between responses to the same stimulus configuration selected from different trials) were computed and found to be flat. This finding strengthens the conclusion that the synchronization phenomenon described here is the result of feature-specific interactions among LGN cells and not the covariation of discharge rates (Brody 1999*a*,*b*).

Synchronization of responses in the LGN could in principle be of cortical, thalamic or retinal origin. A cortical origin of the observed synchronization phenomena is unlikely for two reasons: (i) oscillatory responses in the cortex typically occur at much lower frequencies (30–50 Hz); (ii) the synchronization of geniculate responses resulting from corticofugal inputs is much less precise and not based on phase locking of high-frequency oscillation (Sillito *et al.* 1994). The fact that we have always seen synchronization for cell pairs with the same eye input, regardless of whether the cells were located in the same LGN or in the LGNs of the two hemispheres, makes a thalamic contribution to synchronization in this high-frequency range improbable. This leaves a retinal mechanism as the most likely candidate.

3. RETINAL ORIGIN OF RESPONSE SYNCHRONIZATION

In the retina, precise oscillatory patterns in the spiking activity of ganglion cells were discovered long ago in both vertebrates and invertebrates (Fröhlich 1914; Adrian & Matthews 1928; Granit 1933). Later, several studies described oscillatory activity in the retina of the cat and the monkey in response to luminance modulation (Kuffler 1953; Doty & Kimura 1963; Rodieck 1967; Laufer & Verzeano 1967; Ariel *et al.* 1983). As in the LGN, this oscillatory activity depends on stimulus size and contrast, pointing to the involvement of centre–surround mechanisms (Ariel *et al.* 1983; Przybyszewski *et al.* 1993). Laufer & Verzeano (1967) first suggested that fast oscillations in the retina are likely to result from cooperative

