Behavioral measures such as expectancy and attention have been associated with the strength of synchronous neural activity. On this basis, it is hypothesized that synchronous activity affects our ability to detect and recognize visual objects. To investigate the role of synchronous activity in visual perception, we studied the magnitude and precision of correlated activity, before and after stimulus presentation within the visual cortex (V1), in relation to a monkey’s performance in a figure–ground discrimination task. We show that during the period of stimulus presentation a transition in synchronous activity occurs that is characterized by a reduction of the correlation peak height and width. Before stimulus onset, broad peak correlations are observed that change towards thin peak correlations after stimulus onset, due to a specific decrease of low-frequency components. The magnitude of the transition in correlated activity is larger, i.e. a stronger desynchronization occurs, when the animal perceives the stimulus correctly than when the animal fails to detect the stimulus. These results therefore show that a transition in synchronous firing is important for the detection of sensory stimuli. We hypothesize that the transition in synchrony reflects a change from loose and global neuronal interactions towards a finer temporal and spatial scale of neuronal interactions, and that such a change in neuronal interactions is required for figure–ground discrimination.

Keywords: attention, correlation, cortex, figure–ground, macaque, wavelet

Introduction

A prominent feature of cortical processing is that neurons may engage in synchronous firing. Synchronous activity has been proposed to play a role in many high level processes such as perceptual organization, sensory-motor binding, attention, arousal and even consciousness (Eckhorn et al., 1988; Gray et al., 1989; Riehle et al., 1997; Tallon-Baudry et al., 1999; Gail et al., 2000, 2004; Steinmetz et al., 2000; Von Stein et al., 2000; Engel and Singer, 2001; Engel et al., 2001; Fries et al., 2001, 2002; Mima et al., 2001; Varela et al., 2001; Varela et al., 2001; Varela et al., 2001; Varela et al., 2001). However, the role of neural synchrony remains controversial. In particular, the function of synchrony in perceptual grouping and scene segmentation has been challenged (Lamme and Spekreijse, 1998; Shadlen and Movshon, 1999; Bair et al., 2001; Thiele and Stoner, 2003). An alternative view, not necessarily incompatible with a role in binding (Singer and Gray, 1995; Singer, 1999; Varela et al., 2001), is that fast dynamical changes in synchronous activity occur in relation to changes in attention or expectancy (Lee, 2003; Supér et al., 2003), which may subsequently affect the manner in which sensory input is processed. That fast shifts in cortical mode occur is suggested by human EEG studies that have demonstrated fast desynchronisation of neural activity in the visual cortex in response to visual input (Morrell, 1967; Vijn et al., 1993). Dynamical changes in synchrony are also observed at the level of spike activity and local field potentials in animal studies (Eckhorn et al., 1993; Vaadia et al., 1995; Bressler, 1996; Cardoso de Oliveira et al., 1997). However, the relation between dynamical changes in correlated spike activity and visual perception has received limited attention (Woelbern et al., 2002).

We studied dynamical changes in correlated activity in the visual cortex of monkeys that were engaged in a figure–ground discrimination task. The animals were trained to report the presence or absence of a textured figure within a homogenous textured background. Previously, we have shown that the late responses of V1 neurons segregate figure from background (Lamme, 1995; Zipser et al., 1996) and that these late modulated responses predict the behavioral report of the animal in a figure–ground discrimination task (Supér et al., 2001). Here we show that in such a task correlated activity in V1 changes over time. Before stimulus onset, broad peak correlations are observed that change towards thin peak correlations after stimulus onset. This change in synchronous activity is not a direct result of visual stimulation or small eye movements. Instead, it correlates with the behavioral report of the animal where the transition in correlated activity is stronger when the animal reports the stimulus correctly than when it fails to detect the stimulus. We propose that the dynamical switch in synchronized activity in V1 represent a change in neuronal interactions, and that this change is important for the segregation of figure from background and thus for visual perception.

Materials and Methods

Behavioral Task

Monkeys (Macaca mulatta) were seated in a primate chair 75 cm from a monitor screen, in a dark room. Stimuli were presented on a 21-inch monitor driven by a No. 9 GxITC TIGA graphics board (resolution: 1024 × 768 pixels, refresh: 72.34 Hz, visual angle: 28 × 21°). In each trial, a red fixation dot (0.2°) popped up within a texture of randomly oriented line segments filling the whole screen. After the monkey had fixated for 300 ms (i.e. eye position remained within a 1° × 1° fixation window surrounding the fixation point) the stimulus texture appeared. Stimulus textures consisted of randomly positioned line segments of 16 × 1 pixels (0.44°) with an average density of five line segments per square degree, and an orientation of either 45° or 135°. In figure-present trials, the stimulus could be perceived as a square containing line segments in one orientation on a background of orthogonal line segments (Fig. 1). Both orientations were used for both figure and background, resulting in complementary stimulus pairs (Lamme, 1995). The position of the ‘figure’ square was randomly chosen out of three possible locations with an eccentricity of 2.7–4.4° from the...
Data Recording and Analysis

Neural activity was recorded simultaneously from 16 chronically implanted platinum-iridium micro wires (Trimel coated, diameter 25 μm, tips exposed between 50 and 150 μm, impedances 100-350 kΩ, at 1000 Hz). Multiple unit activity (MUA) was obtained through a four-electrode array. The activity from an electrode is represented as $S_j(t)$ for the $j$th electrode and $R(t)$ for the stimulus. The averaged response or peri-stimulus time histogram (PSTH) can be represented as:

$$P_j(t) = \frac{1}{N} \sum_{i=1}^{N} w(t - t_i) \quad \text{with} \ w(t) \text{ representing averaging over all trials } r.$$ 

The SEM was calculated from the average variance of the samples within each window. To analyze the dynamics of the correlations we calculated a matrix of covariance’s for all combinations of electrodes averaged over all trials. Shuffle-corrected covariance matrices are represented as:

$$J_{jk}(t_1, t_2) = \langle S_j(t_1) S_k(t_2) \rangle - P_j(t_1) P_k(t_2)$$

This denotes the averaged (over all trials $r$) cross product of the responses from electrode $j$ and $k$, minus the cross product of the averaged responses. The cross product of the averaged responses has been termed the shuffle predictor and is used to reduce common input due to the stimulus. This equation is also known as the un-normalized joint peristimulus time histogram (JPTSTH) (Aertsen et al., 1989).

