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RESEARCH ARTICLE

Wolfgang Kruse · Klaus-Peter Hoffmann

Fast gamma oscillations in areas MT and MST occur during visual stimulation, but not during visually guided manual tracking

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Abstract We studied the incidence of oscillatory activity in the gamma range (35–110 Hz) in single cell and multi-unit activity recorded from extrastriate areas MT (middle temporal) and MST (superior middle temporal) while rhesus monkeys performed different behavioural tasks. During full field stimulation by coherent motion of random dots, we observed gamma oscillations in approximately 20% of the cells. The average oscillation frequencies differed considerably between both animals (60 Hz vs 100 Hz). In both animals, oscillatory modulation was particularly strong at sites that showed a strong directional bias to visual stimulation. The amount of oscillatory activity was roughly the same whether stimulus movement was presented during fixation or whether the animal had to perform pursuit movements across a stationary visual pattern. If cells were engaged in gamma oscillations during visual stimulation, the amount of oscillatory modulation was dependent on stimulus direction, stimulus velocity and stimulus contrast. During a visually guided manual tracking task no gamma activity was detectable. Cells with clear oscillatory modulation during the full field stimulation failed to show oscillatory activity when the animal was involved in a motor task in which the visual motion information had to be evaluated for the correct movement of the hand. Our results reaffirm the ubiquitous presence of stimulus-induced gamma oscillation in extrastriate areas MT and MST of the awake monkey during various stimulus conditions, but they fail to support the notion that high-frequency gamma oscillations in this area play a specific role during cortical control of a motor response to visual stimulation.

Keywords Gamma oscillations · Extrastriate cortex; Synchronization · Macaque monkey · Motor task

W. Kruse (✉) · K.-P. Hoffmann
Department of Zoology and Neurobiology,
Ruhr-University Bochum, ND7, 44780 Bochum, Germany
e-mail: kruse@neurobiologie.ruhr-uni-bochum.de
Tel.: +49-234-3228973
Fax: +49-234-3214278

Introduction

The areas MT (middle temporal) and MST (superior middle temporal) located in the "dorsal pathway" of the primate brain are specialized in the processing of visual motion information. Neurons in these areas are highly sensitive for the direction of motion (Dubner and Zeki 1971; Zeki 1974; van Essen et al. 1981; Maunsell and van Essen 1983a, 1983b; Tanaka et al. 1986). Experimental evidence exists indicating that phase coupling of oscillatory activity emerges between spatially separated neurons in area MT in the awake monkey under specific stimulus conditions (Kreiter and Singer 1992, 1996). The stimulus dependence of neuronal coupling led to the notion that the distributed processing of a single object might incorporate a temporal code based on synchronized, phase-coupled activity in area MT, a hypothesis that had been proposed in general for the visual system (Eckhorn et al. 1988; Gray et al. 1989). In contrast, when monkeys performed a motion-direction discrimination task, the amount of non-oscillatory synchronization diminished in area MT and MST with stimulus onset (Cardoso de Oliveira et al. 1997). In this previous study of our group, phase-coupled oscillatory activity was rarely observed. To tackle these controversial results on stimulus-induced synchronization versus desynchronization and the discrepancies in the observation of oscillatory modulation of spike activity in MT and MST, we analysed a large set of data from multi-electrode recordings of MT and MST that were sampled during different behavioural tasks.

Stimulus-dependent phase-coupling in the frequency range 30—120 Hz has been found in visual cortices of cats (Eckhorn et al. 1988, 1993; Gray et al. 1989; Gray and Viana Di Prisco 1997; Molotchnikoff and Shumikhina 2000) and monkeys (Kreiter and Singer 1992, 1996; Eckhorn et al. 1993; Frien et al. 1994, 2000; Frien and Eckhorn 2000; Friedman-Hill et al. 2000; Maldonado et al. 2000; reviewed in Singer 1999). In cat area 17 and 18, stimulation with an unfractured bar elicited higher amounts of oscillatory modulation than stimuli containing discontinuities like a bar disrupted by a gap or stimuli

shaped like an "L" or "T" (Molotchnikoff and Shumikhina 2000). When the uniform, linear movement of a grating was perturbed by a superimposed bidirectional random jitter, oscillatory activity was gradually suppressed with increasing jitter amplitude (Kruse and Eckhorn 1996). These results support the notion that gamma oscillations in visual areas are preferentially induced during sustained activation with coherent stimuli. In the present study, we have analysed separately our data from MT and MST for the overall incidence of oscillatory modulation in the spike activity of single cells, and subsequently tested for synchronized activity in the data obtained during simultaneous recording with multiple electrodes. The analysis of single cell activity allowed us to relate the amount of oscillatory modulation to various parameters of the visual stimulation without being dependent on the relative match of functional properties among different cells in multi-site recordings.

To assess further the possible functional relevance of internally generated gamma oscillations and their cortical synchronization, behavioural tasks are required, in which the animal has to use the visual information provided by the stimulus. We therefore included two different motor tasks in our experimental design. In an oculo-motor task, the animals had to pursue a target moving across a stationary patterned background. A manual motor task required the animal to follow, with its hand, a moving target in different directions. This approach allowed comparison of the incidence of gamma oscillations and the cortical synchronization during passive visual stimulation, during active ocular pursuit as well as during visually guided hand movements requiring a highly attentive state of the animal. Part of the data have been published in abstract form (Kruse and Hoffmann 2000).

Material and methods

Preparation of experimental animals

Experiments were conducted on two adult male rhesus monkeys (*Macaca mulatta*) weighing 5.5 and 6.3 kg, and aged between 4 and 6 years. After initial training, both monkeys had a head restraint, a scleral search coil and a recording chamber implanted while under deep pentobarbital anaesthesia. The recording chamber was placed over occipital cortex in a parasaggital stereotaxic plane tilted 60° back from the vertical. The placing of the chamber was guided by magnetic resonance images (MRI) of each individual animal taken a few weeks before surgery (see details in Paolini et al. 2000). In both animals, a second chamber was implanted above primary motor cortex, and part of the data were collected while simultaneously recording activity from the primary motor cortex. All treatments of experimental animals were performed in full compliance with the guidelines of the National Institutes of Health for the care and use of laboratory animals and of the European Community (EUVD 86/609/EEC).

Behavioural tasks

Both animals were trained to fixate a green fixation spot that was back projected on a tangent screen. Alternatively, a pursuit task was used where the animals had to pursue with their gaze the movement of a small target which was of the same size and colour as the fixation spot. Eye movements were monitored by means of a scleral search coil and sampled by a personal computer at 500 Hz. The direction of gaze was controlled in real-time and any deviation from the target by more than 2° resulted in abandoning the trial. In part of the recordings, a manual motor task was used in which an animal had to track with the right hand a moving target presented on the screen. The target consisted of a bar moving orthogonal to its orientation at constant velocity (7 deg/s) in one of the four cardinal directions. During this visually guided hand-tracking task, the hand position was displayed on the screen as a filled red circle, and the monkey controlled the position of this feedback cursor by means of a 2D-manipulandum, which was movable in the horizontal plane. During the entire task, the monkeys had to keep their gaze on the central fixation spot. After correct completion of a trial a liquid reward was given. In all behavioural tasks, a randomized block design was used and unsuccessful trials were re-randomized and repeated until correct performance of all conditions was achieved. These paradigms were only a part of a larger set of tasks, which the animals had to perform in a study designed to analyse cortical population activity during visually guided hand and eye movements. The results of this study are published separately (Kruse et al. 2002).