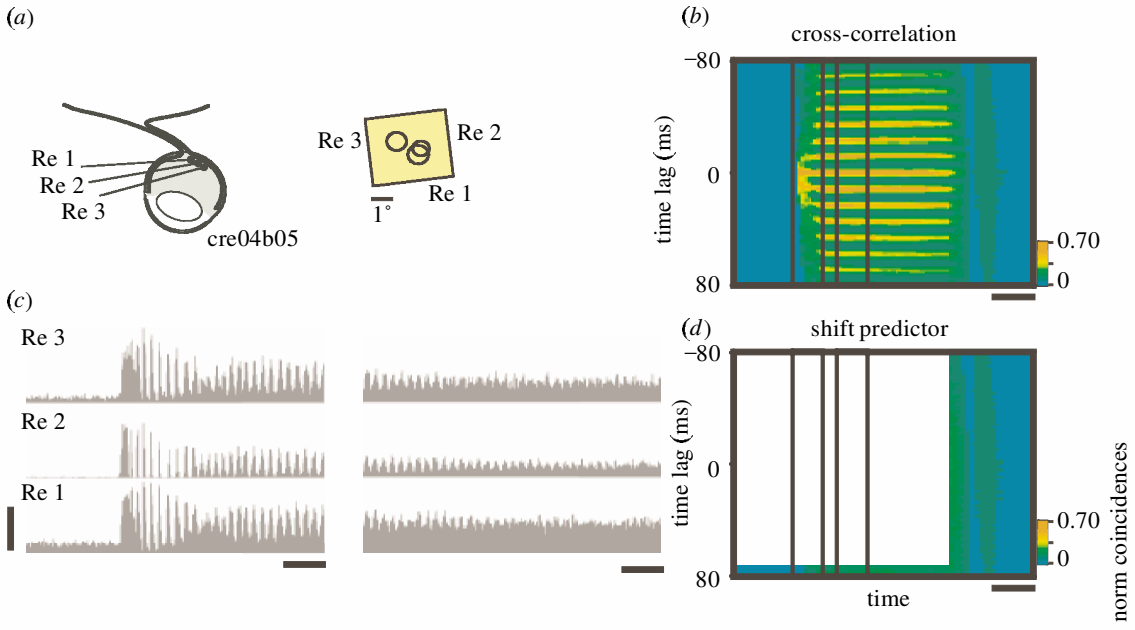

Figure 2. Synchronous oscillatory responses in the retina. Responses to a light stimulus (square) flashed over the receptive fields (circles) were obtained from three simultaneous multi-unit recordings. Receptive fields were located in the central visual field. The stimulus was generated by a direct-current light source and therefore it was free of any oscillatory component. (*c*) Response histograms were computed with a 1 ms resolution (vertical scale bar, 150 spikes s^{-1}; horizontal scale bars, 50 ms). Two distinct 400 ms epochs of the responses are shown at expanded time-scale. A strong oscillatory modulation is visible in the early phase of the responses (to the left), fading completely within a few hundred milliseconds (to the right). The peaks seen in the histograms are precisely aligned in the first few cycles, indicating a strong phase locking to stimulus onset. (*b*,*d*) Cross-correlation functions obtained through a sliding-window analysis are shown for one recording pair. Notice that the shift predictor control explains entirely the correlation pattern during the transient phase of the response (left panel). Thereafter, the modulation persists despite subtraction of the shift predictors from the raw correlograms, indicating that synchronization is no longer stimulus locked but caused by neuronal interactions. Number of stimulus repetitions, 100. Sliding-window analysis, step 50 ms, analysis window 200 ms; normalized amplitude. Scale bars, 500 ms.

interactions among large populations of cells. Later, cross-correlation analysis revealed that neighbouring ganglion cells can exhibit strong correlations among their discharges (Arnett 1978; Arnett & Spraker 1981; Mastronarde 1989; Sakai & Naka 1990; Meister *et al.* 1995; Brivanlou *et al.* 1998). We have extended these observations with multi-electrode recordings performed simultaneously in the retina, the LGN and the visual cortex (Neuenschwander & Singer 1996). The multi-electrode recordings from the retina confirmed the relationship between stimulus continuity and response synchronization observed in the LGN and showed that these interactions occur unattenuated over distances of more than 20° and across all quadrants of the retina. The fact that synchronization depends on the spatial continuity of the stimulus indicates that it results from neuronal interactions within the retina and not from phase locking to stimulus onset. In the latter case, synchronization should persist regardless of the spatial continuity of the stimulus.

A more detailed analysis of the time course of synchronization revealed that the initial component of the response can be precisely phase locked to stimulus onset (figure 2). Such stimulus locking of oscillatory responses in the retina and the LGN has been described in a number of studies (Ariel *et al.* 1983; Ghose & Freeman 1992; Wörgötter & Funke 1995). However, the epoch of stimulus-locked synchronization is of short duration and replaced by a sustained phase of synchronous oscillatory firing that is no longer time locked to stimulus onset and hence needs to be attributed to intraretinal synchronization mechanisms that must be based on horizontal interactions.

Another consistent feature of this intraretinally generated synchronization was its systematic modulation by stimulus size, contrast and velocity. As mentioned above, and described in detail in Castelo-Branco *et al.* (1998), the oscillatory modulation of the responses and the precision of the synchronization increased systematically with the size of the stimulus. A similar positive correlation exists with stimulus contrast. Moreover, oscillation frequency, and thereby also the precision of synchronization, increase with the velocity of moving stimuli (for details see Neuenschwander *et al.* 1999).

4. FEED-FORWARD TRANSMISSION OF OSCILLATORY PATTERNS

Direct evidence for feed-forward synchronization and reliable transmission of oscillatory patterning of ganglion cells to the cortex has been obtained with simultaneous recordings from the retina, the LGN and area 18 (Castelo-Branco *et al.* 1998; figure 3). As expected in case of feed-forward synchronization, relatively large phase shifts characterize cross-correlograms obtained from retina–cortex pairs, with the retinal responses leading in phase. This type of synchronization was more frequent for static than for moving stimuli. Figure 3*c* shows also an example where retino-cortical synchronization occurs for both the onset and offset of a light stimulus. Typically, ON-responses

