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# SHORT COMMUNICATION

# Oscillatory Neuronal Responses in the Visual Cortex of the Awake Macaque Monkey

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## Abstract

An important step in early visual processing is the segmentation of scenes. Features constituting individual objects have to be grouped together and segregated from those of other figures or the background. It has been proposed that this grouping could be achieved by synchronizing the fine temporal structure of responses from neurons excited by an individual figure. In the cat visual cortex evidence has been obtained that responses of feature-selective neurons have a distinctive oscillatory structure and can synchronize both within and across cortical areas, the synchronization depending on stimulus configuration. Here we investigate the generality of oscillatory responses and their synchronization and specifically whether these phenomena occur in extrastriate areas of the visual cortex of the awake behaving primate. We find in the caudal superior temporal sulcus of the macaque monkey (*Macaca fascicularis*) that adjacent neurons can synchronize their responses, in which case their discharges exhibit an oscillatory temporal structure. During such periods of local synchrony spatially separated cell groups can also synchronize their responses if activated with a single stimulus. These findings resemble those described previously for the cat visual cortex, except that in the awake monkey the oscillatory episodes tend to be of shorter duration and exhibit more variability of oscillation frequency.

## Introduction

At an early stage of visual processing the information contained in a visual scene is represented by the responses of feature-selective neurons which are distributed over numerous areas of the visual cortex. These responses signal the presence and location of particular features of the visual scene. It is commonly held that the next step in pattern analysis consists of a grouping operation whereby features constituting a particular figure or object are bound together and get segregated from features belonging to other objects or the embedding background. Based on theoretical considerations it has been proposed that such feature-binding could be accomplished by synchronizing the responses of neurons which are activated by the same figure (von der Malsburg, 1985). The cells encoding a particular figure would thus be distinguished by the temporal coherence of their responses. Compatible with this concept is the recent observation that feature-selective neurons in the visual cortex of anaesthetized cats exhibit oscillatory responses in the range of 30–60 Hz (Gray and Singer, 1989) which can become synchronized both within (Gray *et al.*, 1989; Engel *et al.*, 1990a) and across cortical areas (Eckhorn *et al.*, 1988; Engel *et al.*, 1991a,c). In agreement with the binding hypothesis the strength of synchronization between oscillating cells depends critically on the configuration of the stimuli used to activate the neurons. If cells are activated by contours which, according to common gestaltcriteria, appear as parts of a single figure, they synchronize their responses while cells activated by independent stimuli show less or no response synchronization (Gray *et al.*, 1989; Engel *et al.*, 1990b, 1991b).

If this phenomenon of response synchronization is of functional relevance in cortical processing two predictions follow: First, it should occur also in the visual cortex of non-anaesthetized animals while they are alert and engaged in visually guided behaviour. Second, it should not be confined to the visual cortex of cats. To test these predictions we recorded with multi-electrode arrays from the caudal superior temporal sulcus of an awake, behaving macaque monkey and analysed multi-unit responses to moving light stimuli with auto- and cross-correlation techniques.

## Materials and methods

One male macaque monkey (*Macaca fascicularis*) was trained to maintain fixation of a light spot for up to 6 s and to signal the dimming of the fixation spot (0.2° diameter) within a predetermined interval (0.6 s). Behavioural paradigm and training procedures were similar to those described by Wurtz (1969).

After completion of training the monkey was prepared for chronic recording. For the implantation of the recording chamber anaesthesia was induced with an i.m. injection of Ketamine (10 mg/kg) and after tracheal intubation continued with Halothane and nitrous oxide.

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Postoperative treatment included local and systemic application of antibiotics for 5 days. All surgical procedures were performed in accordance with the guidelines for the welfare of experimental animals issued by the Federal Government of Germany.