Visual stimulation

The visual stimulus was rear-projected on a translucent screen by a video projection system (Electrohome 4100; Kitchener, Ontario, Canada), running with a frame rate of 75 Hz (sometimes 100 Hz) and with 800×600 pixels video resolution. A random square pattern was generated through a personal computer by means of a high performance graphic board (ELSA Winner 2000 Pro/X; Aachen, Germany). The pattern consisted of equally sized squares with adjustable width (typically, 10 pixel=0.7° visual angle, range 5–20 pixel) and randomized luminance (64 grey levels, luminance range: 0.0–0.7 cd/m^2). Accordingly, a typical whole-field pattern contained 4800 equal sized squares (range 19200–1200) with a visual width of 0.7 deg (range 0.35–1.4 deg) and randomized grey levels (see Fig. 1D). The size of the square was adjusted such that it was considerably smaller than the average receptive field (RF) size in a given recording (estimated qualitatively by use of a hand-held projector), but still large enough to drive the cells continuously. For a given square size, the software always generated an identical pattern of pseudo-randomized grey levels. In the pursuit condition, this pattern was presented stationary and the pursuit target (a green dot) was moved in this background. During the fixation task, the pattern was moved by copying the identical pattern from the video memory to a shifted position, and the green dot was superimposed to serve as a fixation point. By this setup, the motion of the pattern seemed to occur behind a large aperture and the size of visual whole-field stimulation remained constant during the time-course of the stimulus. The stimulation with the random pattern moving along the circular path produced – at a fixed position on the screen (for example, at an RF of a neuron) – a movement in continuously changing directions. During completion of a full circle, all possible directions were covered. Similarly, during the circular pursuit across the stationary pattern, the retinal shift of the pattern at a given position on the retina covered all possible directions (Schoppmann and Hoffmann 1976; Hoffmann and Distler 1989).

In the circular stimulation paradigm, a single trial consisted of a reference time where the pattern was stationary for a randomized period of 500–800 ms, and a subsequent motion time when the random dot pattern or the pursuit target moved for 3500 ms. The time for completion of a full cycle was fixed at 3.333 s. The radius of the movement was adjusted according to a qualitative estimate of the preferred velocity of the cell (range r=3.5–10.5 deg, resulting velocity 3.3–10 deg/s). A minimum of five repetitions of the four different stimulus conditions (circular stimulus motion and circular pursuit in clockwise and counterclockwise direction) were always presented in a randomized block design, and unsuccessful trials were repeated until all trials of a given set of conditions were

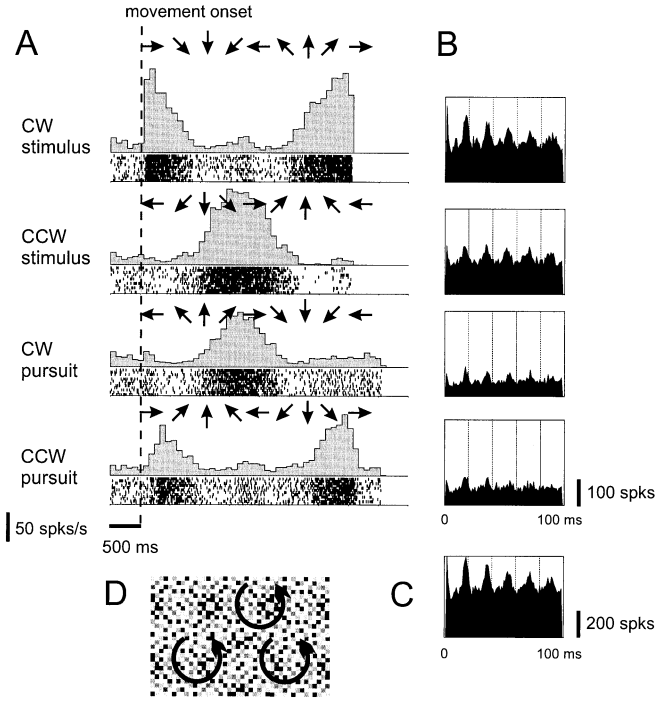

Fig. 1A–D Example for single-cell response during active pursuit and passive stimulation. **A** Raster plots and the corresponding histograms display the activity during the clockwise (*CW*) and counterclockwise (*CCW*) stimulus motion and pursuit condition (12 identical stimulus presentations). Movement of the stimulus pattern or the pursuit target started after a reference period of 500 ms, the pursuit movements are followed by a fixation period of 500 ms. The time-varying direction of the retinal movement of the full-field pattern is indicated by *arrows* above each histogram. Preferred direction of the cell is to the right (358 deg), which corresponds to the vector average of preferred directions obtained from the clockwise and counterclockwise stimulation. **B** Auto-coincidence histograms (ACHs) computed separately for each stimulus condition. **C** ACH computed across all four conditions. Oscillation index for this cell is 4.78; oscillation frequency is 54.7 Hz. **D** Sketch of stimulus pattern. Each part of the pattern was moved on a circular pathway, as indicated by the *black arrows*

successfully completed. Trials in which the monkey broke fixation were abandoned and not included in further analysis.

Extracellular recording and data acquisition

Recording sites were aimed at areas MT and MST using response characteristics (RF size, direction selectivity and velocity tuning) and recording depths as landmarks, in conjunction with the information from the MRI data. Neuronal activity was preferentially recorded from positions showing a clear response to moving stimuli. Extracellular spike activity was recorded with up to four electrodes simultaneously using a multi-electrode manipulator (Thomas Recording, Giessen, Germany) with an inter-electrode distance of 330 µm. Activity of single cells was detected in real-time by means of a computer controlled multi-channel spike sorter (Plexon Inc., Dallas, Tex., USA). Time stamps for detected spikes were stored with 10 µs resolution. Real-time control of the animals' behaviour, data acquisition and visual stimulation was performed by a single personal computer running software developed by one of the authors (W. Kruse). In Fig. 1A, an example for a single cell response during the four different stimulus conditions is depicted.

Calculation of preferred directions

The activity during the circular movement of the pattern in clockwise and counterclockwise direction was used to determine the preferred direction of the cell. For this determination, each spike was encountered as a unitary vector pointing in the actual direction of stimulus motion at the time of spike occurrence. The vector sum **R** of all weighted spikes indicated the optimal direction for one condition. The average of both directions marked the preferred direction of the cell. By this average, any influence of the cell's latency to the visual stimulus is cancelled out. The statistical significance of the directional tuning was tested by applying a non-parametric, statistical bootstrap technique (Lurito et al. 1991) on the data for both stimulus directions separately. If a cell showed a significant tuning during both conditions, the cell was rated as directionally tuned.

Analysis of oscillatory modulation in spike activation

To analyse the temporal structure in the spike train we calculated auto-coincidence histograms (ACHs) from the activity of single cell recordings. The ACH comprises all first-order and higher intervals between the spikes of the cell within the time window under study, up to a maximal delay of typically ±128 ms. All ACHs were computed with a bin width of 1 ms. Only cells with a total of more than 500 spikes recorded during stimulus movement and during the pursuit conditions were included in this analysis (see example in Fig. 1B, C).

To quantify the oscillatory modulation of the cell activity, the counts in each bin of the ACH were taken as a time series and the spectral components of this time-varying function were analysed. The time series has a bin width of 1 ms, equivalent to a sampling frequency of 1 kHz. Before spectral components of such a time series can be analysed by applying a Fourier transformation, precautions have to be taken to ensure that the time-varying signal does not contain frequency components above the Nyquist frequency (500 Hz, half the sampling frequency). We therefore performed two transformations of the data. Firstly, the central peak (±5 ms surrounding the zero bin) was clipped to the averaged value of the neighbouring bins (at +6 ms and –6 ms). By this step the main source of artificial high-frequency components in the ACH was removed, as the zero bin holds the number of spikes analysed. Subsequently, data were smoothed with a three-point triangular filter.

The frequency components of the ACH were evaluated by applying a fast Fourier transformation (FFT) to the 256 data points. In the resulting power spectrum (bin width 3.91 Hz), we searched for pronounced maxima in the frequency range between 31.3 and 132.8 Hz. The lower frequency limit was chosen because many ACHs displayed a single trough of approximately 30-ms width on both sides of the centre without a satellite peak. To avoid influence of such non-oscillatory components, the frequency components below 30 Hz were ignored in further analysis. Frequencies above 130 Hz were usually not present in the data. Peak height in the spectrum was calculated as the average from three FFT bins centred on the oscillation frequency. The average of the remaining spectrum between 31.3 and 132.8 Hz (without the three bins holding the oscillatory peak) was taken as non-oscillatory background, and the ratio between peak power and background level was defined as the oscillation index.

To allow an estimate of the base level of the spectral components in the ACH, we calculated the shift-predictor by correlating subsequent trials with each other and the last one with the first one. We performed the same spectral analysis on the shift-predictor as we did on the ACH. The shift-predictor was usually flat in the gamma range, indicating the neuronal origin of the oscillations and excluding the possibility that oscillatory discharge is locked to the stimulus (e.g. the video refresh rate). The comparison between the spectrum of the shift-predictor and that of the unshuffled ACH was used to define criteria for the significance of possible spectral peaks in the ACHs.