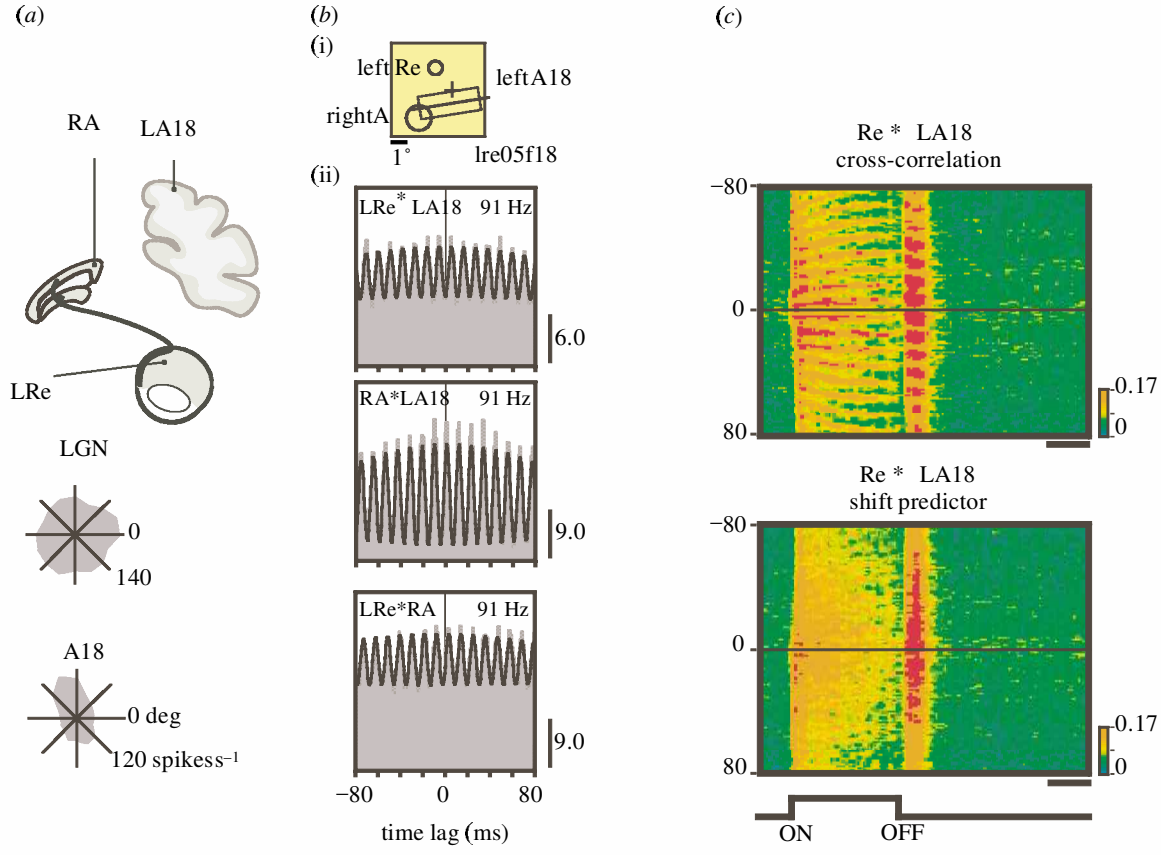

Figure 3. Feed-forward synchronization between the retina, the LGN and the cortex of oscillatory responses evoked by a stationary stimulus. (*a*) and (*b*(i)) Responses were recorded simultaneously from the left retina (LRe), right LGN lamina A (RA) and left A18 (LA18). (*b*(ii)) The onset of the stimulus evokes oscillatory responses at all sites at a frequency of 91 Hz and these oscillations are correlated between all recording pairs. Shift predictor controls (not shown here) indicate that this feed-forward synchronization is not due to stimulus locking. (*c*) Sliding-window analysis for another set of recording sites in area 18 and the retina. The cross-correlation functions show a strong and sustained synchronization of responses to the onset of the stimulus and a more transient synchronization to the offset of the stimulus. Notice that the oscillation frequency for the OFF-responses is lower than the one for the ON-responses (85 and 101 Hz, respectively). Scale bars, 1000 ms.