Within recording sessions, which lasted for ~5 h, the monkey's head was fixed and eye movements were monitored with an infrared eye tracking system. Visual fixation had to be maintained for 4–6 s. Single electrodes or a linear array of two to three glass insulated platinum iridium (Wolbarth *et al.*, 1960) or elgiloy (Suzuki and Azuma, 1976) electrodes with fixed tip separations of 0.33–1.3 mm were used to record multi-unit activity from the caudal superior temporal sulcus. The electrodes were introduced approximately perpendicular to the surface of the brain in a region close to the foveal representation in V1/V2 and the adjoining prelunate gyrus. If electrode arrays were used the plane of the array was oriented roughly in parallel to the superior temporal sulcus to maximize the distance between sites along the tangential extent of the cortex. Since the analysis of the temporal structure of spike trains is often incompatible with averaging, we restricted analysis to recording sites which exhibited vigorous responses to moving light stimuli and provided sufficient spike counts to allow for a trial by trial analysis. For quantitative evaluation of neuronal responses single moving light bars were generated whose location, size and motion parameters were adjusted to evoke maximal responses at a particular recording site. Their dimensions varied from 0.3° × 3° to 2° × 12° and their velocity from 2°/s to 30°/s. Direction of stimulus motion was always orthogonal to the long axis of the light bar. Whenever possible, we tried to elicit simultaneous responses from different sites with a single light stimulus. In this case stimulus orientation and direction of motion were often suboptimal for any of the simultaneously recorded cell groups. A particular stimulus was repeated at least 5 times. Data were rejected when the monkey abandoned fixation before the end of stimulation. Light stimuli including the fixation spot were generated on a CRT display located 57 cm in front of the monkey's head. The CRT subtended a visual angle of 35° × 27° and operated with a frame rate of 80 Hz (non-interlaced), which is well above the temporal resolution of monkey retinal ganglion cells (Boynton and Baron, 1975). Control measurements were made with stimuli provided by an optical bench system and a DC driven light source. The luminance of the background and of the stimuli was $<0.1$ cd/m$^2$ and 0.9–4.1 cd/m$^2$, respectively. For the collection of multi-unit activity the appropriately amplified signals were band pass filtered from 1 to 3 kHz and fed to Schmitt triggers whose thresholds were set to at least 2 times the amplitude of the noise. The resulting pulse sequences were digitized at a rate of 1 kHz and stored on disk.

To describe oscillatory response patterns quantitatively, auto-correlograms averaging over all trials were computed in 500, 700, and 1000 ms windows to avoid lumping together response epochs with differing temporal structure. To cover the whole response period, multiple overlapping windows were shifted over the response in 100 ms steps. The resulting auto-correlograms were fitted with a Gabor function as described in detail elsewhere (Engel *et al.*, 1990a). A response was considered as containing regular oscillations if the Gabor functions in at least two windows of at least one of the three window types fulfilled the following criteria: (i) The amplitude of the modulation had to be significantly greater than zero at the 5% level; (ii) The decay constant of the Gabor function had to be $>0.8$ times the period of the frequency; (iii) The amplitude of the Gabor function had to be $>0.104$ times the offset of the auto-correlogram plus a constant (5 for 500 ms windows; 4 for 700 and 1000 ms windows; all computations in total amount of spikes). The possibility of a false positive classification by bad fitting was excluded by visual inspection of the correlograms and the corresponding shift-predictors (Perkel *et al.*, 1967). As we recorded multi-unit activity, these auto-correlograms indicate not only whether responses have a periodic temporal structure but also whether the simultaneously recorded units discharge in synchrony. Thus, auto-correlograms exhibiting a centre peak broader than the centre bin and flanked by a deep trough indicate that the simultaneously recorded cells have synchronized their activity. If such correlograms exhibit in addition equally spaced side peaks, it can be further inferred that the synchronous activity comprised sequences of regular oscillations. To assess synchronization between responses recorded from different electrodes we computed cross-correlograms between the respective spike trains for windows of 700 ms duration that were centred on the overlapping part of the responses, and identified those with clear peaks and flat shift-predictors.

## Results

Data for quantitative evaluation were taken from 71 sites in 25 tracks through the caudal superior temporal sulcus. The receptive fields of the investigated neurons were all confined to the hemifield contralateral to the recorded hemisphere and had eccentricities of $<20°$. Their size (largest diameter) ranged from 0.5 to 22° and >90% were direction selective. These receptive field properties and the characteristic sequence of response properties of the different visual areas encountered along the electrode penetrations indicate that most of the recording sites were in the motion sensitive area MT and eventually a few in the adjoining areas MST and FST (Van Essen *et al.*, 1981; Desimone and Ungerleider, 1986).

At the majority of recording sites the light-evoked responses contained episodes characterized by grouped discharges which followed at rather regular intervals of 15–35 ms. This grouping resulted from the tendency of different cells recorded from the same electrode to discharge simultaneously with brief bursts or single spikes (Fig. 1 A,B). Response sequences characterized by such a periodic pattern of grouped discharges occurred several times during the whole response period, each sequence lasting for ~100–300 ms. Accordingly, auto-correlograms computed from such response sequences showed an oscillatory modulation. In order to compare the present results with those from anaesthetized cats we averaged the auto-correlograms obtained in the same window from five or ten successive responses and evaluated the oscillatory modulation of these averaged correlograms (Fig. 1C–F) with a method similar to that applied previously to data from cat [see Materials and methods and Engel *et al.* (1990a)]. According to these criteria responses from 41 (58%) of the recording sites gave auto-correlograms with a significant oscillatory modulation indicating that the simultaneously recorded units had synchronized their discharges and that these synchronized discharges occurred at rather regular intervals. Oscillation frequencies ranged from 30 to 60 Hz (average 46.1 ± 8.9 Hz).

