Proc. Natl. Acad. Sci. USA
Vol. 92, pp. 290–294, January 1995
Neurobiology

Relation between oscillatory activity and long-range synchronization in cat visual cortex

(extracellular recording/correlation analysis/temporal coding/cell assembly)

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Communicated by John Eccles, Contra, Switzerland, September 7, 1994

ABSTRACT **Recent theoretical studies have suggested that oscillatory firing patterns with frequencies in the gamma band (30–70 Hz) may be instrumental for the establishment of synchrony among widely distributed neurons if synchrony is to be achieved by reciprocal connections. We have now investigated the relationship between synchrony and oscillations in cat visual cortex. Our results show that when synchronization of neuronal activity occurs over distances of >2 mm in primary visual cortex, or occurs between the two hemispheres, it is almost always associated with oscillatory firing patterns, whereas synchronization over short distances occurs also in the absence of oscillations. Furthermore, our results indicate that short-range interactions affect both the firing rate of the respective neurons and the timing of their discharges, whereas only the latter is influenced by long-range interactions. These data support the hypothesis that oscillatory activity can contribute to the establishment of long-range synchrony in a network of reciprocally coupled neurons.**

Electrophysiological studies indicate that synchronous firing of neurons is a ubiquitous phenomenon in the nervous system (for review, see ref. 1). One specific proposal regarding the function of this phenomenon is that neuronal synchronization may serve to establish dynamic relations between groups of neurons and that such a mechanism could provide a flexible solution to binding problems inherent in perceptual functions such as scene segmentation and object representation (2, 3). In support of this hypothesis, electrophysiological studies have demonstrated a synchronization of spatially separate cell groups with near-zero phase lag, which has been observed both within (4–8) and between (6, 9, 10) areas of the visual cortex and even between different cerebral hemispheres (11). Furthermore, it has been shown that synchronization probability depends on the configuration of visual stimuli and does reflect some of the *Gestalt* criteria that are used for scene segmentation (7, 12). Moreover, a recent investigation of cats with strabismic amblyopia has demonstrated a close correlation between reduced synchrony and perceptual deficits, supporting the hypothesis that synchronization serves a function in visual processing (13).

A striking observation in many of these studies was that synchronization of neurons was frequently associated with oscillatory firing patterns (6–9, 11–13). During such oscillatory epochs, neighboring neurons tend to engage in grouped discharges which recur at frequencies in the gamma range—i.e., between 30 and 70 Hz (14). However, the role of these oscillations, which have also been observed in monkeys (15, 16) and humans (17, 18), has remained controversial. Based on simulation studies (19), we have suggested that these oscillatory firing patterns may offer advantages for the establishment of synchrony by reciprocal connections among spatially distributed neurons (3, 20). Neurons that are endowed with mechanisms that favor oscillatory firing patterns may be synchronized with zero phase lag despite considerable and variable transmission delays in the coupling connections and even if they are only connected through polysynaptic links (19). If it holds true that oscillatory activity is instrumental for the establishment of synchrony among spatially distributed neurons, cortical long-range synchronization should be closely correlated with oscillatory activity, whereas such a relation would not necessarily hold for synchronization over short distances. Here we report physiological evidence obtained in cat striate cortex which supports this hypothesis.

MATERIALS AND METHODS

Data were recorded from 12 adult cats in which anesthesia was induced with ketamine and xylazine (10 mg/kg and 2.5 mg/kg of body weight, respectively) and maintained with 70% N_2O/30% O_2 supplemented by 0.4–2% halothane. After completion of the surgical procedures, the cats were paralyzed with hexacarbacholine bromide (1–2.5 mg/hr) and anesthesia was maintained as before. Multiunit activity was recorded from area 17 with arrays of platinum/iridium electrodes. In 3 cats, simultaneous recordings were made in left and right area 17 close to the 17/18 border (11). After mapping of the receptive fields with hand-held stimuli, light bars were projected from a computer-controlled optical bench onto a tangent screen. Whenever possible, we used coherent visual stimuli, since these, according to our previous studies (7, 12), optimize the probability of synchronization. Thus, neurons having overlapping receptive fields were always activated with a single light bar whose orientation was intermediate between the neurons' preferred orientations, rather than a combination of two optimally oriented bars. When the cells had nonoverlapping receptive fields, we used either a single long light bar or two coherently moving bars of similar orientation. Blocks of 10 responses to the same stimulus configuration were digitized for quantitative analysis. See ref. 8 for further details of preparation and recording procedures.