An ACH was rated oscillatory when the following criteria were met. (1) The power spectrum of the preprocessed ACH contained a prominent peak in the frequency range 31.3–132.8 Hz, i.e. the maximum value had to be higher than the two neighbouring bins above and below. In this case the location of the maximum was taken as the frequency of the oscillatory modulation of the spike activity. (2) The power in this peak had to be at least twice as high as the background level, i.e. the oscillation index had to be greater than 2.0. (3) The power in this peak subtracted by the corresponding bins of the shift-predictor spectrum had to be at least twice as high as the average power obtained from the shift-predictor in this frequency range. This criterion assured that the power of the peak in the ACH is not substantiated by any component time-locked to the stimulus. Multiple peaks were rarely encountered in our data – usually there was only a single prominent peak detectable.

The spectrum obtained from the shift-predictor was taken as a control for the spectral background in the spike train as its calculation is based on the original data and thus incorporates the identical temporal modulation of the overall spike rate caused by the stimulus. This was particularly important as we analysed the responses during the full circular movement, which usually included a strong modulation of the spike rate in the response of a direction selective cell.

Synchronization index

To test whether the oscillatory activity appeared synchronized at different cells, we calculated cross-coincidence histograms (CCHs) between different spike trains. The CCHs were analysed in the same manner as the ACHs, i.e. an FFT was calculated and the corresponding spectra were tested for discernable peaks. Additionally, each CCH was tested for a singular central peak as a sign of non-oscillatory synchronization. This synchronization analysis was guided by a previous study of our group (Cardoso de Oliveira et al. 1997), in which non-oscillatory synchronization has been observed especially during an expectation period when the monkey expected a low contrast pattern in a direction discrimination task. In accord with the previous study, we analysed only CCHs that contained more than 1000 entries with a maximum delay of less than 100 ms. Briefly, the subsequent steps were as follows: the shift-predictor was low-pass filtered (frequency limit 3 dB at 120 Hz) and subtracted from the raw CCH and the resulting difference correlogram was expressed in *Z*-scores, i.e. in units of standard deviation. Only peaks in the difference correlograms that exceeded a *Z*-score of 3.0 were taken as significant. To avoid false positives, two additional criteria had to be fulfilled: (1) the peak had to be significant after filtering the correlogram by a three-point averaging filter (1/4, 1/2, 1/4), which ensured that the peak was not caused by a single bin exceeding the significance level; (2) we tested whether the correlation was consistently detectable when the trials were divided in two subgroups. Only if a significant correlation occurred in both groups, was the cell pair scored as significantly correlated.

Histology

During the last week of experiments in both monkeys electrolytic lesions or dye injections were placed at recording sites of interest. After completion of the experiments, the brain of the first monkey was histologically processed and area boundaries were determined by myeloarchitectural criteria. Recording sites were reconstructed on the basis of penetration tracks and records of recording depths. The histologically derived location of the superior temporal sulcus was in good agreement with the estimate based on the MRI data.

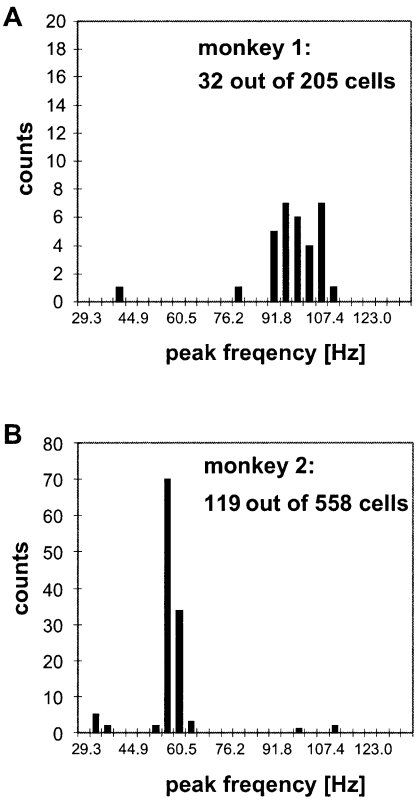

Fig. 2A,B Distribution of oscillation frequencies for cells with significant oscillatory modulation in the auto-coincidence histogram from both animals tested: **A** monkey 1, and **B** monkey 2

Results

Incidences of oscillatory modulation during full-field stimulation

Neuronal activity from 283 sites in the first monkey and 717 sites in the second monkey was recorded during a circular full-field stimulation paradigm containing passive stimulation and active pursuit.

For the analysis of the temporal structure only those data were considered that included more then 500 spikes during presentation of the stimulus (205 from monkey 1 and 558 from monkey 2). In 151 of 763 ACHs (19.8%), an oscillatory modulation was found that was rated as significant according the criteria described in the method section (monkey 1 32 of 205, 15.6%; monkey 2 119 of 558, 21.3%). The dominant frequencies in the oscillatory modulation, 95.7 Hz in monkey 1 and 55.9 Hz in monkey 2, differed significantly (Fig. 2). When we analysed separately the data obtained from the reference period in which the full-field stimulus remained stationary for 500 ms, no significant oscillatory modulation was found in any of the according ACHs.

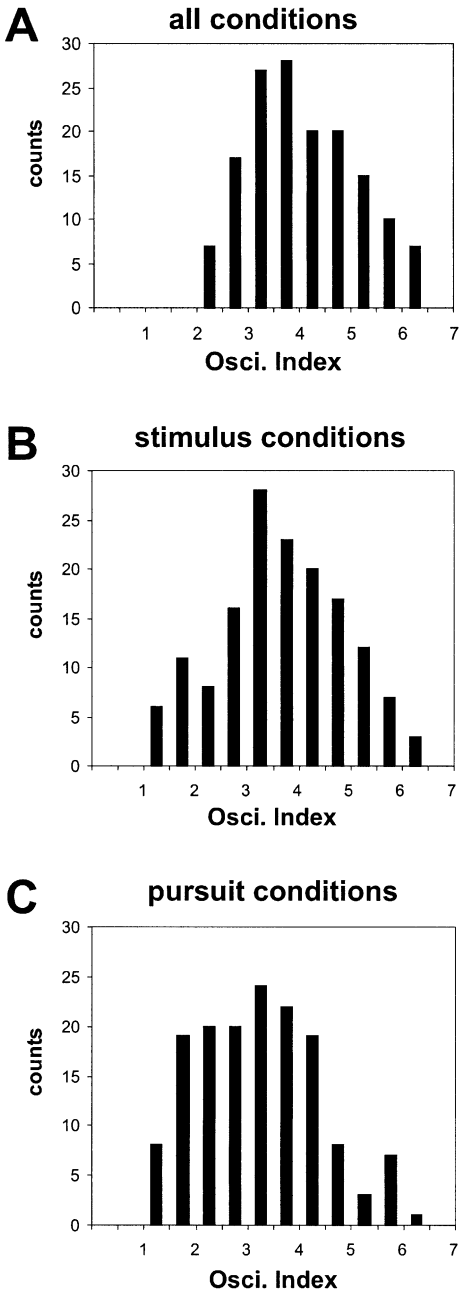

Fig. 3A–C Distribution of oscillation indices obtained from data during passive circular stimulation (**A**), during active pursuit on a circular path (**B**), and when data from these conditions were combined (**C**). Only data from cells which were rated as oscillatory are shown (n=151). Slightly higher values for the oscillation index were reached when data from all conditions were combined

Dependence on active pursuit versus passive stimulus conditions

To test whether we have to distinguish between data obtained during passive stimulation and that during active pursuit conditions or whether we can combine these conditions in further steps of the analysis, we recalculated the oscillation index for each cell for both types of behavioural conditions separately. The ACHs from the passive stimulation and the active pursuit showed no systematic differences. The median values for the distribution of oscillation indices did not show a significant difference, and the distribution of oscillation indices was rather similar. In Fig. 3, the distribution of oscillation indices from all oscillatory cells is shown. For the pursuit data, we observed a slight decrease in occurrence of higher oscillation indices. This difference proved to be significant at the 5% level of probability (Kolmogorov-Smirnov test). Similar results were obtained when data from all 763 cells were included (oscillatory and non-oscillatory cells, data not shown). On the other hand, it becomes obvious from the cumulative distribution of the oscillation indices that we obtained, on average, higher incidences of oscillatory ACHs by combining both subsets of data. Accordingly, the oscillatory modulation was present during both stimulus conditions to a similar extent and does not cancel out in the averaging across conditions (e.g. due to random or systematic changes in the oscillation frequencies).