The (time-dependent) standard error of the electrode response $j$ is derived from the auto-covariance matrix of $j$:

$$\sigma_j(t) = \left( \langle \hat{J}_{jj}(t_1, t_1) \rangle \right)^{1/2} \quad \text{for } t_1 = t_2 = t$$

This is the square root of the values on the main diagonal of the auto-covariance matrix. Normalized covariance matrices or normalized JPTSTHs can then be defined as:

$$R_{jk}(t_1, t_2) = \frac{J_{jk}(t_1, t_2)}{\sigma_j(t_1) \sigma_k(t_2)}$$

In this equation, division with the cross product of the standard deviations of the $j$th and $k$th electrode is used to normalize the covariance matrix and obtain a two dimensional cross-correlogram.

To estimate correlation peak area at time $t$, sample values between −25 and +25 ms lag were summed. Lag is the offset in time from the central diagonal of the correlogram. We define lag as $(t_1 - t_2)$. Lag = 0 ms for $t_1 = t_2$. Peak width and peak area are further estimated for two epochs of 100 ms, corresponding to what we define as the pre-stimulus and late period (see Results). This was done by first averaging the correlation functions in these epochs, followed by normalization with the corresponding auto-covariances resulting in a correlation function for each combination of electrodes. Peak width was then estimated as the number of samples with a value greater or equal to one-third peak height. Peak height is defined as the maximum of the correlation function for these averaged epochs and therefore corresponds to nearly all cases to the correlation coefficient at lag = 0 ms. To compare peak heights in different epochs and conditions, the Fisher $z$-transform was applied to these correlation coefficients, whereby $z$-values are obtained with a normal distribution. Peak area for these two periods was also estimated between −25 and +25 ms lag. Because the range of values differed for the two monkeys, we define normalized area. This is simply obtained by dividing area with the largest value within all combinations.
of electrodes, separately for both monkeys. For example, when comparing pre-stimulus and late correlation peak area for all combinations of electrodes, the largest value was in the pre-stimulus period. We then divided all values in both pre-stimulus and late period with this value. In this manner relative differences are retained and the values for both monkeys may be plotted over each other and statistically combined.

Wavelet Analysis
Additionally we explored the dynamics of the frequency components between 5 and 150 Hz by estimating the time- and frequency-dependent phase clustering index (PCI) (Kalitzin et al., 2002) associated with any pair of electrodes. We define the time-frequency complex amplitudes $F'_j(t, \omega)$ by using a set of normalized Gabor filters:

$$F'_j(t, \omega) = \int dt' g(t, t', \lambda) S'_j(t')$$

where $\lambda = 2\pi/\omega$ is the aperture of the corresponding Gabor-filter, which is directly connected to the filter's frequency. The univariate PCI associated with electrode $j$ can then be defined as:

$$\kappa_j(t, \omega) = \frac{\left\langle F'_j(t, \omega) \right\rangle}{\left\langle |F'_j(t, \omega)| \right\rangle}$$

with $\langle \rangle$ denoting averaging over all trials $r$. The absolute value (amplitude) of this complex number is always smaller than 1 and indicates the degree of consistency between the phases of frequency components over consecutive trials, for a given frequency and time within an epoch. The phase of the PCI represents the average phase among the trials. Similarly, the mutual phase consistency between traces $j$ and $k$ can be quantified by the complex number:

$$\kappa_{jk}(t, \omega) = \frac{\left\langle F'_j(t, \omega) F'_k(t, \omega) \right\rangle}{\left\langle |F'_j(t, \omega) F'_k(t, \omega)| \right\rangle}.$$  

Where $F'_j(t, \omega)$ indicates the complex conjugate of the time-frequency complex amplitude. High mutual phase consistency can result from a 'genuinely' independent phase locking between the signals. To separate these two options, we define the partialized mutual PCI as:

$$\kappa_{jk}^{\text{partial}}(t, \omega) = \kappa_{jk}(t, \omega) - \kappa_j(t, \omega) \kappa_k(t, \omega).$$

Partialized PCI amplitudes close to one would indicate a phase shift between the two signals that cannot be explained by the univariate PCI. Partialized PCI amplitudes close to one would indicate phase locking averaged over different numbers of trials for the Seen and the Not-Seen condition. The univariate PCI is directly connected to the filter's frequency. The univariate PCI corresponding to PCI amplitudes greater than PCIcr. We found $5\%$ in these random sequences. In other words, the PCIcr determines the corresponding distributions of PCI. We simulated sequences representing instantaneous velocity and direction of eye motion. To control for fixational eye movements and to estimate their effect on the correlations we calculated the standard error of the eye position and measured the incidence of fixational saccades within successive epochs, before and after stimulus onset. Fixational saccades were detected using a velocity threshold of $10^7$ s. To investigate the effects of fixational eye motion on synchrony, we split the neural data into two groups containing an equal number of trials. In the first group (High) the standard error of the eye position of each trial was larger than the median standard error of all trials and in the second group (Low) the standard error of each trial was lower than the median standard error of all trials. We also calculated the strength of correlations between eye velocity and neural response strength over time. For this purpose, two-dimensional cross-correlograms with time versus lag on the $x$-axis and $y$-axis and correlation strength on the vertical axis were calculated.

Results
Figure-ground evoked multi-unit responses from the primary visual cortex are characterized by an initial transient followed by a late modulated response, commencing 70–100 ms after stimulus onset (Fig. 2A). Previously, we have reported that the modulated response is a neural correlate of figure–ground segregation, where the responses to figure elements are stronger than the responses to identical ground elements (also termed contextual modulation and is indicated by the blue shading in Fig. 2A; see Lamme, 1995; Lamme et al., 1998; Zipser et al., 1996).