For the recorded spike trains, we computed peristimulus–time histograms, autocorrelation functions (ACFs), and cross-correlation functions (CCFs). As a control, we also computed shift predictors for all correlograms (8), which never showed a significant modulation in the cases included here. To quantify the temporal modulation of the responses and the strength of synchronization, we used a new version of a method described previously (8, 21). To each of the correlograms we fitted a generalized Gabor function,

$$F(t) = A \cdot \exp\left[-\left(\frac{|t-\varphi|}{\sigma}\right)^{\lambda}\right] \cdot \cos[2\pi\nu(t-\varphi)] + O,$$

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Abbreviations: ACF, autocorrelation function; CCF, crosscorrelation function; RMA, relative modulation amplitude; EoA, effect on activity; EoT, effect on timing.

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with variable amplitude (A), offset (O), phase shift (φ), frequency (ν), decay (σ), and exponent (λ). Using this type of generalized sinusoid as a model allowed the appropriate description of ACFs and CCFs with quite different morphologies. In particular, center peaks in the correlogram modulation could be detected independently of eventually occurring satellite peaks (21). To be accepted, the fitted function had to account for at least 15% of the variance of the data points. The fit was performed with the Marquardt–Levenberg algorithm (22), which was modified to supply not only error estimates for the parameters of the fitted function but also the complete covariance matrix. This allowed us to determine the value of the fitted function at each point together with the respective confidence limits and, thus, to test different aspects of the function separately. With this approach, the significance of the center peak and that of the first satellite peak were tested independently against zero at the 5% level for successfully fitted functions (21). Significant center peaks in the CCFs were taken as evidence for synchronization between the recorded cell groups; significant satellite peaks in both ACFs and CCFs were taken as indicators of an oscillatory temporal structure. To be flagged as oscillatory, at least one significant satellite peak had to be detected in ACFs or CCFs on either side of the center peak. As a quantitative measure, we computed a relative modulation amplitude (RMA) for center and satellite peaks by calculating the ratio of their amplitude over the offset of the fitted function.

In addition, the fitted function was employed to assess the area of the peaks and troughs of the correlogram modulation, which we used to compute the effect on activity (EoA) and effect on timing (EoT) as shown in Fig. 1. EoA was defined as the difference of peak and trough area divided by the geometric mean of the total number of spikes present in the responses of the two cell groups (GMR, Fig. 1*B*). Thus, EoA represents the fraction of coincidences which are added to the offset in the correlogram. These coincidences are presumed to be due to neuronal interactions, and the spikes involved contribute to an increase of the firing rate of the respective neurons on a short time scale. Effects on a longer time scale (several hundred milliseconds) would result in a change of the offset in the correlogram and are not detected by our methods. EoA is equivalent to the geometric mean of "contribution" and "efficiency" as defined by Levick *et al.* (23), but in contrast to these measures it does not imply asymmetric interactions in the network. For the computation of EoT, the absolute value of EoA was subtracted from the sum of peak and trough areas, which had been normalized with GMR, and the result was divided by 2 (Fig. 1*B*). Mathematically this measure is equivalent to the minimum of either peak area or trough area in the CCF and is related to the "event coherence" as used by Neven and Aertsen (24). In contrast to EoA, EoT describes the part of the correlogram modulation which results from mere shifting of coincidences along the time axis and not from adding coincidences to the offset.