Dependence on direction selectivity

From our sample of 763 cells analysed for oscillatory modulation during the circular stimulus conditions, a total of 534 (70.0%) showed a significant directional tuning (160 of 205, 78.0%, from monkey 1; 374 of 558, 67.0%, from monkey 2). Our overall impression during recordings was that oscillatory modulation appeared with some prevalence at positions showing a particular strong directional tuning. We therefore divided our sample into recordings where a significant directional bias was found and those without a strong directional tuning. Additionally, the amount of direction selectivity of single units was assessed by calculating the activity during the time when the direction of the stimulus was close to the preferred direction of the cell (PD rate, difference between stimulus direction and cell's preferred direction less then 45°) and during the time when the direction of the stimulus was close to the reverse of the preferred direction (anti-PD rate). The direction selectivity index was defined as DI = 1–(anti-PD rate/PD rate). Plotting the oscillation index against the direction selectivity index (Fig. 4) revealed that, indeed, strong oscillations were preferably present in both monkeys at positions with pronounced direction selectivity, i.e. with a directionality index larger than 0.75. From the 151 cells that were classified as oscillatory in our sample (circles in Fig. 4), 134 (88.7%) showed a statistically significant directional bias (see Materials and methods section) during the circular stimulus condition, whereas from the non-oscillatory cells, only 65.4% (400 of 612) were directionally tuned. Cells with a directional tuning were significantly more often rated as oscillatory than cells without a significant preferred direction ($\chi 2$ test, P<0.0001).

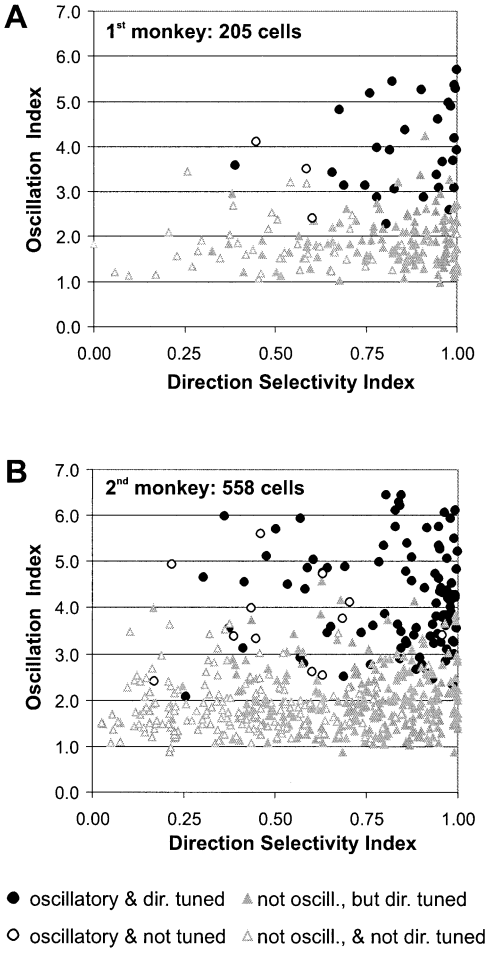

Fig. 4A,B Scatter plot showing the influence of the directional bias of the cells on the amount of oscillatory modulation. Cells with a statistically significant preferred direction (*filled symbols*) show in average a higher amount of oscillatory activity than cells without significant directional tuning (*open symbols*). Similar trends are present for data from both monkeys: **A** monkey 1, and **B** monkey 2

Dependence on activation strength

The correlation between directional selectivity of the cells and the oscillatory modulation in the spike activity led to the assumption that oscillatory modulation might be particularly confined to times of strong activation during the visual response. We therefore separated the responses during the time-course of visual stimulation into two periods containing similar numbers of spikes: the "peak" period, which was centred on the peak of activation of the peri-stimulus time histogram (PSTH) for each stimulus condition (and was therefore equivalent to the time period when the direction of retinal pattern motion was close to the preferred direction of the cell), and the "off-peak" period, containing the remainder of spikes recorded during each stimulus condition. For the population of 134 cells showing strong oscillatory modulation and a significant preferred direction, we could not confirm that oscillatory modulation was stronger during the maximal

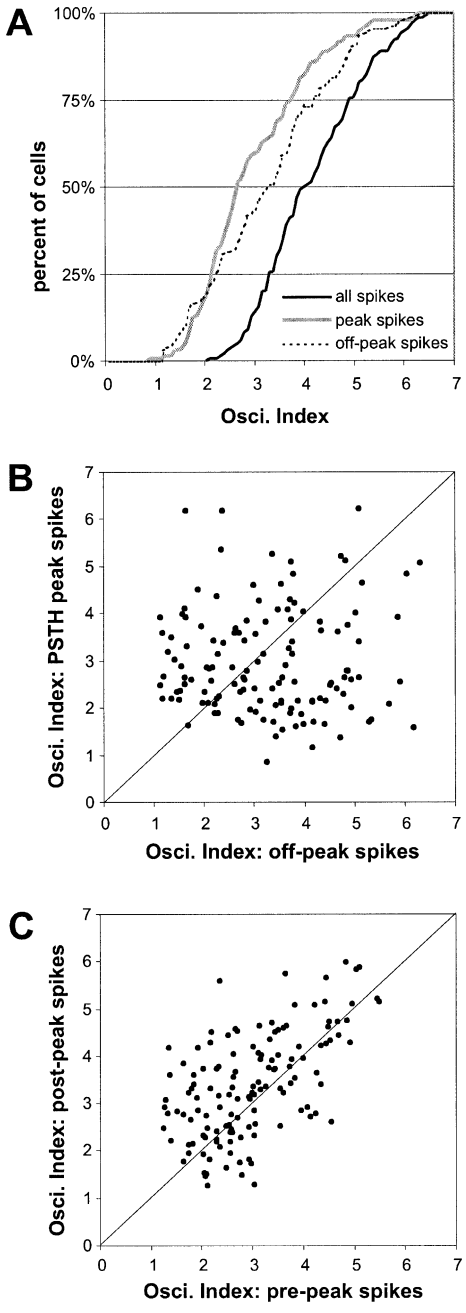

Fig. 5A–C Comparison of oscillatory modulation during times of maximal response (peak spikes) and during the remaining time of visual stimulation (off-peak spikes). For each cell, spike data were separated into two subgroups each containing a similar number of spikes. Only cells with significant preferred direction and significant oscillations are included (n=134). **A** Cumulative distribution of oscillation indices from different parts of the data. **B** Lack of correlation for the oscillation index obtained from peak spikes and off-peak spikes (*PSTH* peri-stimulus time histogram). **C** Comparison of oscillation index during pre-peak period and post-peak period

activation. The median value of the oscillation index was even smaller for the peak period data than for the off-peak data, as can be seen in the cumulative distributions of the corresponding oscillation indices (Fig. 5A). A scatter-plot

of the population of 134 cells does not indicate a correlation between the oscillation index obtained for the peak and off-peak data (Fig. 5B). The relative large scatter indicates that cells might switch between oscillatory and non-oscillatory activity in both periods. The median response rate in this population was 58.4 spikes/s during the peak period and 14.7 spikes/s during the off-peak period.

We also compared the amount of oscillatory activity in periods of rising spike rates and during falling spike rates. For this, we separated the sampled spikes into two halves, distributed symmetrically around the location of the maximum. For the same population of 134 cells showing strong oscillations mentioned above, oscillations were significantly intensified (paired *t*-test, $P<0.0001$) in the period following the maximal activation compared with the period of rising rates (Fig. 5C).