Here we investigated the time course of correlation coefficients within two-dimensional (time versus lag) cross-correlograms (2D-CC) and compared this with the time course of averaged multi-unit activity responses. This was done for two monkeys (denoted as T and U), and based on trials within the 'seen' condition. The 'seen' condition represented those trials in which the monkeys correctly identified the target position. In the first part of this analysis 2D-CCs were averaged over figure and ground responses grouped together.

Dynamics of Correlated Activity
Characteristically, a correlation peak centered at 0 ms lag can be observed during the total period of analysis, i.e. 250 ms before stimulus until 250 ms after stimulus onset. We define this type of correlated activity, due to the occurrence of peaks with a maximum at zero time lag, as synchrony. Correlated activity was found to reach a maximum before stimulus onset, which then decreases in height and sinks to a minimum well after the initial response transient within the late response period.
As a parameter of the magnitude of synchrony we measured area under the peak between $-25$ to $+25$ ms lag for both monkeys. Consistent with the changes in peak height, a maximum in peak area was found before stimulus onset in both animals ($T: -55 \pm 16$ ms; $U: -43 \pm 17$ ms; time relative to stimulus onset). Following this maximum, the correlations decrease and a minimum in average peak area occurs at $164 \pm 20$ and $124 \pm 30$ ms after stimulus onset for $T$ and $U$, respectively. In addition, the 2D-CCs (Fig. 2B lower panels) indicate that narrowing of the correlations contribute to the decrease of area in the late period.

To quantify the differences between the pre-stimulus and late activity period we averaged auto- and cross-covariance matrices for all electrode combinations (120 per animal) in two 100 ms periods. The first period ending at stimulus onset and incorporating the pre-stimulus maximum and a second period centered on the peak minimum after stimulus onset for $T$ and $U$, respectively. In addition, the 2D-CCs (Fig. 2B lower panels) indicate that narrowing of the correlations contribute to the decrease of area in the late period.

To quantify the differences between the pre-stimulus and late activity period we averaged auto- and cross-covariance matrices for all electrode combinations (120 per animal) in two 100 ms periods. The first period ending at stimulus onset and incorporating the pre-stimulus maximum and a second period centered on the peak minimum after stimulus onset. Due to differences in the time course of the synchrony the second period is thus different for both monkeys ($T: 115–215$ ms; $U: 75–175$ ms after stimulus onset). Both monkeys display a decrease in peak height and peak width in the late (post-) stimulus period in comparison with the pre-stimulus period (Fig. 3A). Correlated activity therefore desynchronizes within most electrode combinations. To capture this transition in correlated activity, the correlation functions were analyzed with respect to three parameters: peak width, peak height and peak area.

As Figure 3A shows, the correlation functions in both monkeys indicate the superposition of a thin correlation peak on a broad correlation peak and it seems that only the broad part of the correlation functions is modulated. Therefore we used peak width at one-third peak height as a measure of peak width. Using this measure, a significant decrease in peak width was found for both animals (sign test, MATLAB: $T: P < 2.5 \times 10^{-11}$, $U: P < 2.0 \times 10^{-7}$). Within a total of 240 correlation peaks, 153 became thinner, 15 became wider, 22 became non-significant and 50 showed no difference in the late period. Since the change was restricted to the lower part of the correlation peaks this suggests a loss of synchrony (desynchronisation) for low-frequency components only.

We then estimated peak height for all combinations of electrodes (Fig. 3B), and found that peak height was significantly smaller in the late period compared to the pre-stimulus period (Sign test: $T: P < 3.2 \times 10^{-11}$, $U: P < 2.0 \times 10^{-5}$). To estimate the significance of the difference between pre-stimulus and late peak height, we used a z-score obtained by $(Z_{pre} - Z_{post})/\sqrt{(2/n - 3)}$, where $n$ = number of trials, for each combination of channels. $Z_{pre}$-values of correlation peak height were obtained after Fisher z-transform of the correlation coefficients. These results show that a large proportion of the channel combinations have a significant ($P < 0.05$) decrease in

(Fig. 2B). As a parameter of the magnitude of synchrony we measured area under the peak between $-25$ to $+25$ ms lag for both monkeys. Consistent with the changes in peak height, a maximum in peak area was found before stimulus onset in both animals ($T: -55 \pm 16$ ms; $U: -43 \pm 17$ ms; time relative to stimulus onset). Following this maximum, the correlations decrease and a minimum in average peak area occurs at $164 \pm 20$ and $124 \pm 30$ ms after stimulus onset for $T$ and $U$, respectively. In addition, the 2D-CCs (Fig. 2B lower panels) indicate that narrowing of the correlations contribute to the decrease of area in the late period.

To quantify the differences between the pre-stimulus and late activity period we averaged auto- and cross-covariance matrices for all electrode combinations (120 per animal) in two 100 ms periods. The first period ending at stimulus onset and incorporating the pre-stimulus maximum and a second period centered on the peak minimum after stimulus onset. Due to differences in the time course of the synchrony the second period is thus different for both monkeys ($T: 115–215$ ms; $U: 75–175$ ms after stimulus onset). Both monkeys display a decrease in peak height and peak width in the late (post-) stimulus period in comparison with the pre-stimulus period (Fig. 3A). Correlated activity therefore desynchronizes within most electrode combinations. To capture this transition in correlated activity, the correlation functions were analyzed with respect to three parameters: peak width, peak height and peak area.

As Figure 3A shows, the correlation functions in both monkeys indicate the superposition of a thin correlation peak on a broad correlation peak and it seems that only the broad part of the correlation functions is modulated. Therefore we used peak width at one-third peak height as a measure of peak width. Using this measure, a significant decrease in peak width was found for both animals (sign test, MATLAB: $T: P < 2.5 \times 10^{-11}$, $U: P < 2.0 \times 10^{-7}$). Within a total of 240 correlation peaks, 153 became thinner, 15 became wider, 22 became non-significant and 50 showed no difference in the late period. Since the change was restricted to the lower part of the correlation peaks this suggests a loss of synchrony (desynchronisation) for low-frequency components only.