oscillated at significantly higher frequencies than OFF-responses (mean *ca*. 90 Hz for ON- and *ca*. 80 Hz for OFF-responses; Neuenschwander *et al.* 1999). By contrast, cortico-cortical synchronization usually occurs between 30 and 50 Hz, and is more pronounced for moving than for stationary stimuli. Figure 4 exemplifies the difference between retinal and cortical synchronization mechanisms. Two pairs of simultaneous recordings were obtained from area 17 and the LGN, respectively. At the cortical site, moving gratings induced a strong synchronization of oscillatory responses at 33 Hz and this synchronization persisted throughout the duration of the response. By contrast, in the LGN, synchronization was very transient and occurred at a much higher frequency (106 Hz). No significant correlations were found in this case between the slow cortical and the fast thalamic oscillatory responses, indicating that the cortical oscillations and their synchronization are largely independent of the oscillatory patterning of afferent activity.

The distribution of oscillation frequencies assessed from cross-correlograms of retinal, thalamic and cortical responses is summarized in figure 5. This comparison confirms that cortico-cortical synchronization occurs on the basis of oscillations in the frequency range of 30–50 Hz while the synchronization that originates in the retina and propagates through the LGN to cortex occurs at much higher oscillation frequencies (60–120 Hz). The finding that retino-cortical correlations occur only in the high-frequency range is in agreement with a feed-forward propagation of synchronous oscillatory activity. Thalamocortical cross-correlograms covered a much broader frequency range, including both the retinal and the cortical range. This suggests two possibilities: (i) cortical oscillations may sometimes back-propagate to the LGN via the cortico-thalamic projection and synchronize a fraction of the thalamic spikes to the cortical rhythm; (ii) the slow cortical oscillation may on occasions be triggered or reset by one of the synchronous volleys arriving from the thalamus.

5. FUNCTIONAL IMPLICATIONS

At first sight, synchronization of ganglion cell discharges appears poorly adapted, as the information transmittable across parallel channels is maximal if the activity in these channels is statistically independent. However, if the target cells in the LGN and the visual cortex can distinguish between and respond differentially to synchronized and non-synchronized activity, additional information can be conveyed by modulating the degree of synchronization among ganglion cells. Several findings indicate that thalamic and cortical neurons distinguish with high selectivity between synchronous and non-synchronous input. Analy-