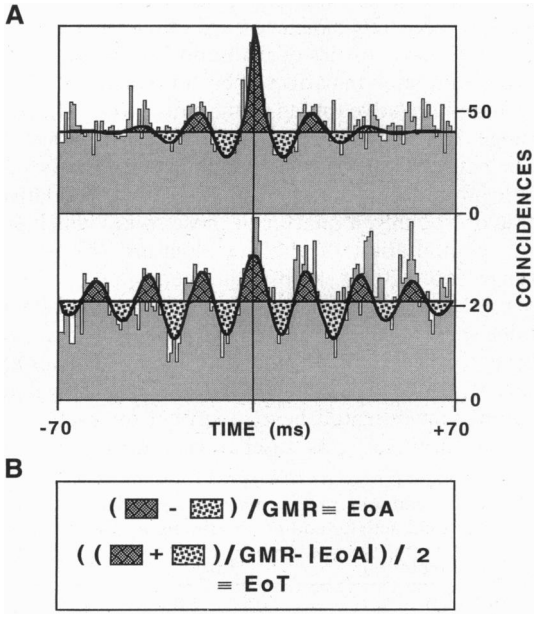

FIG. 1. Computation of EoA and EoT. (*A*) Typical short-range (*Upper*) and long-range (*Lower*) correlograms obtained for cell groups recorded in area 17. The generalized Gabor function (thick continuous line) fitted to the correlograms was used to estimate the surface of peaks (cross-hatched) and troughs (stippled) with respect to the offset of the modulation. (*B*) Definition of EoA and EoT. For details see text.

RESULTS

Two hundred thirty-eight pairs of recording sites were analyzed. To investigate the relation of synchrony and oscillations, short-range interactions (electrode separation ≤2 mm, overlapping receptive fields), long-range interactions (recording distance between 2 and 7 mm, nonoverlapping receptive fields), and interhemispheric interactions were considered separately. For each case, we selected the data set where the best coactivation of the respective cell groups had been achieved. If multiple blocks of 10 trials to the same stimulus were available, these were pooled for the analysis of averaged correlograms. With the fit method described above, each case was tested for the occurrence of a significant center peak in the respective CCF and of significant satellite peaks in both CCF and the respective ACFs. As shown in Table 1, we observed a clear difference between the samples of short- and long-range interactions. Significant short-range synchronization occurred both with and without oscillatory modulation of the CCFs. In contrast, when synchronization was observed over large distances within striate cortex or across the hemispheres, it was almost always accompanied by an oscillatory component in the CCF. Evaluation of oscillatory components in the ACFs revealed a similar relationship. In cases with significant long-range synchronization, the incidence of ACFs showing an oscillatory modulation was much higher than in those without synchronization or in the sample exhibiting short-range synchronization (Table 1). In all cases, the observed oscillations had frequencies in the range 30–70 Hz. These data demonstrate a clear relation between long-range synchronization and oscillatory firing patterns. This observation suggests that the establishment of synchrony between widely separate neuronal populations may indeed be facilitated if these do not discharge their spikes at random, but in a temporally structured manner. The fact that in the two samples with long-range intra-area and interhemispheric synchronization the ACFs were not always

Table 1. Relationship between synchrony and oscillatory activity

Data sample (n)	% oscillatory CCF	% oscillatory ACF
SHORT sync (50)	66	45
SHORT not sync (23)	0	22
LONG sync (21)	100	81
LONG not sync (21)	0	41
INTER sync (61)	95	82
INTER not sync (62)	0	44

SHORT, short-range correlations within area 17; LONG, long-range correlations within area 17; INTER, interhemispheric correlations; osci, at least one significant satellite peak present; sync, significant center peak present. For counting the incidence of oscillatory ACFs, those cases where only one ACF was flagged as oscillatory were weighted with a factor of 0.5.