However, oscillatory responses are more frequent than suggested by the evaluation of averaged auto-correlograms. Oscillatory response episodes were often of short duration ($<300$ ms), did not occur on each trial and could vary in their oscillation frequency both within and between trials. In these cases, averaging across trials led to blurring of the sidepeaks and troughs of the auto-correlograms (Fig. 2A,B). As illustrated in Figure 2 C,D interburst intervals could vary even within individual oscillatory episodes. The spike trains shown in Figure 2 C,D closely resemble those in Figure 1A,B with respect to the synchronization of spikes from different cells and the repetitive character of these grouped discharges. Accordingly, the auto-correlograms possess a broad centre peak and flanking troughs, features which are characteristic for

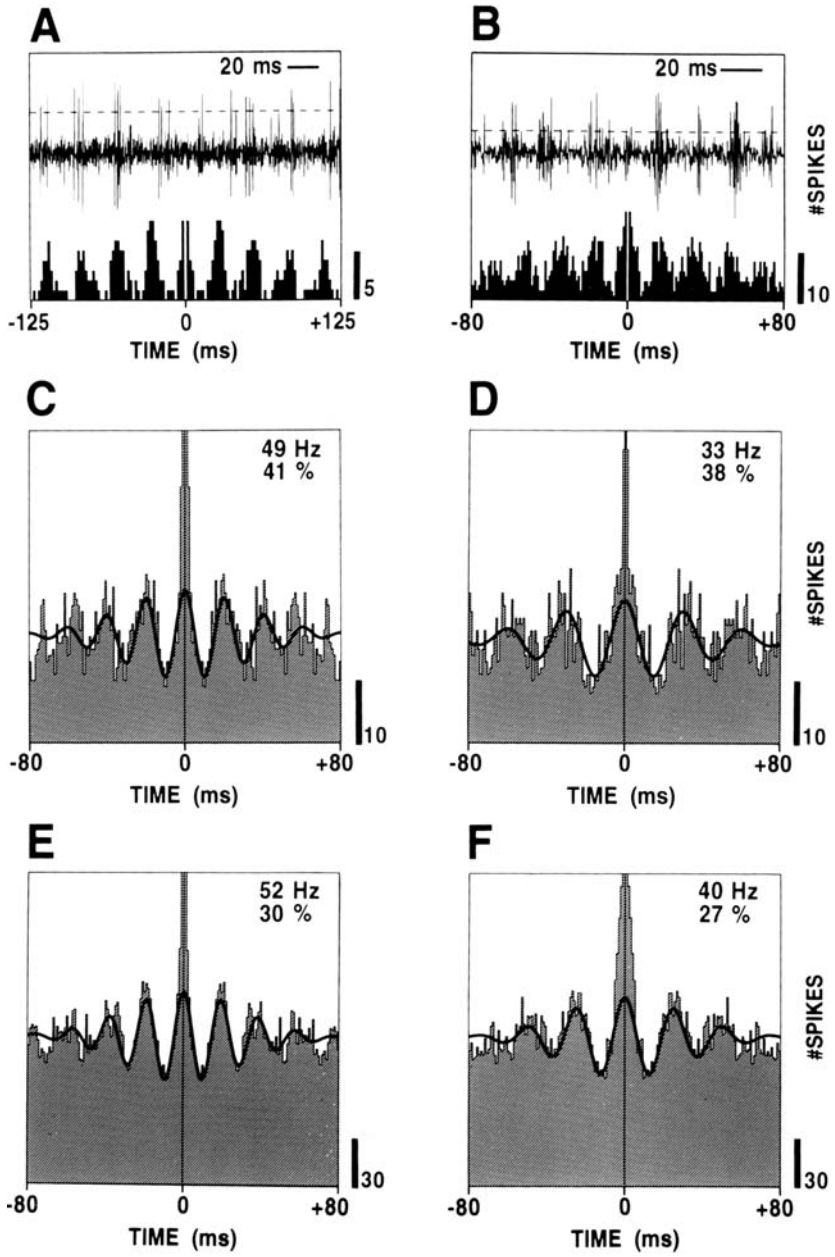


FIG. 1. (A,B) Two examples of spike trains from response episodes with an oscillatory discharge pattern (upper trace) and corresponding auto-correlograms (lower trace). The dashed line indicates the trigger level. (C–F) Auto-correlograms of oscillatory response episodes within a 500 ms (C–E) and 800 ms window (F) averaged over five (D–F) or 10 (C) trials. Recordings in (A–F) are from six different sites.

synchronized multi-unit activity. However, due to the jitter of intervals between the multi-unit bursts, the auto-correlograms lack periodic sidepeaks. Nevertheless, these response episodes have to be addressed as oscillatory. They are simply somewhat less regular and stable than those leading to multiple sidepeaks in averaged auto-correlograms.