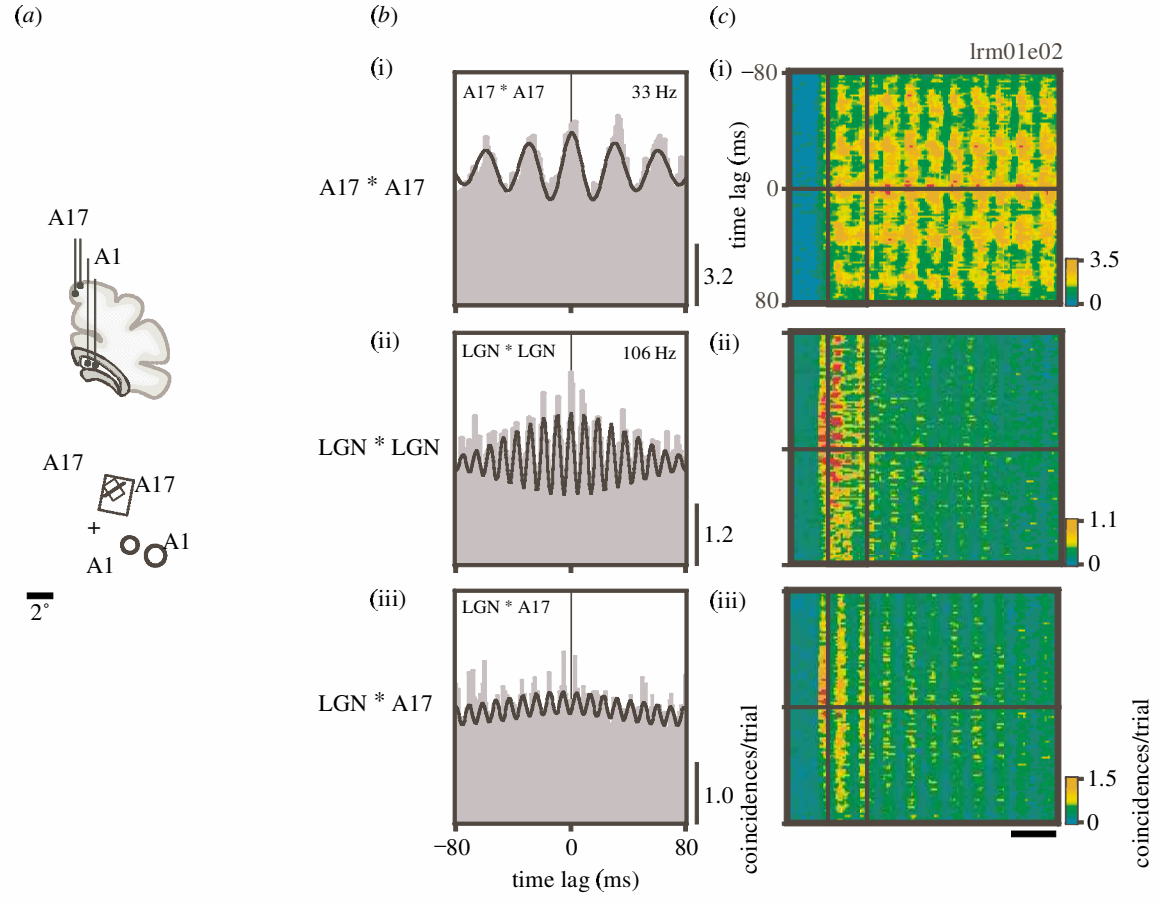

Figure 4. Relation between cortico-cortical and intrathalamic synchronization. (*a*) Responses to drifting gratings were recorded simultaneously from four separate sites, two in the left A17 and two in the left LGN lamina A1. The orientation of the gratings was always intermediate to the optimal orientation of the cortical neurons. Strong and stable cortico-cortical synchronization at a frequency of 33 Hz and a phase shift of 0.8 ms were induced by the stimuli (cross-correlation function, (*b*(i)). The sliding-window cross-correlation (analysis window, 250 ms; step, 50 ms) shows that synchronous oscillations do not decay over time (*c*(i)). By contrast, intrageniculate synchronization occurs only during the initial response epoch (*b*(ii),*c*(ii)), at a much higher frequency of 106 Hz. There is no significant correlation between the responses of cortical and LGN neurons in this case (*b*(iii),(*c*(iii)), indicating that cortical synchronization is independent of oscillatory LGN input. Average cross-correlation functions were computed from the 1000 ms window as shown in (*c*). Scale bar, 1000 ms.

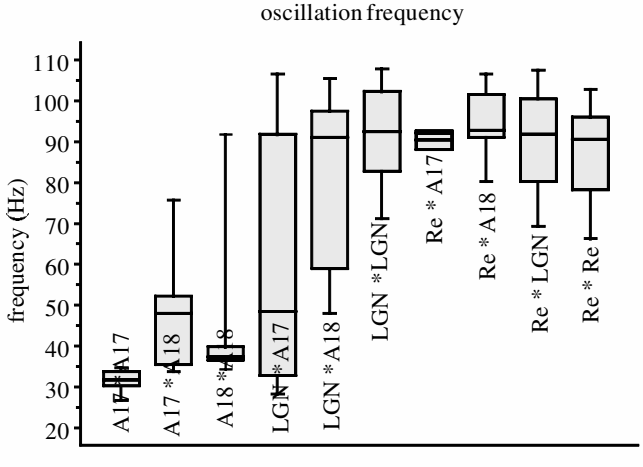

Figure 5. Box plot of the distribution of oscillation frequencies for all cases of synchronous oscillations. The horizontal bars depict the median (50th centile), the boundaries of the boxes the 25th centile, and the error bars the 10th centile. Note that the oscillatory patterns in thalamocortical correlations span a larger frequency range than in subcortical and intracortical correlograms.