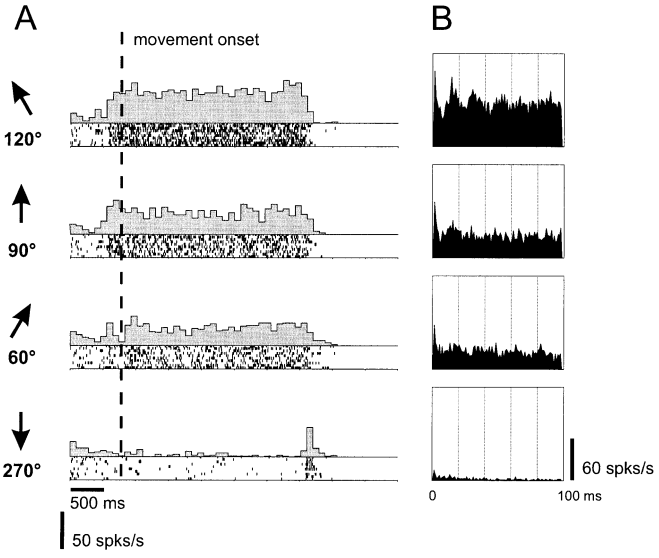

Fig. 6A,B Example of influence of direction of linear motion on oscillatory modulation. In this example, deviation of direction of the stimulus caused a gradual decrease of oscillatory modulation in the spike rate. Preferred direction of the cell was 120.1°. **A** Cell response (raster plot and peri-stimulus time histogram) during stimulation with full-field random dot pattern moving in four different directions (as indicated by *arrows*). **B** Auto-coincidence histograms calculated separately for each direction of stimulus movement

Specificity of oscillatory activity for stimulus direction, velocity and contrast

During recordings from the second monkey, we were able to analyse the recorded data immediately after data collection had been completed. This allowed us to identify oscillatory activity during the time-course of an experiment and provided the possibility to customize the visual stimulus in order to selectively test single recording positions that showed oscillatory activity. One of these customized stimuli consisted of a linear movement of the same random pattern that was used for the circular stimulation. To test the influence of stimulus direction during linear movements, the pattern moved uniformly in the preferred direction of the cell, the reverse direction to the preferred one, and two directions close to the preferred direction. Figure 6 depicts an example in which the oscillatory activity was clearly modulated by the direction of the linear stimulus movement. Oscillatory modulation of the ACH was highest when the stimulus moved in directions close to the preferred direction of the cell, and was gradually diminished when the direction of stimulus movement deviated from the preferred direction. We only tested a small subgroup of cells with this customized stimulus moving linearly in the preferred direction. We observed a co-variation between the response rate and the amount of oscillatory modulation (quantified by the oscillation index) for all six cells that showed a clear oscillatory response during at least one linear movement. When the stimulus direction matched the preferred direction of the cell, the oscillatory modulation was most pronounced, and the oscillatory modulation decreased when the response rate was diminished due to a deviation from the preferred direction of the cell. The seemingly different result in this linear motion test to that in the circular stimulus motion will be taken up in the Discussion section.

In addition to stimulus direction, we varied stimulus velocity during linear stimulus movements for a subset of recordings. In 33 cells, we elicited oscillatory modulation in the spike activity by selecting an appropriate stimulus direction and varying the velocity of the stimulus in logarithmic steps (overall range 3.5–140 deg/s). When oscillatory modulation was present for the particular direction of linear movement, the amount of modulation was always strongly affected by a change of stimulus velocity. In most cases (22 of 33 cells), strongest oscillations were present when the maximum response rate was elicited, i.e. the oscillation index followed broadly the velocity tuning of the cell. However, in one-third of the cells (11 of 33), the highest response rate and the highest oscillation index were observed at different stimulus velocities. According to previous results from work done on anaesthetized cats (Eckhorn et al. 1988; Gray et al. 1990), awake cats (Gray and Viana Di Prisco 1997) and awake monkeys (Eckhorn et al. 1993), we expected that stimulus velocity might influence the frequency of the gamma oscillations. This was generally not the case (e.g. see Fig. 7). Only in one case did we observe a continuous increase of oscillation frequencies when stimulus velocity was increased. In two cases, we observed at high stimulus velocities an additional high frequency component in the ACH, which occurred at twice the frequency present during slower movements.

In a few recordings, we tested whether the video frame rate had any influence on the neuronal activity in area MT. We therefore compared the data obtained during stimulation with two different frame rates (75 and 100 Hz), but we did not observe any influence of the

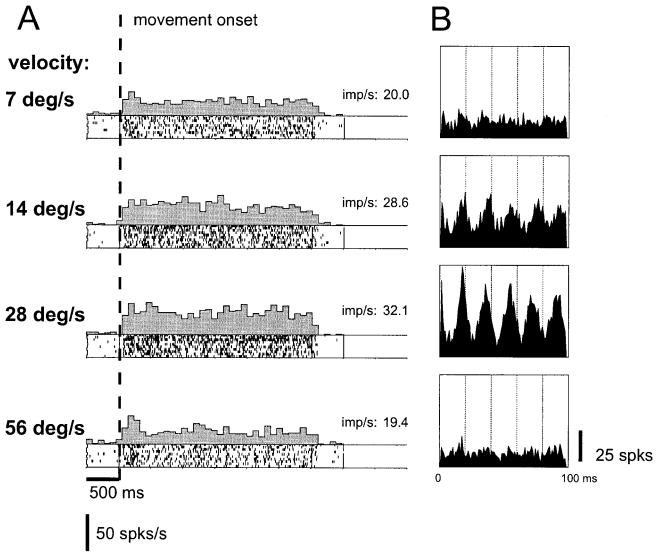

Fig. 7A,B Example of influence of velocity of linear motion on oscillatory modulation. Stimulus pattern moved in constant direction with four different velocities. **A** Cell response (raster plot and peri-stimulus time histogram) during stimulation with full-field random dot pattern moving at four different velocities. **B** Auto-coincidence histograms calculated separately for each velocity of stimulus movement

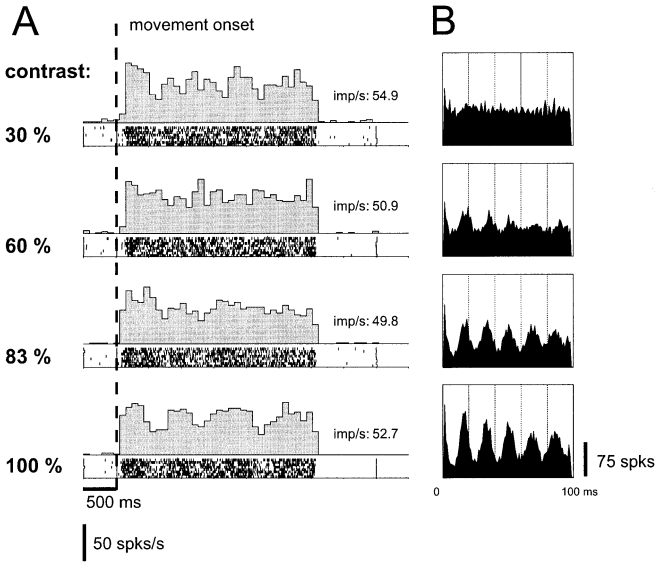

Fig. 8A,B Example of influence of stimulus contrast on oscillatory modulation. The stimulus pattern contained different levels of luminance contrast and was moved linearly with constant speed in the preferred direction of the cell. **A** Cell response (raster plot and peri-stimulus time histogram) during stimulation with full-field random dot pattern at four different contrast levels. **B** Auto-coincidence histograms calculated separately for each contrast level of stimulus pattern

video frame rate, neither in the overall activity nor in the gamma oscillations.

As a third parameter, we varied the contrast in our random pattern by reducing the total span of grey levels used for the pattern (in four logarithmic steps, from 64 grey levels down to the medial 8 levels). With this stimulus we obtained examples of neuronal responses that varied more in the oscillatory modulation than in the overall response rate. In the example shown in Fig. 8, the cell responded vigorously even when the random pattern contained only a small luminance modulation (contrast range 30–100%, mean luminance 0.1 cd/m^2). When the luminance contrast was restored by increasing the difference in luminance between the squares of the pattern, the response rate was not changed but the amount of oscillatory modulation increased considerably.

Synchronized oscillations in simultaneous recordings from separate positions

As most of the data were sampled during multi-electrode recordings, we were able to analyse whether oscillatory activity is synchronized between different cells and between different positions. From the 763 datasets that were analysed for oscillatory activity during the circular stimulus condition, we could combine 998 pairs of simultaneously recorded cells (228 from monkey 1, 770 from monkey 2). From these pairs, 159 were collected through a single electrode and the remaining 839 were collected from spatially separate electrodes with an inter-electrode distance of up to 2 mm.