For the cross-correlation analysis of responses recorded from different electrodes we selected cases where simultaneous responses could be evoked at both sites with a single stimulus ($n = 15$) (Fig. 3 A,B,G,H). In 11 out of these cases the average cross-correlograms showed a clear peak, indicating that the spike trains recorded from the two locations were correlated. This peak had a half width of 5–10 ms and was centred around zero phase indicating that the correlated events had occurred essentially without a phase lag (Fig. 3 E,L). This synchronization was not due to phase locking of the individual responses to the stimulus because it was no longer visible in the shift-predictor (Perkel *et al.*, 1967) (Fig. 3 F,M), i.e. the cross-correlograms computed between responses to successively presented stimuli were flat. As exemplified in Figure 3, some cross-correlograms showed in addition signs of a periodic modulation and in most cross-correlograms the centre peak was flanked by troughs. The latter indicates that during the epochs where the responses at the two sites were synchronized, the multi-unit activities at the respective sites exhibited the characteristic synchronous oscillations

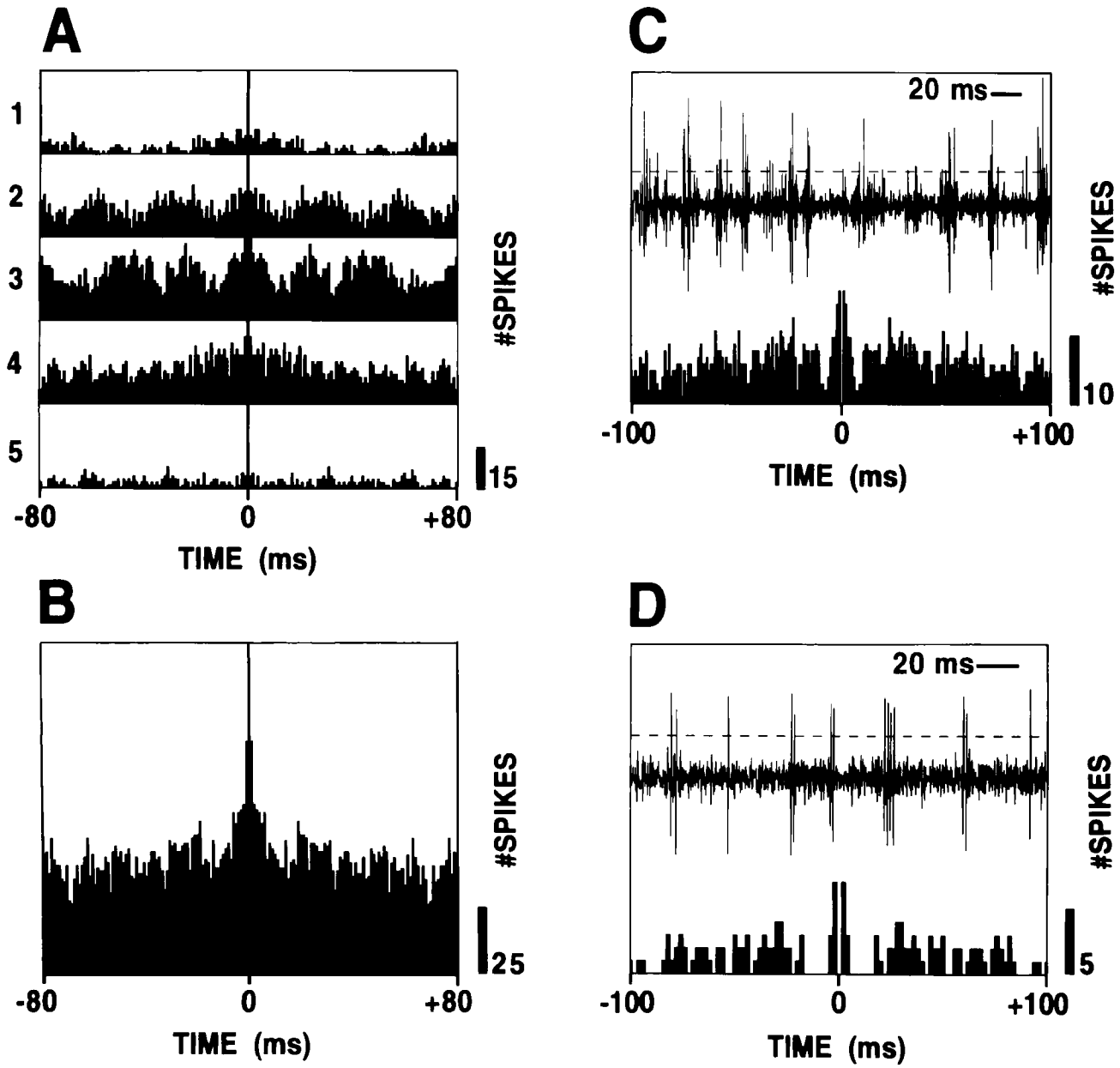


FIG. 2. Frequency variability in oscillatory spike trains. (A)1 – 5 Auto-correlograms computed from the same 500 ms long response segments for five successive trials. (B) Sum of the auto-correlograms (A1 – 5). The oscillatory modulation apparent in the auto-correlations from single sweeps is lost in the average. (C,D) Examples of frequency variability within individual oscillatory response episodes from two different recording sites. The clustered occurrence of the spikes is reflected in the auto-correlograms by broad centre peaks and adjacent troughs but due to variable intervals between clusters the auto-correlograms show no periodic modulation.

illustrated in Figures 1 and 2. In cases where the correlograms exhibited additional side peaks the synchronous discharges of the local cell groups must furthermore have occurred at regular intervals. The respective auto-correlograms are compatible with this interpretation. They have a broad centre peak which is flanked by a trough and they exhibit indications of an oscillatory modulation.

## Discussion

The results of this study demonstrate for the first time that in the caudal superior temporal sulcus of awake, behaving monkeys neurons spaced sufficiently close to be recorded with a single electrode can synchronize their responses when presented with their preferred stimulus. In multi-unit recordings this synchronization was reflected by repeated groups of simultaneous discharges which occurred at rather regular intervals. These episodes of synchronized activity often lasted for only 100 to 300 ms and could occur several times during a single stimulus passage. The average interval between successive bursts was in the range of 23 ms which is equivalent to an oscillation frequency of ~ 45 Hz. But there was substantial variability of interburst intervals, both within and between responses to the same stimulus. In addition to these indications for local synchronization we obtained evidence from multi-electrode recordings