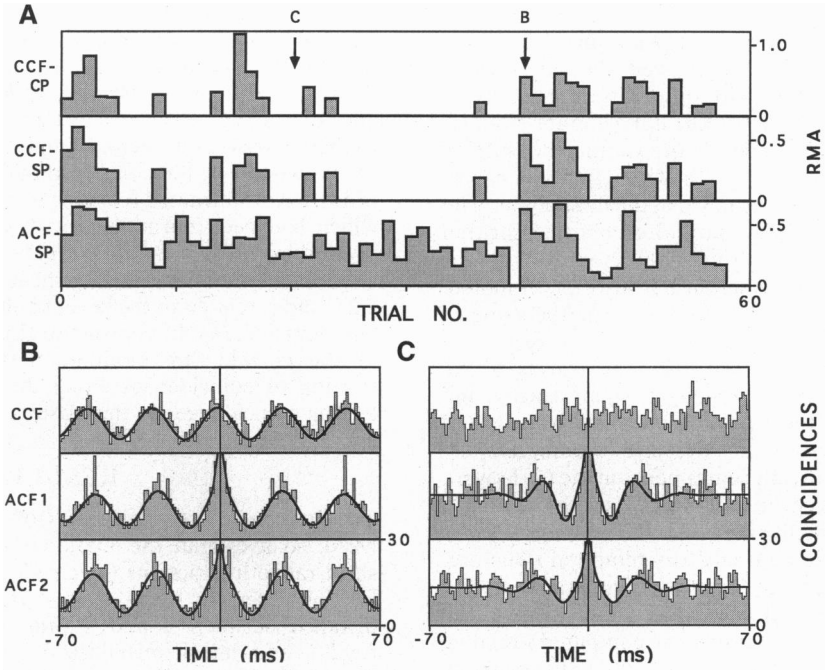

FIG. 2. Single-sweep analysis of interhemispheric interactions. The cells at the two recording sites had the same orientation preference but nonoverlapping receptive fields. For both recording sites, the averaged ACFs (all trials pooled) were flagged as oscillatory. (*A*) Intertrial variability of the RMA of the center peak (CP) (*Top*) and the satellite peak (SP) (*Middle*) of the CCF and of the arithmetic mean of the satellite-peak RMAs in the two respective ACFs (*Bottom*). Note the strong quantitative covariance of CCF-CP with CCF-SP. The arrows indicate two representative trials which are illustrated in *B* and *C*. (*B*) Example of a trial where both cell groups showed narrow-banded oscillations, as indicated by the presence of multiple peaks and troughs in the ACFs (*Middle* and *Bottom*). This is reflected in a strong modulation of the corresponding CCF (*Top*). (*C*) Example of a sweep where no temporal correlation was evident in the CCF (*Top*). The two ACFs (*Middle* and *Bottom*) were still flagged as oscillatory by our rating procedure, but the center peak was flanked by only one satellite peak with a reduced amplitude. Where present, the thick continuous line represents the generalized Gabor function that was fitted to the underlying correlogram.

flagged as oscillatory (Table 1) need not contradict this principal conclusion. Either these ACFs were contaminated by noise and thus failed to pass our significance criteria although they showed some modulation, or the respective responses had been too weak for a reliable assessment of their temporal structure.

In 13 cases exhibiting interhemispheric synchronization the relationship of oscillations and synchrony was, in addition, examined on a trial-by-trial basis. In these cases, 60 consecutive trials had been recorded with similar stimulation. For each trial, the RMA was computed for the center peak and the first satellite peak of the CCF. In addition, we calculated the arithmetic mean of the RMAs of the first satellite peaks in the two respective ACFs. As shown for one of these cases in Fig. 2, this analysis revealed a quantitative relationship between synchrony and oscillatory components (Fig. 2*A*). In this particular example, the ACFs almost always showed at least one significant satellite peak. However, strong correlation between the two recording sites occurred mainly when the ACFs exhibited a strong modulation with more than one satellite peak (Fig. 2*B*). If the temporal structure of the responses happened to be less regular, synchrony between the recorded cells disappeared (Fig. 2*C*). In all 13 cases, the RMAs of the CCF center peaks were clearly correlated with the RMAs of the satellite peaks of both the CCFs and the ACFs. The averaged correlation coefficients were 0.74 ± 0.13 and 0.55 ± 0.06, respectively (mean ± SD). These data clearly indicate that for long-range synchronization there is not only a qualitative relation between synchrony and oscillations but also a quantitative covariance between the strength of synchronization and the degree of rhythmicity of the respective spike trains.

As described in *Materials and Methods* we finally determined whether the interactions between simultaneously activated cell groups affected only the relative timing of their respective discharges (EoT) or whether they actually contributed to the responses of the cells on a short time scale (EoA). Fig. 1*A* shows typical examples of short- and long-range interactions. Usually, in the short-range CCFs the peak area exceeded that of the troughs, whereas in the long-range CCFs the peaks and troughs approximately balanced each other. This observation is reflected in the statistics of EoA and EoT values (Table 2). Short-range interactions affected both the activity of the cell groups and the relative timing of their discharges. In contrast, long-range interactions within striate cortex, which occur between neurons with nonoverlapping receptive fields, had only little influence on the activity but still led to a relative shift in timing of, roughly, a quarter of those spikes which entered into the computation of the correlogram. In the case of long-range interactions across the hemispheres, EoT was clearly predominant. However, also the interhemispheric interactions showed some EoA when the neurons had overlapping receptive fields. When the fields were nonoverlapping, EoA was negligible. Taken together, these data show that in all data samples investigated here, neuronal interactions affect the relative timing of spike discharges and that they may, in

Table 2. Short- and long-range synchronization have different effects on neuronal activity and on the timing of discharges

Data sample (*n*)	EoA	EoT
SHORT (50)	0.22 ± 0.06	0.25 ± 0.03
LONG (21)	0.03 ± 0.01	0.22 ± 0.01
INTER overlap (53)	0.12 ± 0.03	0.36 ± 0.04
INTER no overlap (8)	0.02 ± 0.01	0.27 ± 0.03

Data are means ± SEM. Only cases with significant temporal correlations were included. Overlap, overlapping receptive fields; no overlap, nonoverlapping receptive fields. Other abbreviations are as in Table 1.

addition, change the firing rate of the respective neurons if these have overlapping receptive fields.