Corresponding to the result that oscillatory activity was present in approximately 20% of the cells, in the majority of pairs (664 analysed for synchronized oscillations) neither of the cells showed oscillatory activity. Of these 664 pairs, not a single pair showed oscillatory activity in the CCH when the same criteria were used as for the ACHs. From the 282 pairs that contained one oscillatory cell, the CCH was rated as oscillatory in 28 cases (28 of 282, 9.9%). The remaining 52 pairs comprised two oscillatory cells, and 23 of those (44.2%) showed oscillatory activity (Fig. 9). From these numbers one can conclude that oscillatory modulation in the single spike trains was a prerequisite for the occurrence of oscillatory modulation in the CCHs computed from two cells. There was no case where the oscillatory modulation in the CCH appeared de novo and was not present in the respective ACHs. From the total number of 43 pairs that showed significant oscillatory modulation in the CCH together with a significant preferred direction in both single cells, 13 had a difference in preferred directions between 45° and 90°, and 4 pairs of cells differed by more than 90° in their preferred directions. Therefore, similarity of preferred directions obviously increases the probability for synchronized oscillations – partly due to the co-activation through the large field stimulus – but it does not seem to be a necessary condition for the synchronization of oscillatory activity. However, when two oscillatory cells did not show oscillations in the corresponding CCH, both cells usually had differences in the preferred directions greater than 45°.

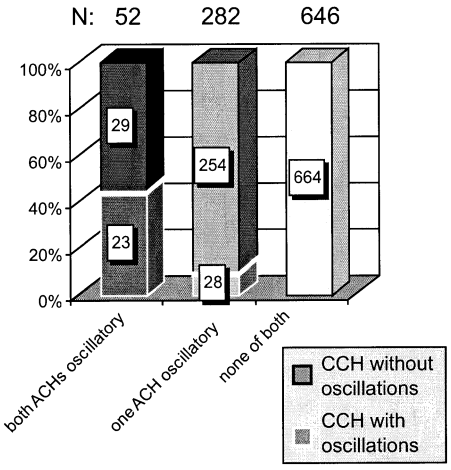

Fig. 9 Synchronized oscillation in simultaneous recordings from separate positions were found in pairs of cells only when at least one of both cells showed oscillations in the auto-coincidence histogram (*ACH*). When both cells showed oscillations, 44.2% of the analysed cross-coincidence histograms (*CCHs*) were oscillatory (*left bar*), compared to 9.9% when only one of both cells showed oscillations (*middle bar*). When no oscillations in the corresponding ACHs were present, the CCHs showed no oscillatory modulation either (*right bar*)

Non-oscillatory synchronization

We analysed whether non-oscillatory synchronization was present in the simultaneously recorded data by testing the CCHs for significant singular peaks (see Materials and methods section). During the circular stimulus conditions, only 42 pairs (4.2%) showed a pronounced peak that was scored as a significant correlation according to similar criteria as those used in the previous study by Cardoso de Oliveira et al. (1997). In the previous study, a higher ratio of cell pairs showed synchronized activity. Particularly during an "expectation period" when no stimulus was present and when the monkey waited for a behaviourally relevant stimulus, they observed synchronized activity in area MT and MST in 72 of 160 pairs. We therefore analysed separately the data from the reference period when the monkey only had to fixate and the visual stimulus was stationary. In our paradigm where the stimulus had no behavioural meaning, we found no indication of a higher probability of non-oscillatory synchronization during the reference period. In general, the pairs that showed a clear peak during the circular stimulus conditions showed synchronization during the reference period as well, and the degree of synchronization measured as the normalized peak height was very similar for a given cell pair during the stimulation period and during the reference period.

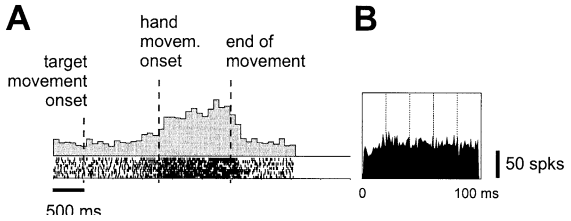

Fig. 10A,B Example of cell activity in MT during the manual tracking task. Data are from the same cell as in Fig. 1, preferred direction to the right. **A** Raster plots and histograms during tracking movements to the right. When a bar symbol started to move from left to right with constant velocity, the animal had to track the target with a manually controlled feedback cursor during the second half of the target movement. The monkey fixated at the centre of the screen during the entire task. The moving target, together with the tracking feedback cursor, crossed the receptive field during the second half of the target movement. **B** Corresponding auto-coincidence histograms for the data shown in **A**. In contrast to the activity shown in Fig. 1, the cell does not exhibit oscillatory modulation in the auto-coincidence histogram

Lack of gamma oscillations during visually guided tracking

After we reaffirmed the presence of high-frequency gamma oscillation and their synchronization in area MT and MST during various visual stimulus conditions, we set out to elucidate whether comparable gamma oscillations could be found in single cell activity when the animals were involved in a visually guided manual tracking task. It has been proposed before that stimulus induced oscillations and synchronization might play a functional role especially in behaviourally demanding situations in which integrative processing of sensory information is required (Roelfsma et al. 1997; Classen et al. 1998; Singer 1999; Fries et al. 2001). A motor task directly related to visual motion should be an appropriate behavioural condition for the occurrence and synchronization of oscillatory activity in area MT and MST. We designed a motor task in which a moving bar had to be tracked with the hand by means of a manually controlled visual feedback cursor. During the complete time-course of the tracking task, the monkey always had to fixate the centre of the screen (radius of fixation window 2.1°), otherwise a trial was aborted immediately. After a reference period of 500 ms, a moving target appeared in the periphery and moved uniformly towards the centre of the screen. When the target passed the centre, the monkey tracked the target with a feedback cursor, which was controlled by hand movements in the corresponding direction.

In Fig. 10, single-cell activity during the tracking movement in the preferred direction of the cell (horizontal to the right) is exemplified. Activity from the same cell during the circular stimulus condition is shown in Fig. 1. The cell fires vigorously when the bar moves through the receptive field. At the same time, the animal has to follow the moving target with its hand. During the visually guided tracking, the firing rate covers a similar range as

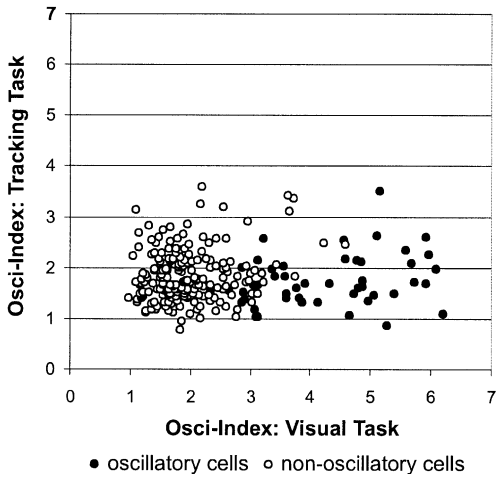

Fig. 11 Scatter diagram for the oscillation index obtained during circular stimulation (*Visual Task*) and during visually guided manual tracking (*Tracking Task*). Data combined from 247 cells, from which 49 showed significant oscillations