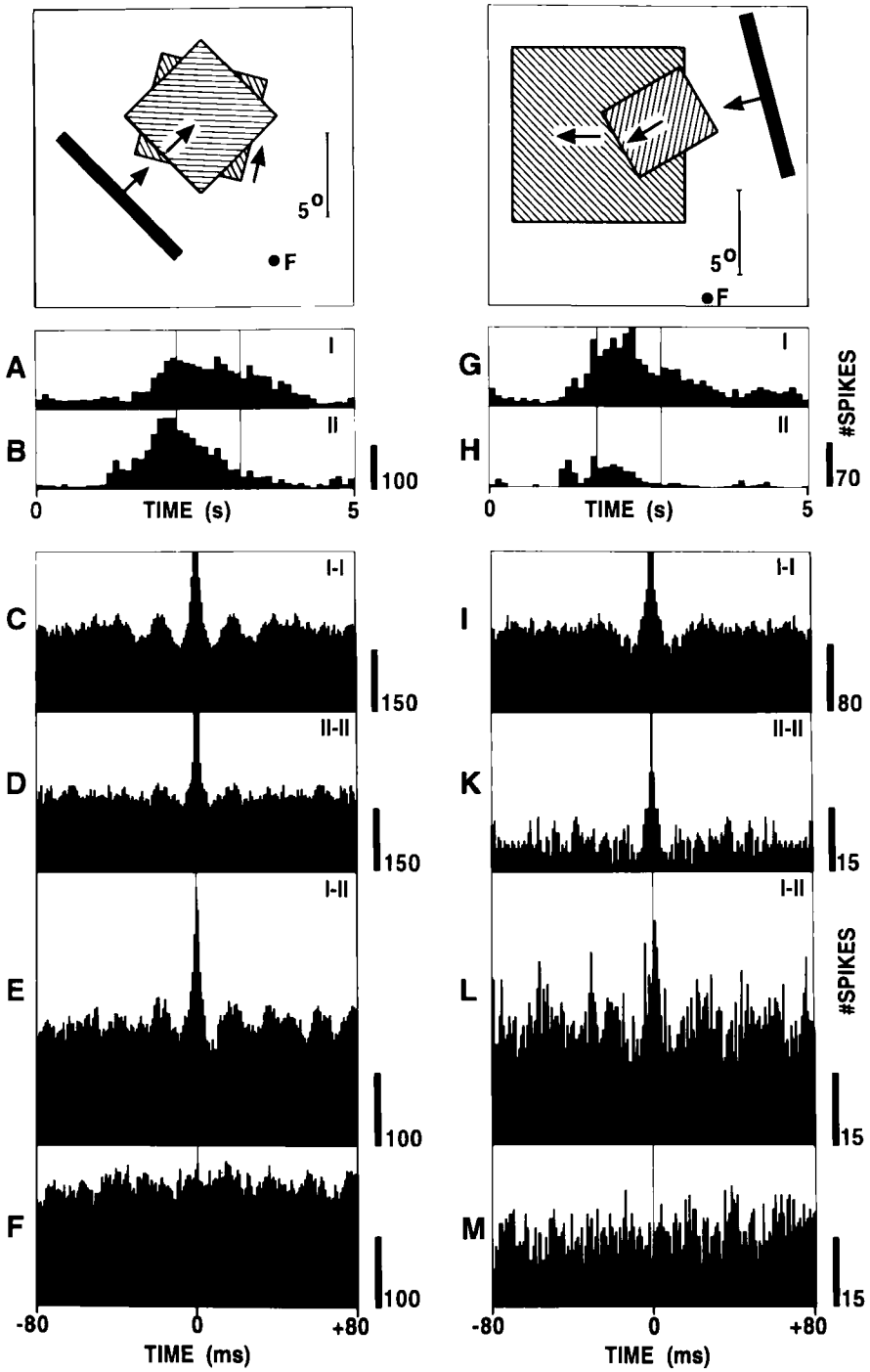


FIG. 3. Cross-correlation between spike trains recorded from two different electrodes spaced at 0.33 mm (left column) and 1.3 mm (right column). The graphs at the top show the position of the RFs relative to the fovea and the stimulus. Little arrows in the RFs indicate preferred direction of movement. (A,B) and (G,H) show the post-stimulus time histograms for the corresponding responses to forward movements of the stimulus. (C,D) and (I,K) show the average auto-correlograms and (E,L) the average cross-correlograms for the response segments in the window indicated by the vertical lines in (A,B) and (G,H), respectively. (F,M) shift-predictor cross-correlograms computed from responses to successive stimuli.

that spatially segregated cells can also synchronize their respective responses at a fine time scale of milliseconds when activated simultaneously with the same stimulus. This synchronization over distance seems to occur mainly when the respective local cell groups engage in synchronous oscillatory activity but it does not appear to be a prerequisite either for local or for distant synchronization that the oscillation frequency remains constant throughout the sequence of grouped discharges. Thus, with respect to the occurrence of synchronized episodes in the responses of both adjacent and spatially segregated cell groups the present data closely resemble those obtained previously from

anaesthetized cats (Gray and Singer, 1989; Gray *et al.*, 1990; Engel *et al.*, 1990a). However, as we applied only single stimuli in the present study we cannot tell whether the observed response synchronization in MT of the awake macaque is sensitive to changes in stimulus configuration.

Until now only a few multi-electrode studies have been performed in search for correlated neuronal responses in monkey visual cortex. Ts'o and Gilbert (1988) found correlations between the responses of spatially segregated neurons in V1 of anaesthetized monkeys. These correlations occurred preferentially between cells showing the same feature preference. Because the peaks in the correlograms were centred around zero the obtained correlations were attributed to common input. As the purpose of the study was the search for a physiological correlate of the anatomically demonstrated selective intracortical connections (Livingstone and Hubel, 1984) no attempts were made to determine whether response synchronization depended on stimulus configuration. Recently Livingstone (1991) performed cross-correlation analysis in V1 of anaesthetized Saimiri monkeys confirming some of the phenomena of response synchronization described previously for the cat. Similarities included the tendency of neurons to engage in rhythmic discharge patterns and to synchronize their responses if activated with coherently moving stimuli.