We then estimated peak height for all combinations of electrodes (Fig. 3B), and found that peak height was significantly smaller in the late period compared to the pre-stimulus period (Sign test: $T: P < 3.2 \times 10^{-11}$, $U: P < 2.0 \times 10^{-5}$). To estimate the significance of the difference between pre-stimulus and late peak height, we used a z-score obtained by $(Z_{pre} - Z_{post})/\sqrt{(2/n - 3)}$, where $n$ = number of trials, for each combination of channels. $Z_{pre}$-values of correlation peak height were obtained after Fisher z-transform of the correlation coefficients. These results show that a large proportion of the channel combinations have a significant ($P < 0.05$) decrease in

(Fig. 2B). As a parameter of the magnitude of synchrony we measured area under the peak between $-25$ to $+25$ ms lag for both monkeys. Consistent with the changes in peak height, a maximum in peak area was found before stimulus onset in both animals ($T: -55 \pm 16$ ms; $U: -43 \pm 17$ ms; time relative to stimulus onset). Following this maximum, the correlations decrease and a minimum in average peak area occurs at $164 \pm 20$ and $124 \pm 30$ ms after stimulus onset for $T$ and $U$, respectively. In addition, the 2D-CCs (Fig. 2B lower panels) indicate that narrowing of the correlations contribute to the decrease of area in the late period.

To quantify the differences between the pre-stimulus and late activity period we averaged auto- and cross-covariance matrices for all electrode combinations (120 per animal) in two 100 ms periods. The first period ending at stimulus onset and incorporating the pre-stimulus maximum and a second period centered on the peak minimum after stimulus onset. Due to differences in the time course of the synchrony the second period is thus different for both monkeys ($T: 115–215$ ms; $U: 75–175$ ms after stimulus onset). Both monkeys display a decrease in peak height and peak width in the late (post-) stimulus period in comparison with the pre-stimulus period (Fig. 3A). Correlated activity therefore desynchronizes within most electrode combinations. To capture this transition in correlated activity, the correlation functions were analyzed with respect to three parameters: peak width, peak height and peak area.
peak height (T: 60/120; U: 34/120). In contrast, only few channel combinations were found with a significant ($P < 0.05$) increase in peak height (T: 4/120; U: 0/120).

Finally, as a measure of the difference between pre-stimulus and late activity, we estimated area under the peak (Fig. 3C). To estimate area we summed the averaged correlation functions between $-25$ and $+25$ ms lag and normalized these values to obtain similar ranges of values in both animals. Normalization was done by division with the maximum area found within all combinations of electrodes in the pre-stimulus period (this was done for both monkeys separately). Relative differences between periods remain unaffected in this way. A significant decrease of area from pre-stimulus to late activity can be observed (Signed Rank Test: T: $P < 3.5 	imes 10^{-3}$; U: $P < 1.3 	imes 10^{-3}$). This measure gave the most robust difference between pre-stimulus and late activity, which is not surprising because this measure incorporates both height and width changes. This is corroborated by our spectral analysis, showing that the transition in correlated activity involves mainly a decrease of power for frequency components below 40 Hz (Fig. 3D).

Previously we have reported a relation between spatial scale and synchrony (van der Togt et al., 1998). In that study, we provide evidence that broad correlation peaks (low-frequency synchrony) represent common input to a large number of neurons whereas thin peaks are generated within small assemblies of neurons. In the present study, we implanted all the electrodes within an area of $<2$ cm$^2$ of V1 and we selected electrodes that have adjacent or overlapping receptive fields, which fall within a square of $3^\circ$ of visual angle. Based on a cortical magnification factor of 2.5--5.0 mm/degree (Tootell et al., 1988), we estimate that the majority of the electrode pairs have an inter electrode distance of $<1$ cm, approximately half of the pairs $<0.5$ cm and the smallest inter electrode distances $\sim1$ mm. The largest transitions generally occurred within electrode combinations with the largest pre-stimulus peaks. Assuming that stronger synchrony is observed when distances between electrodes become smaller (Das and Gilbert, 1999) then even for nearest electrode pairs a transition in their neural interactions occurs.

**Figure-Ground Responses**

Next we analyzed figure and ground responses separately and compared the 2D-CCs of figure and ground responses within the pre-stimulus and late period, when figure-ground segregation is expressed in the firing rate of the recorded neurons (Fig. 2A). For both the figure and ground conditions a strong transition in synchrony was found in both animals (Fig. 4A shown only for monkey T). Thus, a large decrease in synchrony from pre-stimulus to late post-stimulus activity occurs irrespective of the location of the figure.

![Figure 3](image1)

**Figure 3.** Differences between pre-stimulus and late correlated activity. (A) Averaged cross-correlation functions from the pre-stimulus and late period. Note that the difference is mainly due to change within the lower part of the correlation functions. (B) Scatter plots showing the difference between the heights of the central peak in the pre-stimulus period versus the late period. Black dots show combinations of electrodes with significant changes in peak height, i.e. correlation strength (R). (C) Scatter plot of peak area in pre-stimulus period versus late period. Peak area was calculated between $-25$ and $25$ ms lag and normalized by division with the largest area (pre-stimulus) within all combinations of electrodes. (D) Power of averaged and normalized cross-spectral density functions between 6 and 200 Hz. Black lines denote the pre-stimulus spectral power and gray lines the spectral power within the late activity.