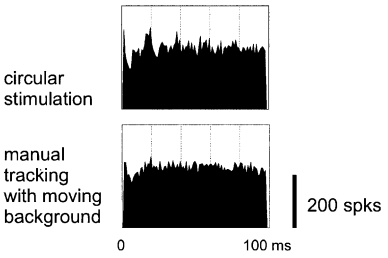

Fig. 12 Auto-coincidence histograms (ACHs) obtained from a single cell during circular stimulation and during manual tracking across a linearly moving background. Data from five repetitions of four different conditions are included in each ACH. During circular stimulation, the pursuit and passive stimulation in clockwise and counterclockwise directions were combined, whereas during the manual tracking task, a cumulative ACH was calculated during upward tracking while the full-field pattern moved in the four cardinal directions. During the circular stimulation, the ACH was rated as oscillatory (oscillation index 2.51), whereas during the tracking task, the resulting ACH failed to show significant oscillatory modulation (oscillation index 1.69)

during the circular stimulus conditions (Fig. 1). Despite the comparable firing rate, the cell does not engage in oscillatory activity and the corresponding ACH remains flat. A similar effect was observed in all cells that showed oscillatory activity during the circular stimulation. We recorded a total of 315 cells during the tracking task (124 cells from monkey 1, 191 cells from monkey 2). From 247 cells, we collected more than 500 spikes in at least five repetitions of the four tracking conditions, and these data were subsequently analysed for oscillatory modulation in the ACH. The median discharge rate across all four directions was 10.7 spikes/s for the tracking task, whereas during the full-field stimulation we obtained a median discharge rate of 12.8 spikes/s. From the 247 cells, 49 showed significant oscillatory modulation during the circular stimulation. None of these 49 cells responded with a oscillatory activity during the manual tracking task. When the corresponding ACHs were analysed, not a single one was rated as showing significant oscillatory modulation by applying the same criteria as for the data obtained during circular stimulation. When we compared the oscillation index for both conditions, the scatter diagram (Fig. 11) demonstrates this lack of gamma oscillations during the tracking condition. In our sample, several ACHs achieved an oscillation index greater than 2.0, but the cell activity was not rated as oscillatory because the other criteria based on the shift predictor and the presence of a distinct spectral maximum were not met.

Although many cells responded vigorously during the tracking task, it should be noted that the visual input during the circular full-field stimulation differs considerably from the manual tracking. In the tracking task, a light bar moves in one of four cardinal directions, and the bar might cover the receptive field of a particular cell only during a fraction of the stimulus movement. In contrast, during circular visual stimulation, the random pattern always covered the whole screen. To test whether this difference in visual input might account for the observed differences in oscillatory activity, we combined the tracking movement in the upwards direction with a background pattern moving in the four cardinal directions. The same random dot pattern that was used in the circular stimulus condition moved linearly with constant speed during the entire task, i.e. during a reference period when no tracking target was present, and during the tracking phase when an additional bar was moving through the visual field. In recordings from the second monkey it has been shown that the linear moving stimulus is capable of eliciting oscillations to a similar degree as the circular stimulus (see, for example, Fig. 6). However, when we combined the linear-moving stimulus with the tracking task, no oscillatory activity was observed. The ACHs from the spike activity of a single cell during circular stimulation and during manual tracking with a linearly moving background are exemplified in Fig. 12. Whereas during the circular stimulation condition, satellite peaks are evident in the ACH indicating oscillatory activity, the same cell failed to elicit oscillatory activity during the combination of a linear full-field motion with a manual tracking movement. As the linearly moving full-field pattern matched the preferred direction of the cell (96.1°, close to upwards), one should expect that the linearly moving full-field pattern is capable of eliciting oscillatory activity, similar to the responses to linear full-field stimuli described above (Fig. 6). This was not the case for the cell shown in Fig. 12 and was not seen either in any of the other cells tested during this combined task. We recorded 126 cells in this task, and obtained oscillatory activity during the circular stimulation in 16 cells. Not a single one of these cells showed comparable oscillations when the linear full-field motion was combined with a motor tracking task. This was true even for conditions in which the direction of linear pattern movement matched the preferred direction of the visual cell.

Discussion

In the current study, the incidence and strength of oscillatory modulation in the spike activity in areas MT and MST was measured during different behavioural conditions. We found stimulus-induced gamma oscillations in approximately 20% of the recordings when monkeys were stimulated with a full-field random dot pattern during a fixation task. Oscillatory activity was dependent on stimulus features like direction of movement, velocity, and stimulus contrast. However, when animals had to use the information from the visual stimuli for the ongoing control of a manual tracking task – by having to keep their attention on a moving bar – no oscillatory modulation of cell activity was detected.

Methodological considerations

It has been shown before (Kreiter and Singer 1992, 1996) that stimulus-dependent synchronization is present in area MT of awake monkeys when animals perform a visual fixation task. The study by Kreiter and Singer (1992) found that data from the awake monkey showed, in general, higher variability in the occurrence and the frequency of oscillations compared with that in the anaesthetized cat. In contrast, we observed only very little variation of the gamma oscillations. When we divided our data into subgroups of trials and analysed different temporal epochs separately, similar oscillation frequencies were measured in each epoch. Even during different full-field stimulus conditions, the oscillation frequencies remained surprisingly stable. Due to this stability of the gamma oscillation frequencies, we do not expect that the incidence of cells with significant gamma oscillations would have increased considerably if our analysis had been based on shorter epochs. However, considerable differences in the dominant oscillation frequency were found between the two monkeys.

The observation that gamma oscillations can be found not only during periods of high activation when the direction of the circular stimulation matches the preferred direction of the cell, but also at times when the cell is responding only moderately to non-optimal stimuli seems contradictory to the dependencies seen during the linear stimulation. When the stimuli were moved linearly in different directions, oscillatory activity co-varied with the response rate of the cell and was usually absent during weak responses. During circular stimulation, the occurrence of oscillatory activity in phases of low activation might be due to a longer persistence of oscillatory activity compared to the overall spike rate. The slight increase in oscillatory activity in the period following the maximal activation (Fig. 5C) supports this notion. During the linear stimulus condition, such a putative persistence of oscillatory activity has no effect on the directional tuning of the gamma oscillations. Therefore, during tests with linear-moving stimuli, a better match between the directional tuning of gamma oscillations and the rate-based directional tuning can be expected. In a recent study by Frien et al. (2000), it was shown that gamma oscillations in area V1, observed in multi-unit activity of the awake monkey, have even sharper orientation tunings than the corresponding multi-unit activity. One possible reason for this discrepancy is the different signals on which the different results are based. The multi-unit spike rates and the local field potentials analysed by Frien et al. (2000) encompass a local average of neuronal activity. Oscillatory activity might be specifically detectable in such local averages, which could result in a higher specificity of gamma oscillations to stimulus orientation than in the in the overall rate of the ensemble. A recent study by Volgushev et al. (2002) investigated the transformation of the membrane potential changes into the spiking of a cell. Results from these intracellular recordings support the notion that occurrence of oscillatory activity in the gamma range is coupled to changes in this transformation (Volgushev et al. 2002), and they suggest that oscillatory activity in the gamma range is most pronounced during states of optimal neuronal activation.

Oscillations as a prerequisite for synchronized activity

In several previous studies, it has been mentioned that oscillatory modulation in local group activities in the gamma range can be taken as a sign of synchronized ensemble activity, because strong synchronization often occurs during phases of oscillatory activity (Frien et al. 1994; König et al. 1995; Gray and Viana Di Prisco 1997; Maldonado et al. 2000). This notion has been additionally supported by the fact that oscillatory modulation appears usually in a fixed phase relationship at different recording sites, in most cases at zero phase lag, on average. In our data, synchronized oscillations in separate positions were only observed when the spike train from at least one cell showed a significant oscillatory modulation (Fig. 9). Significant oscillatory modulation in one of the two cells evident in the cross-correlogram was a necessary prerequisite for the occurrence of synchronized oscillations in the gamma range. This argues against the possibility that oscillatory modulation might be caused by a covert, third source (neuronal or artificial in origin). If such "subthreshold" inputs were present to both cells they should become more pronounced in the cross-correlograms than in the ACHs describing single cell data.

On the other hand, it is obvious that oscillatory activity in both neurons does not automatically lead to synchronized oscillations. In our sample, we obtained 29 CCHs without significant oscillations, while both underlying single cells did oscillate. For 22 of these pairs, the preferred directions differed by more than 90°, which caused a considerable temporal offset of the maximal activation during the circular stimulation. As we did not specifically optimize our stimulus to the particular combination of RF properties (e.g. preferred direction) of the single cells, we obtained a lower percentage of synchronized oscillatory pairs than in other studies (e.g.

Kreiter and Singer 1996) that always optimized the stimulus for the particular RF properties.