The only conspicuous difference between the awake, behaving monkey and the anaesthetized cat is that in the former the episodes of synchronous activity are shorter and exhibit a higher variability of oscillation frequencies than in the latter. This difference was not unexpected since systems dynamics is likely to be more complex in a performing than in an anaesthetized brain. The binding hypothesis even predicts that during visual processing synchronization and desynchronization of responses should occur at a time scale of a few hundred milliseconds at most because pattern specific states of neuronal assemblies should change at least at the rate at which saccades can be performed and different successive images processed. This rate is estimated to be in the order of 5/s. As a consequence, individual cells or groups of cells must be able to rapidly switch between different assemblies (Singer, 1990). This will in most instances require rapid phase shifts leading to variable interburst-intervals of individual oscillatory responses. In this context it needs to be emphasized that regular oscillations, i.e. fixed interburst intervals in the respective spike trains, are by no means a necessary prerequisite for binding by synchronization (Crick, 1984; von der Malsburg, 1985; Abeles, 1982). On the contrary, the instabilities observed in the frequency domain may actually be advantageous for several reasons. First, networks capable of engaging in synchronous activity tend to enter states of total coherence which are inappropriate for information processing. In artificial systems this problem is usually circumvented by adding noise in the amplitude domain (von der Malsburg and Schneider, 1986; Sporns *et al.*, 1989). An alternative possibility is to introduce noise in the frequency domain (Sompolinsky *et al.*, 1990), or to implement mechanisms for active desynchronization (Schillen and König, 1991). This introduces instabilities in the frequency domain and has the additional advantage of preserving amplitude coded information from degradation by noise. Second, if cell assemblies engaged always in oscillatory modes with similar and time invariant frequency, aliasing phenomena would lead to strong but accidental correlations between neurons participating in different, simultaneously active assemblies. This would substantially reduce the number of assemblies that can be generated simultaneously without becoming confounded.

Evidence for oscillatory activity in the gamma-range has been obtained previously with EEG-recordings from awake cats (Bouyer *et al.*, 1987), monkeys (Rougeul *et al.*, 1979; Freeman and van Dijk, 1987) and humans (Sheer, 1989). The fact that such activity was visible in field potential recordings indicates that large numbers of neurons must have synchronized their activities in this frequency range. The same conclusion must be drawn from the recent observation that large amplitude oscillatory field potentials occur in the 30 Hz range in the somatosensory and motor cortex of monkeys when they perform a novel and difficult grasping movement (Murthy and Fetz, 1991). This finding is particularly intriguing as these oscillatory signals can synchronize between the two cortical areas and hence between recording sites which are more than a centimetre apart. The present results provide direct evidence for such synchronization phenomena at the single cell level by demonstrating that spatially segregated neurons in the visual cortex of an awake, behaving primate can synchronize their respective oscillatory responses to visual stimuli. Thus, our data are compatible with the conjecture derived from previous measurements in anaesthetized cats that response synchronization in the millisecond range might serve as a mechanism for feature binding and perceptual grouping (Gray *et al.*, 1989; Engel *et al.*, 1990b, 1991b). The fact that such synchronization occurs also in a cortical area remote from primary visual cortex may be taken as indication for the generality of the phenomenon. It is compatible with the proposal that synchronization of temporally structured responses at a fine time scale could serve as a basic binding mechanism to establish relations between distributed neuronal responses (Singer, 1990; Crick, 1984; Damasio, 1989).

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## References

Abeles, M. (1982) *Local Cortical Circuits*. Springer-Verlag, Berlin Heidelberg New York.

Bouyer, J. J., Montaron, M. F., Vahnée, J. M., Albert, M. P. and Rougeul, A. (1987) Anatomical localization of cortical beta rhythms in cat. *Neuroscience*, **22**, 863–869.

Boynton, R. M. and Baron, W. S. (1975) Sinusoidal flicker characteristics of primate cones in response to heterochromatic stimuli. *J. Opt. Soc. Am.*, **65**, 1091–1100.

Crick, F. (1984) Function of the thalamic reticular complex: the search light hypothesis. *Proc. Natl. Acad. Sci. USA*, **81**, 4586–4590.

Damasio, A. R. (1989) The brain binds entities and events by multiregional activation from convergence zones. *Neural Computation*, **1**, 123–132.

Desimone, R. and Ungerleider, L. G. (1986) Multiple visual areas in the caudal superior temporal sulcus of the macaque. *J. Comp. Neurol.*, **248**, 164–189.

Eckhorn, R., Bauer, R., Jordan, W., Brosch, M., Kruse, W., Munk, M. and Reitboeck, H. J. (1988) Coherent oscillations: a mechanism of feature linking in the visual cortex? *Biol. Cybern.*, **60**, 121–130.

Engel, A. K., König, P., Gray, C. M. and Singer, W. (1990a) Stimulus-dependent neuronal oscillations in cat visual cortex: intercolumnar interaction as determined by cross-correlation analysis. *Eur. J. Neurosci.*, **2**, 588–606.

Engel, A. K., König, P., Gray, C. M. and Singer, W. (1990b) Synchronization of oscillatory responses: a mechanism for stimulus-dependent assembly formation in cat visual cortex. In Eckmiller, R., Hartmann, G. and Hauske, G. (eds), *Parallel Processing in Neural Systems and Computers*. Elsevier Science Publishers B.V., North Holland, Amsterdam, pp. 105–108.

Engel, A. K., König, P., Kreiter, A. K. and Singer, W. (1991a) Interhemispheric synchronization of oscillatory neuronal responses in cat visual cortex. *Science*, **252**, 1177–1179.