DISCUSSION

Our data demonstrate that the occurrence of long-range synchrony in cat visual cortex is associated with oscillatory discharge patterns in the respective cell groups. Some of the earlier studies of neuronal interactions in cat visual cortex (4, 5, 10, 25) did not report such correlations between synchrony and oscillations. For this, several reasons may be considered. First, in two studies crosscorrelograms with additional satellite peaks had actually been observed but were excluded from further analysis because they were considered to be artefactual (5, 25). Second, oscillatory firing patterns may have escaped analysis because of excessive averaging over long sampling periods (10). Averaging tends to blur satellite peaks in CCFs and ACFs because oscillatory activity in the gamma range can show considerable frequency variations even in relatively short data epochs (15, 26). Finally, most studies have actually been confined to short-range interactions at distances below 1 mm (e.g., refs. 4 and 25), in which case significant interactions can occur without concomitant oscillatory firing patterns.

Our result that long-range synchrony is nearly always accompanied by oscillatory firing patterns is compatible with the hypothesis that an oscillatory temporal pattern in neuronal responses may be instrumental for the establishment of long-distance synchrony and, hence, for the binding of distributed neurons into cell assemblies (3, 20). Previously, we have obtained evidence that long-range synchronization is mediated by connections at the cortical level and not by synchronous drive from subcortical afferents (11). Interestingly, long-range synchrony in the cortex occurs consistently with near-zero phase lag (6–11), although the underlying connections, especially those between the two hemispheres, are known to exhibit considerable transmission delays (27). As suggested by simulation studies (19), the establishment of synchrony without phase lag may be facilitated under these conditions if the respective neurons show oscillatory firing patterns. These models demonstrate that, owing to the recurrent temporal structure of such patterns, reciprocally coupled neurons can entrain each other into synchrony within a few oscillatory bursts despite considerable and variable conduction delays of synchronizing connections (19). Furthermore, robust synchrony can even be established across polysynaptically linked cells without adding up of small phase lags. When considered in the context of these modeling studies, the present data suggest that oscillatory firing patterns may indeed be a prerequisite for the establishment of long-range synchrony in the cortex. Apparently, this would not hold for interactions between closely spaced cells (Table 1), since these tend to be strongly coupled without major delays in the respective connections.

However, we wish to emphasize that the potential role of oscillatory firing patterns needs to be substantiated by further experiments. Based on the present data, which merely demonstrate a correlation of synchrony with the appearance of oscillatory firing patterns, we cannot rule out the possibility that synchrony is achieved by other mechanisms which do not require a band-limited temporal structure of neuronal responses. Indeed, this possibility might be inferred from a previous study (28) of sensorimotor synchronization in awake behaving monkeys performing a visual discrimination task. In that study, Bressler *et al.* (28) observed an increased coherence between field potentials recorded from visual and motor areas, which did not only involve the gamma band but also occurred in the alpha and beta range. Although this finding seems at first sight hard to reconcile with the data presented here, we do not believe that it provides a refutation of our hypothesis that band-limited oscillatory signals may facilitate long-range synchronization. First, direct comparison of these results with our data is hampered by the fact that field potential recordings do not reflect spike activity, but mainly dendritic processes, and thus, the results are more difficult to interpret. Second, it seems conceivable that the broad-band coherence observed by Bressler *et al.* does actually result from multiple binding processes occurring in parallel in different frequency bands. Yet for each of these processes some band-limited temporal structure may be required for the establishment of coherence. Finally, evidence in support of our hypothesis has been obtained by another group using a similar sensorimotor paradigm in awake behaving monkeys. Extending their earlier work (16), Murthy and Fetz have recently observed that synchrony between somatosensory and motor sites as well as between motor areas of different hemispheres occurs only during episodes of oscillatory neuronal firing (V. N. Murthy and E. E. Fetz, personal communication). However, further experiments are clearly required to elucidate the potential role of oscillatory activity. With respect to the visual modality, the present results need to be complemented by studies in awake behaving animals, where band-limited neuronal oscillations should occur with prevalence when the animal successfully binds features over large distances in the visual field.