sis of transfer functions between simultaneously recorded retinal afferents and LGN cells (Singer *et al.* 1972; Levick *et al.* 1972; Usrey 2002) revealed that EPSPs arriving within intervals shorter than 3–4 ms summate much more effectively than temporally dispersed EPSPs. As LGN cells receive convergent input from several ganglion cells of the same functional type (Singer *et al.* 1972; Levick *et al.* 1972; Usrey 2002) this implies that transmission of retinal signals through the LGN is also likely to be influenced, apart from numerous other variables, by the amount and precision of retinal synchrony. The same argument applies to thalamocortical transmission as cortical cells have been shown to exhibit similar sensitivity to synchronized inputs as thalamic cells (Usrey & Reid 1999). Thus, synchronization of activity in parallel channels could be used to increase the safety factor of synaptic transmission and hence the sensitivity of the visual system. Another function could be to improve the precision with which the temporal features of stimuli are transmitted. Due to stimulus locking of the early components of the synchronized oscillatory responses, stimulus transients lead to highly synchronized volleys of high frequency discharges. Because of the synergy between temporal

and spatial summation, these volleys trigger postsynaptic responses with minimal latency and latency jitter. In analogy to synfire chains (Abeles 1991; Diesmann *et al.* 1999) the time-stamps of response transients get reliably transmitted across successive processing stages if discharges are synchronized across channels. Thus, synchronization of retinal responses could contribute to raise the precision with which temporal signatures of stimuli are encoded and transmitted. The finding that retino-cortical response synchronization was particularly precise in the pathway to area 18, which receives input exclusively from the phasic Y-system and seems to be specialized in the analysis of fast motion, is in agreement with this theory.

However, since retinal synchrony is modulated by stimulus features, such as size, contrast, continuity and movement velocity, it is likely that it also contributes to the encoding of these variables. As discussed above, synchronization of responses raises their saliency above the level that is attainable by joint rate increases and the concomitant increase of spurious coincidences. Kenyon *et al.* (2001) have simulated a retinal network that exhibits the feature-dependent synchronization properties described by Castelo-Branco *et al.* (1998) and Neuenschwander *et al.* (1999) and fed the output of this retinal model to a cortical network of simple cells which received a convergent input of elongated arrays of ganglion cells, as proposed initially by Hubel & Wiesel (1962). These simulations provided several important insights.

First, they identified the network of amacrine cells as the substrate for the horizontal interactions that generate the oscillatory patterning of ganglion cell responses and the synchronization of spike discharges. Essential components were the inhibitory interactions between amacrine cells and the coupling via gap junctions. Second, it was shown that the model that incorporated known anatomical and physiological parameters reproduced, with surprising precision, the stimulus dependency of the retinal oscillations and synchronization. Third, the analysis of the simple cell responses revealed that the synchronization of the retinal responses enhances considerably the dynamic range over which simple cells can encode stimulus features. By inactivating the synchronization mechanisms in the retina, it was possible to assess the amount of information transmittable by rate modulation alone and to determine the additional modulation of simple-cell responses caused by synchronization. The simple cells were implemented as conventional integrate-and-fire units and no special attempts were made to increase their coincidence sensitivity by implementing regenerative dendritic responses. Thus, it appears that neuronal networks consisting of neurons with conventional time-constants and exhibiting the usual degree of convergence and divergence of input connections are sensitive not only to the rate variations of input signals, but also to the degree of synchrony due to neuronal interactions, and do not simply reflect the level of spurious coincidences characteristic for a particular discharge rate.