Engel, A. K., König, P. and Singer, W. (1991b) Direct physiological evidence for scene segmentation by temporal coding. *Proc. Natl. Acad. Sci. USA*, **88**,

9136–9140.

Engel, A. K., Kreiter, A. K., König, P. and Singer, W. (1991c) Synchronization of oscillatory neuronal responses between striate and extrastriate visual cortical areas of the cat. *Proc. Natl. Acad. Sci. USA*, **88**, 6048–6052.

Freeman, W. J. and van Dijk, B. W. (1987) Spatial patterns of visual cortical fast eeg during conditioned reflex in a rhesus monkey. *Brain Res.*, **422**, 267–276.

Gray, C. M. and Singer, W. (1989) Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex. *Proc. Natl. Acad. Sci. USA*, **86**, 1698–1702.

Gray, C. M., König, P., Engel, A. K. and Singer, W. (1989) Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus patterns. *Nature*, **338**, 334–337.

Gray, C. M., Engel, A. K., König, P. and Singer, W. (1990) Stimulus-dependent neuronal oscillations in cat visual cortex: receptive field properties and feature dependence. *Eur. J. Neurosci.*, **2**, 607–619.

Livingstone, M. S. (1991) Visually-evoked oscillations in monkey striate cortex. *Soc. Neurosci. Abstr.*, **17**, 176.(Abstract)

Livingstone, M. S. and Hubel, D. H. (1984) Specificity of intrinsic connections in primate primary visual cortex. *J. Neurosci.*, **4**, 2830–2835.

Murthy, V. N. and Fetz, E. E. (1991) Synchronized 25–35 Hz oscillations in sensorimotor cortex of awake monkeys. *Soc. Neurosci. Abstr.*, **17**, 310.(Abstract)

Perkel, D. H., Gerstein, G. L. and Moore, G. P. (1967) Neuronal spike trains and stochastic point processes II. Simultaneous spike trains. *Biophys. J.*, **7**, 419–440.

Rougeul, A., Bouyer, J. J., Dedet, L. and Debray, O. (1979) Fast somato-parietal rhythms during combined focal attention and immobility in baboon and squirrel monkey. *Electroenceph. Clin. Neurophysiol.*, **46**, 310–319.

Schillen, T. B. and König, P. (1991) Stimulus-dependent assembly formation of oscillatory responses: II. Desynchronization. *Neural Computation*, **3**, 167–177.

Sheer, D. E. (1989) Sensory and cognitive 40-Hz event related potentials: behavioral correlates, brain function, and clinical application. In Basar, E. and Bullock, T. H. (eds), *Brain Dynamics*. Springer-Verlag, Berlin Heidelberg New York, pp. 339–374.

Singer, W. (1990) Search for coherence: a basic principle of cortical self-organization. *Concepts Neurosci.*, **1**, 1–26.

Sompolinsky, H., Golomb, D. and Kleinfeld, D. (1990) Global processing of visual stimuli in a neural network of coupled oscillators. *Proc. Natl. Acad. Sci. USA*, **87**, 7200–7204.

Sporns, O., Gally, J. A., Reeke, G. N., Jr and Edelman, G. M. (1989) Reentrant signaling among simulated neuronal groups leads to coherency in their oscillatory activity. *Proc. Natl. Acad. Sci. USA*, **86**, 7265–7269.

Suzuki, H. and Azuma, M. (1976) A glass-insulated 'elgiloy' microelectrode for recording unit activity in chronic monkey experiments. *Electroenceph. Clin. Neurophysiol.*, **41**, 93–95.

Ts'o, D. Y. and Gilbert, C. D. (1988) The organization of chromatic and spatial interactions in the primate striate cortex. *J. Neurosci.*, **8**, 1712–1727.

Van Essen, D. C., Maunsell, J. H. R. and Bixby, J. L. (1981) The middle temporal visual area in the macaque: myeloarchitecture, connections, functional properties and topographic organization. *J. Comp. Neurol.*, **199**, 293–326.

von der Malsburg, C. (1985) Nervous structures with dynamical links. *Ber. Bunsenges. Phys. Chem.*, **89**, 703–710.

von der Malsburg, C. and Schneider, W. (1986) A neural cocktail-party processor. *Biol. Cybern.*, **54**, 29–40.

Wolbarth, M. L., MacNichol, E. F., Jr and Wagner, H. G. (1960) Glass insulated platinum microelectrode. *Science*, **132**, 1309–1310.

Wurtz, R. H. (1969) Visual receptive fields of striate cortex neurons in awake monkeys. *J. Neurophysiol.*, **32**, 727–742.