![Figure 4](image2)

**Figure 4.** Cross-correlations of figure and ground. (A) Time course of the correlation coefficient of peak area (calculated from $-25$ and 25 ms lag) for figure and ground trials separately. (B) Strength of figure-ground responses versus strength of the synchrony transition (peak area in pre-stimulus period minus peak area in post stimulus period, see Fig. 3C). Line is linear regression line.
Furthermore, there appears to be a correspondence between the onset of figure–ground modulation (T: 94 ms; U: 62 ms) and the time of the minimum in the late post-stimulus synchrony (T: 164 ms; U: 124 ms). To explore the possible relation between synchrony transition and figure–ground signal, we measured the correlation strength between the amount of figure–ground activity and the extent of desynchronization (change of area under the peak from pre-stimulus to late post-stimulus period). This correlation was weakly positive for both animals within all electrode pairs (Fig. 4B; T: $r = 0.62$, df = 14, $P < 0.005$, n = 120; U: $r = 0.42$, df = 14, $P < 0.05$, n = 120, Spearman Rank). This finding suggests that the strength of contextual modulation depends on the magnitude of desynchronization. To test this further we calculated synchrony in separate figure and ground trials. In monkey U a significant difference in correlation peak area between figure and ground responses was not found (not shown). For monkey T only a small difference in correlation peak area was found in the late period (115–215 ms: $t$-test, $P < 0.05$, $n = 120$). This difference is short lasting and therefore did not reflect the difference in figure and ground responses found earlier (Lamme, 1995; Zipser et al., 1996; Lamme et al., 1998).

**Eye Movements**

A potential concern is that differences in eye position or eye movements during the pre-stimulus and late post-stimulus periods can cause synchrony changes. For example, eye motion may induce common input to neurons leading to an increase in synchrony even without changes in their level of activity. To control for differences in fixation behavior we first determined the distribution of fixation saccades from 200 ms before stimulus onset to 200 ms after stimulus onset. We divided the data into four groups (200–100 and 100–0 ms before stimulus onset, and 0–100 and 100–200 ms after stimulus onset). Microsaccades mainly occurred at the start of fixation (200–100 ms before stimulus onset) and declined to a constant level (Fig. 5B). This finding was confirmed by comparing the averaged standard deviations of the eye positions during four periods. Note that a trial starts after the monkey’s eyes enter the fixation window and that the stimuli are presented 300 ms after correct fixation. We also determined the strength of neural synchrony during these four intervals (Fig. 5C). The neural correlation strength shows a different distribution where the strongest correlations are observed 100 ms before stimulus onset and gradually decrease thereafter (Fig. 5C).

We then divided trials in two groups based on the quality of fixation; one group with relatively good fixation (Low) and one with poor fixation (High; see Materials and Methods). Both saccades and drifting fixational eye movements have been shown to induce neuronal firing in V1 neurons (Snodderly et al., 2001). The standard error of the eye position signal captures both types of eye motion, whereas the velocity threshold method only captures saccade onset and frequency. We present statistics on both measures and it can be seen that the standard error of eye motion is largely reflected in saccade frequency. In fact in the low motion group the majority of the trials have no saccades at all, whereas in the high velocity group the majority of trials contain one or more saccades. On average, saccade frequency in the low motion group is 0.9 in the high motion group 2.7, which shows that the number of saccades in the two groups differed by at least a factor 3. If eye motion is the main cause for the synchrony transition we should see a difference in synchrony between these two groups. In both groups however we found a clear transition in synchrony, i.e. both groups show a significant difference between the pre-stimulus period (100–0 ms) and the late period [100–200 ms after stimulus onset; analysis of variance (ANOVA), $P < 0.05$]. In addition, the transitions in correlated activity were not significantly different between the two groups (Fig. 5C). We also calculated the correlation between eye velocity and neural activity. These results show that eye velocity from pre-stimulus up to 200 ms following stimulus onset was minimally correlated with neural activity. In fact, no transition is noticeable at any time lag up to the time the monkey makes a saccade (Fig. 6A,B). Thus, these results indicate that the desynchronization is not an effect of small eye movements during fixation.

To investigate whether the synchrony transition is related to the target saccade towards the figure location, we analyzed the responses from a delayed figure–ground task where visual responses are separated from saccade related responses (Supér et al., 2004). Here we analyzed the data from the start of fixation (= 300 ms before stimulus onset) until the end of the trial. This analysis shows that also in such a task desynchronization occurs at the time of stimulus presentation (Fig. 6C, lower panel). The fact that desynchronization starts around stimulus onset indicates that the transition is not directly related to the target saccade, which occurs much later (after 1 s). Desynchronized activity continues at a constant level during the entire delay period. In this period a large variation in spike rate occurs. This shows that the transition is not an artifact of the partialization procedure to remove stimulus induced synchrony, since then we would expect a decrease of synchrony only to occur just after response onset, where the highest spike rate levels are reached. We also correlated the eye velocity with neural responses during this task (Fig. 6C, upper panel). Note that the synchrony increase at the end of the trial compares favorably with the synchrony increase between eye motion and neural activity, suggesting that here the neural correlations are related to eye motion. In contrast, although saccades to the fixation point were aligned with trial onset (300 ms before stimulus onset) the correlation between eye motion and neural activity is not comparable to neural–neural correlated activity in the pre-stimulus period (lower panel). These results corroborate earlier findings suggesting that the transition in synchrony is not an effect of small fixational eye movements, and that saccades to the fixation window also cannot explain our results.

**Wavelet Analysis**

Overall, during the trial, the correlations become reduced in size, with significantly thinner peaks at the end of the trial. The power spectra in Figure 3D indicate that this change is caused mainly by a decrease of frequency components below 40 Hz. As described above, the pre-stimulus correlation functions in both monkeys seem to be a superposition of a narrow on a broad correlation peak (Gochin et al., 1991; Nowak et al., 1999). This suggests different modes of neural interaction in the pre-stimulus period, one of which (associated with broad peaks, and low-frequency components) is strongly reduced after the appearance of the stimulus, while the other (narrow peaks) seemingly remains constant. To investigate whether differences in the modulation of frequency components between 5 and 150 Hz occur, we applied wavelet analysis. In this study we use,
as a measure of coherency of any frequency component, the phase clustering index (PCI; Kalitzin et al., 2002; see also Materials and Methods). Without further measures this index would be greatly dominated by the visual response. Therefore, to investigate the mutual (between electrodes) PCIs, independent of the visual response, the effect of the visual response was removed by partialization (see methods). This method is comparable to subtracting the shuffle predictor as was applied to the two-dimensional cross-correlograms (2D-CC).