The question, whether the dependency of synchronization on the continuity of visual stimuli is exploited by the visual system to extract information about the relations among contours, remains unresolved. Following the discovery of stimulus-related response synchronization in the cat visual cortex (Gray & Singer 1989), we proposed that precise synchronization of spike discharges could serve as a code to signal the relatedness of stimuli. The theory is that synchronization might be used to jointly raise the saliency of distributed responses, thereby enhancing the probability that these synchronized responses are selected for further joint processing. Since that time, a large number of studies have been performed to examine this possibility (for reviews see Singer 1999; Gray 1999; Tallon-Baudry & Bertrand 1999; Engel *et al.* 2001). These have provided ample evidence for tight correlations between response synchronization in the cerebral cortex, especially the synchrony associated with oscillatory responses in the beta- and gamma-frequency range, and a wide range of cognitive phenomena requiring response selection and binding. These include perceptual grouping and figure–ground segregation (reviewed in Singer 1999; Tallon-Baudry & Bertrand 1999), stimulus selection in perceptual rivalry (Fries *et al.* 1997, 2002), attention-dependent stimulus selection (Roelfsema *et al.* 1997; Gruber *et al.* 1999; Steinmetz *et al.* 2000; Fries *et al.* 2001), maintenance of stimulus-related information in short-term memory (Tallon-Baudry *et al.* 2001), establishment of stimulus–stimulus associations in associative learning (Miltner *et al.* 1999) and the preparation and execution of movements (Riehle *et al.* 1997; Maynard *et al.* 1999; Kilner *et al.* 2000). In many of these experiments, it was possible to infer, from the occurrence and precision of synchrony, the nature of the applied stimuli and the attention state of the tested subjects. Occasionally, it was also possible to predict behavioural responses. However, it has so far proved difficult to manipulate synchrony without affecting other response variables, so that direct evidence for a causal role of synchrony in neuronal processing is still lacking. Accordingly, it is difficult to counter the often-raised argument that oscillatory patterning and synchronization of responses are functionally irrelevant epiphenomena (for a collection of these arguments see Shadlen & Movshon 1999). However, if one considers that most of the evidence relating rate changes of neuronal responses to cognitive or motor processes is also correlative in nature—if one excludes the trivial case of silencing neurons—this difficulty in providing causal proof should not discourage the search for putative functions of synchrony.

The data presented in this review indicate clearly that even widely segregated ganglion cells exhibit precisely synchronized discharges when activated by a continuous contour and that this internally generated synchrony breaks down for responses to spatially separate contours. The data also show that the signature of synchrony is reliably transmitted to the visual cortex. Other data (Herculano-Houzel *et al.* 1999; Neuenschwander *et al.* 1999) indicate that the occurrence of cortically generated response synchronization, although it is based on much slower rhythms, develops out of the synchronous volleys of afferent LGN activity. It is, thus, conceivable that the synchronization patterns provided by the retina bias the emergence of corresponding synchronization patterns at the cortical level. If so, retinal preprocessing could, at least in part, be responsible for the fact that cortical cells tend to synchronize their responses when stimulated with a continuous contour, while they synchronize less, or not at all, when responding to spatially segregated contours (Gray *et al.* 1989; Freiwald *et al.* 1995; Kreiter & Singer

1996). Synchronization of retinal responses evoked by continuous contours is likely to favour synchronization of cortical responses to continuous contours; and, vice versa, the non-synchronized retinal responses to spatially segregated contours are likely to reduce the probability of cortical synchronization. Synchronization probability among cortical neurons is, of course, also dependent on numerous other factors, such as the functional architecture of intrinsic cortico-cortical connections and patterned input from top-down projections. The dependence of synchronization patterns on stimulus features such as orientation, collinearity and common fate, and the attention and state dependence of synchrony, are attributed to these cortical mechanisms (for review see Engel *et al.* 2001).

It remains as an attractive possibility, however, that very basic stimulus features, such as continuity, are already evaluated in the retina and translated into a code that is ideally suited to bias synchrony in the visual cortex. It will be interesting to examine in simulation studies whether implementation of continuity-dependent retinal synchrony facilitates scene segmentation operations in machine vision. Since the retinal mechanisms responsible for synchronization can perhaps be influenced pharmacologically, or through genetic manipulations without affecting the discharge rates of ganglion cells, there might be the possibility to obtain direct experimental evidence on the putative function of the synchronization phenomena described in this review.

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GLOSSARY

EPSP: excitatory postsynaptic potential
LGN: lateral geniculate nucleus
RF: receptive field