Stimulus specificity of gamma oscillations

The incidence of gamma oscillations was highly sensitive to the variation of different features of the full-field stimulus. Stimulus direction, stimulus velocity and stimulus contrast proved to influence the amount of oscillatory modulation of a given cell, and, in part, this modulation was independent of the overall response rate of the cell. Despite this stimulus dependency of the gamma oscillations, we observed only very little variability in the oscillation frequencies. An influence of stimulus velocity on the frequency of the gamma oscillations has been described for cat visual cortex (Eckhorn et al 1988; Gray et al. 1990; Gray and Viana Di Prisco 1997) and for monkey primary visual cortex (Eckhorn et al. 1993). Among our data, we sometimes observed a doubling in the oscillation frequencies when higher stimulus velocities were presented, which was manifested in small peaks intercalated between the main peaks in the ACH. The stability of the frequency components observed in both animals suggests that these dominant frequencies are individual characteristics of each monkey. Whether this frequency "lock-in" reflects any functional properties of the involved neuronal network or an intrinsic feature of the cells under study, and whether these fixed frequencies have further functional implications remains unclear.

In the study by Kreiter and Singer (1992), gamma oscillations were seen during visual stimulation with moving bars. From various studies in cat visual areas 17 and 18 (Bauer et al. 1995; Molotchnikoff and Shumikhina 2000), it can be concluded that in these areas moving large-field stimuli were more efficient in eliciting gamma oscillations than single bars. In regard to our data, one might argue that the lack of gamma oscillations during the tracking task is partially caused by the smaller size of the bar stimulus compared to that of the full-field pattern. However, when we combined the tracking task with a large background pattern moving linearly in the four cardinal directions we did not observe gamma oscillations even in recordings that showed oscillatory activity during circular stimulation. Moreover, the results by Kreiter and Singer (1992, 1996) proved that, during a pure fixation task, gamma oscillations can be evoked readily in area MT by a moving bar. We therefore conclude that the most important difference between the circular visual stimulation and the manual tracking is the increased behavioural relevance of the stimulus, which obliterates oscillations in the gamma range.

Non-oscillatory synchronization

We found only a low proportion (4.2%) of pairs of cells showing significant non-oscillatory synchronization, in contrast to the previous study by Cardoso de Oliveira et al. (1997), in which 45.0% of all pairs from MT and MST were rated as synchronized. Vice versa, oscillatory activity was observed only occasionally in the previous study. These discrepancies might be due to methodological differences. As we were looking mainly for stimulus-dependent activities, we have biased our selection of recording sites to cells showing a clear response to the visual stimulation. The situation was different in the previous study, in which all units that could be well isolated were included. We assume that the bias towards cells coding for the visual stimulus increased the incidence of cells showing stimulus-driven gamma oscillations and probably diminished the number of cells showing non-oscillatory synchronization. The different sampling bias may also have yielded to the different observations of stimulus dependency: whereas in the previous study the non-oscillatory synchronization was not stimulus-specific and decreased with stimulus contrast, we here describe stimulus-driven gamma oscillations, which are more pronounced with strong-contrast stimulation and tend to synchronize between cells driven by the same stimulus.

A further methodological difference regards the behavioural tasks. In the current study, most of the data were obtained during visual stimulation and only short epochs (500–800 ms) of "spontaneous activity" were collected. The study by Cardoso de Oliveira et al. (1997) used an "expectation period" of up to 3000 ms where the animal was waiting for the behaviourally important stimulus. In the previous study, non-oscillatory synchronization was more pronounced during the expectation period than during the visual stimulation one. For our data, it seems as if the dominance of the visual stimulus has occluded non-oscillatory synchronization.

In a recent study analysing the synchronization in area MT, monkeys were trained to discriminate a direction in moving random dot displays, and it was tested whether the synchronization between pairs of neurons coding for a particular direction was increased when the animals decided for this direction (Bair et al. 2001). The analysis of non-oscillatory synchronization could not find any influence on the CCHs when data from trials with different behavioural outcome were compared, i.e. trials where the monkey opted for the preferred direction did not differ from trials where the monkeys opted for the opposite direction. The lack of a relationship of synchronized activity to the animals behaviour in a direction-discrimination task is an additional result that calls into question the importance of synchronized activity for the behaviour of the animal. However, this study did not report any oscillatory modulation in their ACHs and CCHs, which might indicate that the data were obtained at a different level of activation from that of the full-field coherent motion stimuli used in our study.

Lack of oscillatory activity during motor behaviour

It is obvious from our own data and from previously published results that linear motion alone was able to induce gamma oscillations. We do not think that the lack of gamma oscillations during the manual tracking task is caused by the fact that we used a linear stimulus movement rather than a circular motion. We instead assume that the higher difficulty of the manual tracking task, which still required continuous visual fixation, is likely to enhance the attention towards the moving target. By contrast, during the circular stimulus conditions, the monkey had to actively suppress the influence of the "background" pattern. This was true for the stimulus conditions where the moving full-field pattern induced a strong optokinetic nystagmus making it difficult for the monkey to maintain fixation on the stationary fixation point. In the pursuit conditions, the monkey had to take the moving green dot as the target for the ocular pursuit movement. In both circular conditions, the background pattern (either moving or stationary) had to be ignored to perform the accurate behaviour. Both circular conditions are comparable in this aspect because the background pattern had to be ignored, and this is paralleled by a comparable amount of oscillatory activity during both conditions (see Fig. 3).

In an accompanying study we analysed the synchronization between motor cortex and visual areas MT/MST during the manual tracking task. In this work we focussed on possible neuronal interactions between these visual and motor areas (Kruse et al. 2002). A total of 744 intermodal cell pairs was recorded during visually guided tracking movements. From 328 pairs, sufficient spikes were recorded to result in CCHs that hold more than 1000 entries. None of these CCHs showed a clear and significant peak that could be interpreted as a significant sign of synchronized activity during the performance of visually guided movements.

The lack of gamma oscillations during the motor task is, at first glance, in contrast to observations described by Roelfsema et al. (1997) in which synchronized oscillations were found in multi-modal recordings from multiple cortical areas while cats had to react with paw movements to a visual stimulus. In their study, synchronization among visual and parietal areas in the behaving cat was particularly present during periods when a visual stimulus triggered a motor reaction of the animal. However, the synchronization appeared to be restricted to the beta frequency range below 30 Hz and might therefore be based on other sources than the high-frequency stimulus-induced gamma oscillations in the spike activity described here. The results from Roelfsema et al. (1997) were obtained from multi-unit and local field potential recordings, which again might account for a higher probability of finding synchronized oscillations than in single cell recordings.

In electroencephalographic (EEG) recordings from human subjects performing a visually instructed force-tracking task, coherence between scalp regions overlying the visual and motor cortex increased in comparison with that a resting condition (Classen et al. 1998). Comparable to the tracking task used in our study, the authors designed a task that requires a functional cooperation of visual and motor areas. Task-specific changes of EEG coherence were best differentiated in the low beta frequency range between 12 and 21 Hz (Classen et al. 1998; see also Toro et al. 1994). Oscillatory activity in the frequency range below 35 Hz was also measured in local field potentials from motor and sensorimotor cortex of the monkey (Murthy and Fetz 1992; Sanes and Donoghue 1993) as well as in parietal areas (MacKay and Mendonça 1995) and in the cerebellum (Pellerin and Lamarre 1997). The occurrence of oscillations up to 35 Hz (beta range) and their cortical synchronization (Murthy and Fetz 1996a, 1996b; Donoghue et al. 1998) seems to be linked mainly to the preparation for movement. By contrast, the stimulus-induced fast gamma oscillations in cell activity of areas MT and MST described in the current paper appear to be broadly diminished while the animal prepares for a motor reaction.

This possible dichotomy between low frequency oscillations in the beta range and fast gamma oscillations is mirrored in part by theoretical considerations about possible sources of short range and long range synchronization (Kopell et al. 2000). From experimental data and simulations it was concluded that oscillations in the beta range have a different dynamical structure than that of gamma. The beta frequency is able to synchronize over long conduction delays that cannot be tolerated by gamma oscillations because such delays would result in cancellation of oscillations due to 180° phase shifts. From this perspective it seems likely that the stimulus-induced high frequency gamma oscillations in areas MT and MST are related to local processing of global motion stimuli. Gamma oscillations are coupled to a change in the transfer function describing the transformation of membrane potential changes into trains of action potentials (Volgushev et al. 2002). In the light of these results, it seems questionable whether fast gamma oscillations are involved in higher level interactions between distant cortical areas that are needed during integrative control of behaviour.

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