A good correspondence with the synchrony transition in the 2D-CCs is observed after applying this method (S in Fig. 7). Pre-stimulus PCI amplitudes are large over a wide range of frequency components (5–40 Hz). In one monkey (U) there is also a relatively strong frequency component around 70 Hz, but this neural activity is induced by the monitor frequency.

Following stimulus onset a decrease is observed to non-significant values over the whole frequency range with an incomplete rebound at intermediate frequencies (20–50 Hz) before the monkeys start to make eye movements. Thus, similar to the 2D-CC results, a desynchronization of activity occurs after the stimulus. Furthermore, it can be observed that frequencies below 20 Hz show the greatest difference between pre-stimulus and late activity. These findings agree with the disappearance of the broad part of the correlation functions in the late activity period.

**Seen versus Not-Seen**

On most figure present trials, the monkeys were able to detect the figure (84%, 'Seen' trials), but on some instances (16%, 'Not-Seen' trials). Fixational eye movements. 

Figure 5. Fixational eye movements. (A) Example of eye traces during fixation. Left panel shows traces of the group (High) with relatively many fixational eye movements and right of the group (Low) with few fixational eye movements. Numbers 1–4 represent time period of data analysis (see B–E). Time is relative to stimulus onset. (B,C) Distribution of saccade frequency (B) and peak area (C) during the four periods indicated in (A). Black bars represent data from the group with many fixational eye movements and gray bars the group with few eye movements. Note extraordinarily high frequency of saccades (7/s) in the first bin in (B). This high value is due to the many cases in which one or two small correctional eye shifts follow the main saccade to the fixation window. Overall we find a saccade frequency of 1–3/s in accordance with other studies. This indicates that our velocity threshold of 10°/s is sufficiently above the noise of the eye position data (D,E). Distribution of fixational saccades in the Seen (black) and Not-Seen (gray) condition (D) and of the standard deviation of the eye position (E). NS and * signify no significant and a significant (P < 0.05) difference between conditions within one period, respectively.
’Not-Seen’ trials) the figure was not detected (Supèr et al., 2001). Since the stimulus was identical in both conditions, differences in behavioral responses must have been due to some difference in cortical state, possibly reflecting changes in attention or expectancy (Fries et al., 2001). We were therefore interested in whether the synchrony transition varies with the ability of the monkey to detect the stimulus. This was done by comparing two dimensional cross-correlation functions (2D-CCs) for Seen versus Not-Seen trials and, as will be described below, by differences in the magnitude of the spectral components (PCI) for these two-conditions.

Figure 8A,B shows an example of the difference in this transition for averaged Seen and Not-Seen trials. In the Not-Seen condition a clear transition is lacking. Since area under the peak was by far the most robust parameter of the difference between pre-stimulus and late activity and a good estimate of the total correlated activity, we analyzed the development of peak area between -25 and 25 ms delay for Seen and Not-Seen trials. Seen trials start out with a higher area under the peak than Not-Seen trials, yet end up with a smaller area under the peak during the late period (Fig. 9A). For the Not-Seen condition there was a significant reduction in synchrony in the pre-stimulus period (Fig. 9B; Student’s t-test; T: \( P < 5.0 \times 10^{-5} \); U: \( P < 1.0 \times 10^{-14} \), \( n = 120 \)) and a significantly stronger synchrony in the late period (Fig. 9C; Student’s t-test; T: \( P < 1.5 \times 10^{-15} \); U: \( P = 0.019 \), \( n = 120 \)). The distribution of differences for Seen versus Not-Seen was skewed in several instances. Although tests for normality did not show that these distributions significantly differed from normal distributions, we nevertheless applied a nonparametric Sign test. A non-significant difference was only found monkey U in the late period between Seen and Not-Seen. When values from both animals were combined significant differences were found for both pre-stimulus (Sign test; \( P < 8.0 \times 10^{-6} \), \( n = 240 \)) and late period (Sign test; \( P < 3.0 \times 10^{-13} \), \( n = 240 \)). These results indicate significantly higher synchrony in the pre-stimulus period and lower synchrony in the late poststimulus period for Seen versus Not-Seen.

Finally, subtracting late peak area from pre-stimulus peak area yields the transition difference for each combination of electrodes (Fig. 9D). The transition was stronger for Seen trials compared with Not-Seen trials. The difference in transition was highly significant (Sign test: T: \( P < 3.0 \times 10^{-13} \), \( n = 120 \); U: \( P < 3.0 \times 10^{-13} \), \( n = 120 \)). Even if we assume that the synchrony transition is evoked by the stimulus, these results suggest that it is modulated by attention or expectancy. Note also that our statistics may underestimate this proposed effect of attention. A number of electrode combinations that were included in the analysis have small insignificant correlation peaks in the pre-stimulus period and show indeterminate differences in the late period. We have not excluded these cases and they possibly reflect combinations of electrodes with the largest separations since correlations between neurons have been shown to decrease with cortical distance (Das and Gilbert, 1999).

Similar differences are also found in the time–frequency plane between Seen and Not-Seen trials using the PCI (Fig. 7). Analysis of the differences between Seen and Not-Seen trials was done by subtracting Not-Seen from Seen PCI amplitudes for all channel combinations and all components in the time–frequency plane (see Materials and Methods). For each component in the time–frequency plane a distribution of differences was thus obtained for all electrode combinations. Figure 7D shows t-scores for the mean of each distribution in the time–frequency plane. In the figures we show areas of values where the most significant differences were found (absolute value \( >3, \)
corresponding to a confidence level with $\alpha = 0.005\%$, for $n = 120)$. The results of this analysis show that in monkey U the greatest difference between Seen and Not-Seen trials occurred immediately after stimulus onset, and is expressed as a larger decrease in phase consistency around 10 Hz for Seen trials. In the other monkey (T) the predominant difference is an enhancement of synchrony for Seen trials in the pre-stimulus period, for frequency components between 10 and 20 Hz. Thus, the results show that the main effects of the difference in synchrony transition between Seen and Not-Seen condition is found in the low-frequency components. In both monkeys these differences support...
a synchrony transition with greater magnitude for the Seen case, although time of occurrence and sign are seemingly different. Note also that the differences do not seem to be well associated with stimulus or response onset, which suggests a role for attention as a cause for these differences.