Interestingly, in our data sample the oscillations associated with long-range synchrony always showed frequencies in the gamma range. If our hypothesis about the potential role of oscillatory firing patterns turns out to be correct, several theoretical arguments could be forwarded to explain why the oscillations required for the establishment of cell assemblies in sensory systems should be in the gamma range (20). Psychophysical studies indicate that scene segmentation and binding of the features of complex objects can be accomplished within 100–200 ms (29). If binding is achieved by synchronization and if oscillatory activity is instrumental in establishment of synchrony, a sufficient number of oscillatory cycles must be accommodated in this time span. This imposes a lower limit to the oscillation frequency, and oscillatory activity with frequencies in the alpha or beta range would be too slow to establish synchrony within the available time. On the other hand, the modeling studies indicate that the oscillations must not be too fast, either. They show that reciprocally coupled oscillators can be synchronized only if the conduction delays in the network do not exceed about one-third of the average period time (19). For much larger delays, zero-phase synchrony cannot be established. Given this constraint and the known coupling delays, transcallosal synchronization and other long-range interactions could presumably not be achieved if the neurons were oscillating at frequencies above 80 or 90 Hz. Taken together, these considerations suggest that, if oscillations do indeed facilitate long-range synchrony, gamma frequencies would seem most appropriate for the establishment of sensory representations.

It should be noted, however, that the potential contribution of oscillations to the establishment of synchrony does not imply that the occurrence of these discharge patterns would alone be sufficient to achieve synchrony. Previous studies have disclosed a number of additional factors, such as the coherence of visual stimuli, the proximity of receptive fields, or the similarity of response properties, which all influence the temporal correlation between responses of spatially separate neurons (7, 8, 12). Changes in synchronization probability among pairs of neurons are not necessarily associated with changes of oscillatory firing patterns, and it is not possible to infer from the presence of oscillatory firing patterns as such whether spatially separate cells discharge in synchrony. However, it should be emphasized that this argument applies specifically to microelectrode studies, which assess responses of only a small number of cells. The situation is different for recordings of mass activity such as electro- or magnetoencephalography (17, 18). Since these recordings reveal the

summed activity of many neurons, the occurrence of event-related gamma components always implies that large neuronal populations have synchronized their activities.

The results of the present study indicate also that short-range interactions within the primary visual cortex affect both the firing rate and the relative timing of discharges, whereas only the latter is influenced by long-range interactions. That interhemispheric interactions also show some effect on the firing rate when the recorded neurons have overlapping receptive fields suggests that the strength of EoA is primarily related to the retinotopic neighborhood, rather than to the average conduction delays in the underlying network. In teleological terms, it makes sense that interactions between neurons with overlapping receptive fields affect their mean activity, since these interactions contribute to the shaping of receptive-field properties (30). Indeed, this holds also true for those callosal projections (31) which link neurons with receptive fields contiguous or overlapping at the midline of the visual field. In contrast, interactions from outside of the classical receptive field, by definition, exert only a weak modulatory influence on the response strength, which is often only measurable when the whole surround is massively stimulated (32). As predicted by our hypothesis, such long-range interactions may rather serve for the binding of distributed neurons into coherently active assemblies (1, 3). Since this is assumed to occur by response synchronization, the principal function of long-distance interactions should indeed be to influence the relative timing of spikes rather than the amplitude of responses, as confirmed by the present data.

In conclusion, the results of this study suggest that fast oscillations of neocortical responses may not be a mere epiphenomenon of cortical processing. The oscillations as such do not seem to represent particular features of the visual stimuli, since they vary only slightly with changes of stimulus parameters such as length or orientation (33). However, these firing patterns may facilitate the establishment of synchrony over large distances in the cortex, and they provide one way to allow for interactions which change temporal relations between discharges without affecting response amplitudes. Thus, oscillatory firing patterns may be well suited as a "carrier signal" for the establishment of long-distance synchronization and, hence, may be crucial for the binding of widely distributed neurons into coherently active assemblies.

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