The differences in correlated responses between Seen and Not-Seen condition are not likely caused by differences in eye movements. We measured both the probability of fixational saccades and standard error of eye position (Fig. 5D, E) and compared the differences between Seen and Not-Seen trials. The findings show that fixational eye movements do not significantly differ between the Seen and the Not-Seen condition during the pre-stimulus and late periods (ANOVA, P > 0.05).

Interestingly during the correlation transition, a short enhancement of broad peak synchrony (80–100 ms after stimulus onset) can be observed for Seen trials and not for Not-Seen trials (Figs 2B, 8 and 9A). To analyze this enhancement, the difference in area was estimated between this and the preceding window of 20 ms for all combinations of electrodes. Comparison between Seen and Not-Seen trials demonstrated a significant enhancement of broad peak synchrony for Seen trials (Sign test; T: P < 5.0 × 10^{-4}; U: P < 3.2 × 10^{-12}). Thus during the longer decrease of synchrony around stimulus onset, a transient increase in synchrony is observed which may be related to the detection of the figure.

### Discussion

We have studied the dynamical changes in synchronous activity that occur in the primary visual cortex during figure-ground discrimination, within 2D-CC and within the time–frequency plane based on the distribution of mutual phase consistency (PCI). Our correlation functions are comparable to the JPSTH developed by Aertsen et al. (1989) to study dynamical changes in correlated activity. We prefer the term two-dimensional cross-correlogram because our sampled signals represent a continuous waveform of the neural firing rate (see Materials and Methods) and not single spikes, binned into discrete epochs. With both methods (2D-CC and PCI) we find an increase in synchronous activity before stimulus onset and a desynchronization of activity following stimulus onset. Nevertheless, overall changes in synchrony are better reflected by the 2D-CCs than the PCI distribution. The latter gives an indication of the dominant frequency components within dynamical changes of synchronous activity. Since both increases and decreases of coherency for different frequency components may occur during a perceptual task, the impact of changes in synchrony is better reflected in terms of change in correlation peak area.

The partialization procedure we applied removes stimulus locked synchrony. How much synchrony is removed depends on the spike level in the PSTH of both MUA traces. The desynchronization we observe could therefore be an artifact of this procedure since the spike rate increases greatly after stimulus onset. A large peak of spike firing occurs in the average PSTH of monkey T between 50 and 100 ms after stimulus onset, and around 100 ms in the PSTH of monkey U. If partialization has this effect it should lead to a particularly strong, albeit short desynchronization at these same time periods. Within the 2D-CCs this does not seem to be the case. On average maximal desynchronization occurs later as spike rate decreases. The same logic can be applied to the PCI. Indeed, here a short, sudden and complete desynchronization can be seen at these moments in time. However, beyond these periods the spike rate can even be lower than in the pre-stimulus period (Fig. 2A), nevertheless PCI amplitudes remain lower (<20 Hz) in the late period than in the pre-stimulus period. This is even more striking in a delayed response task where synchrony remains at a low level until the monkey makes a saccade to a visual target. This shows that the synchrony transient is not an artifact due to partialization.
Figure-Ground and Synchrony Transition

Our results are in agreement with previous reports which show a desynchronization at stimulus onset within area MT/MST (Cardoso de Oliveira et al., 1997) and in visual areas (EEG, MEG) in association with a perceptual response (Rodriguez et al., 1999). Our results show that the transition mainly involves frequency components below 20 Hz. As a consequence, synchrony evolves from broad correlation peaks before stimulus onset to small, thin peaks during the late response period.

We did not find an increase in high-frequency synchrony for figure versus ground responses nor changes in high-frequency coherency as a perceptual correlate of stimulus detection. This seems to conflict with a substantial amount of literature that shows modulation of gamma oscillations induced by visual stimulation (Eckhorn et al., 1988, 1993; Gray et al., 1989; Engel et al., 1991), related to changes in attention (Steinmetz et al., 2000; Fries et al., 2001) or associated with a perceptual task (Tallon-Baudry et al., 1997, 1998; Rodriguez et al., 1999; Gail et al., 2000; Fries et al., 2002; Woelbern et al., 2002; but see Gail et al., 2004; Gross et al., 2004). We note, however, that the type of stimulus used in the present study is fundamentally different from those in the cited literature. The texture elements that make up the figure evoke a strong activation of V1 neurons. However, particularly for the receptive fields that were recorded from (either in the center of the figure or in the background), local feature interactions are completely irrelevant for identifying the figure or making a perceptual choice. Contextual information well beyond the receptive fields (see Fig. 1) and well beyond possible intra-cortical lateral interactions (Das and Gilbert, 1999) determine the presence of a figure. Whether gamma oscillations develop representing feature combinations at the contours of the stimulus, or in higher order visual regions, where large figure features are bound, cannot be tested nor refuted with the present study. Feedforward activation and local feature combinations within the stimuli used here are identical irrespective of all conditions in the present study (figure versus ground, Seen versus Not-Seen). This underscores that the effects we observe are mediated by feedback connections.

Evidence shows that figure-ground discrimination depends on the presence of late modulated activity (Supér et al., 2001), which is probably mediated by feedback projections (Lamme et al., 1998). The synchrony transition is not spatially selective and occurs irrespective of the figure location. This indicates that the transition in synchronous activity does not represent figure-ground segregation, which is consistent with psychophysical (Kiper et al., 1996; Farid and Adelson, 2001) and earlier neurophysiological studies (Lamme and Spekreijse, 1998; Shadlen and Movshon, 1999; Bair et al., 2001; Thiele and Stoner, 2003). However, a transition in synchronous activity may be essential for detecting the stimulus. We showed a significant correlation between the strength of the synchrony transition and the strength of the figure-ground activity, and if no or weak desynchronization occurs the figure will not be perceived (present study). Therefore, the role of desynchronization in figure-ground discrimination may be to facilitate its occurrence.

Fixational Eye Movements and Feedforward Signals

Fixational eye movements have been shown to evoke bursts of activity in single neurons when an optimally oriented stimulus is within their receptive field (Martinez-Conde et al., 2000, 2002; Snodderly et al., 2001). Since fixational eye movements affect the whole visual field, they could induce wide scale synchronous activity in the visual cortex. However, the single unit data from these studies may not be directly applicable to our results. Visual stimulation in our multi-unit recordings was on average non-optimal, which ameliorates the effects of fixational eye movements on neural activity (Martinez-Conde et al., 2002). This may explain why we did not observe any correlation between eye movement and neural activity, which is in agreement with an earlier report (Supér et al., 2004). Moreover, during the period of fixation we did not find any difference in fixational eye motion for the Seen and Not-Seen conditions, whereas we did find a difference in synchrony transition between these two conditions. In contrast, if we compare trials with a relatively high amount of eye movements to trials with a low amount of eye movements we find a transition in neural synchrony in both conditions that is equally strong.

Could the transition in synchrony be due to the stimulus? Not as a by-product of the partialization but as an actual decrease of correlated activity evoked by the stimulus. It has long been known that visual stimulation evokes a desynchronization of the EEG (Moruzzi and Magoun, 1949; Morell, 1967; Vijn et al., 1991), and this is confirmed by recent findings showing that an appropriate stimulus has a very strong desynchronizing effect on the cortex (Miller and Schreiner, 2000). The change in synchrony we observe may thus well be partly due to the stimulus. However, several observations indicate that the stimulus alone cannot explain the changes we observe. For example, whereas the visual response onset is at ~40 ms in both monkeys, the time course of the transition not only completely differs from the time course of the response, but is also different for both monkeys (see Fig. 2). In addition, we observed a difference in the strength of the synchrony transition between Seen and Not-Seen cases whereas the visual stimuli are identical and the visual evoked responses are not significantly different for these two conditions (see also Supér et al., 2003). Finally, the enhancement of synchrony before the presentation of the stimulus and its precocious decline cannot be induced by the change in stimulus configuration (= appearance of the figure-ground texture).

Altogether, this strongly suggests that visual stimulation and small eye movements cannot explain our results.

Low-frequency Components

Correlated activity has been interpreted as a global state reflecting task engagement (Rougeul et al., 1979; Donoghue et al., 1989) or attentional state (Murthy and Fetz, 1996) in the motor cortex and expectation (Cardoso de Oliveira et al., 1997; Worden et al., 2000) or attention (Fries et al., 2001) in the visual cortex. Such interpretations are consistent with a modulation of synchrony before stimulus onset. Previous findings show that synchronous activity in the median (8–20 Hz) frequency range occurs in alert subjects in various cortical areas (Mima et al., 2001), which may reflect top-down feedback (Vanni et al., 1997; Watanabe et al., 1998; Siegel et al., 2000; Pessoa et al., 2003) and affect the discrimination and detection of stimuli (Von Stein et al., 2000; Fanselow et al., 2001; Sherman, 2001; Weyand et al., 2001; Gross et al., 2004). In our study, frequency components below 20 Hz also play a prominent role in the synchrony transition. Since low-frequency activity is generally associated with less attentive states, a larger decrease in low-frequency synchrony after
stimulus onset is consistent with the notion that the monkeys have a higher level of attention in the Seen condition. However, the increase of low-frequency synchrony before stimulus onset for the Seen condition is surprising in this context. Note also that due to the difficulty of the task, the monkeys had to maintain a high level of attention. This suggests that the state of the visual cortex does not reflect general attentiveness but rather momentary demands of a perceptual task. Since the visual task was repeatedly done with an identical fixation period, the pre-stimulus increase of synchrony may therefore reflect the expectancy of the monkey, in the sense that the stimulus is not expected within that period of time. In this period, visual cortical activity may reflect a state of idleness or some kind of resetting (Rodriguez et al., 1999; Gross et al., 2004).

Hypothesis

In order to explain the results, we propose that the transition in synchrony reflects a state change of the cortex. This process might be envisioned in the following manner. Pre-stimulus synchronization of low-frequency activity reflects anticipatory feedback from higher visual areas (Von Stein et al., 2000). This feedback suppresses local (high-frequency) dependencies between visual neurons (a cleaning of the slate, reset), that are associated with local feature combinations in former sensory input. When new sensory information arrives this low-frequency activity disappears (desynchronization) and new, local and possibly even inter-areal high-frequency dependencies may develop (Frien et al., 1994; Roelfsema et al., 1997; Tallon-Baudry et al., 1997). This type of activity may be more optimal for selective modes of information transfer (Azouz and Gray, 2000), and facilitates figure–ground perception (Supér et al., 2001; present study). With new incoming visual information this process is then repeated iteratively.

Conclusion

In conclusion, our results show that during figure–ground discrimination a transition in synchronized activity occurs. This transition is characterized by a change from broad correlation peaks before stimulus onset towards thin correlation peaks after stimulus onset, suggesting a break down in the spatial scale of neural interactions (Silberstein, 1995; Steriade et al., 1996; Van der Togt et al., 1998). The strength of this transition predicts whether the monkey will detect the stimulus correctly or not. We propose that the change in synchronized activity reflects a change in visual cortical state.

Notes

We would like to thank Dr Pieter Roelfsema for helpful comments on earlier versions of this manuscript. We also thank Kor Brandsma and Jacques de Feiter for biotechnical support, and Peter Brassinga and Hans Meester for technical assistance. This study was supported by a Medical Science (MW) grant from the Netherlands Organization for Scientific Research (NWO).

Address correspondence to Chris van der Togt, Department of Vision and Cognition, The Netherlands Ophthalmic Research Institute, Meibergdreef 47, 1105BA Amsterdam, The Netherlands. Email: c.vandertogt@ioi.knaw.nl.

References


