nature neuroscience

Synchrony and covariation of firing rates in the primary visual cortex during contour grouping

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The visual system imposes structure onto incoming information, by grouping image elements of a single object together, and by segregating them from elements that belong to other objects and the background. One influential theory holds that the code for grouping and segmentation is carried by the synchrony of neuronal discharges on a millisecond time scale. We tested this theory by recording neuronal activity in the primary visual cortex (area V1) of monkeys engaged in a contour-grouping task. We found that synchrony was unrelated to contour grouping. The firing rates of V1 neurons are also correlated across trials. We demonstrate that this rate covariation is mainly determined by fluctuations in visual attention. Moreover, we show that rate covariation depends on perceptual grouping, as it is strongest between neurons that respond to features of the same object.

The binding-by-synchronization hypothesis holds that neurons that respond to features of one object fire their action potentials at the same time, but neurons responding to features of different objects do not[1–4]. In vision, neuronal synchrony could thereby bind together all the features of one object and segregate them from features of other objects and the background. Several studies have supported this hypothesis by showing that synchrony between neuronal responses to the same perceptual object is stronger than synchrony between responses to different objects[3–8]. There are, however, also conflicting results that cast some doubt on the generality of the role of synchrony in feature binding[9–11]. These discrepancies may be related, in part, to the use of awake animals in some studies and the use of anesthetized animals in others. Moreover, studies with awake animals usually did not involve tasks that require perceptual grouping, and it is therefore unclear which features were bound in the animal's perception. One exception is a recent study[11] that used plaid patterns composed of moving gratings that can be perceived as moving either coherently or incoherently. Synchrony among neurons in the middle temporal visual area (MT), a motion sensitive area, was not enhanced for the coherently moving gratings, which provides evidence against binding-by-synchronization. Even in this study[11], however, perceptual grouping of the gratings was tested before, not during, measurement of synchrony.

In the present study, we investigated contour grouping in monkeys by using a curve-tracing task. In this task, the monkeys indicate which of two red circles is connected to a fixation point by a curve (target curve in **Fig. 1a**). To solve this task, the animals have to group together all contour segments that belong to the target curve. We recorded neuronal responses in area V1 and investigated whether or not there is a difference in synchrony between responses evoked by grouped contours and those evoked by nongrouped contours. This task has three main advantages over tasks used in previous studies. First, the monkeys report about perceptual grouping on every trial, and we can therefore be confident about their perceptual organization. Second, we can change the grouping by varying the stimulus at locations remote from the receptive fields (RFs), while keeping the RF contours constant. Third, we can make grouping difficult or even ambiguous by changing the stimulus at locations where curves come close together.

In addition to synchronization of neuronal activity within trials, we also investigated correlations across trials. If a neuron's response strength is above average on a particular trial, then the responses of other neurons also tend to be stronger[12–17]. At present, little is known about the factors that cause this covariation of firing rates. A previous study suggests that rate covariation and synchrony might be manifestations of a single process[16]. A process that causes correlated fluctuations in neuronal activity within trials could, in principle, also cause correlated fluctuations in spike count across trials. We investigated whether the factors that influence synchrony also affect rate covariation.

Another factor that may cause rate covariation is fluctuations in the animal's attentional state. We distinguished between the possible effects of arousal and selective attention. On the one hand, fluctuations in the animal's arousal may influence the general excitability of cortical neurons, and thereby cause a nonspecific rate covariation. On the other hand, fluctuations in selective attention may enhance responses evoked by one curve at the expense of responses evoked by the other curve, and thereby cause a rate covariation that is specific, because it would only occur among neuronal responses evoked by the same curve. It has been shown[18] that curve tracing is associated with shifts of selective attention. In this previous study, human observers were presented with a dual-task situation, where the primary task was to trace a target curve flanked by one or two distracting curves, and the secondary task was to report a color on one of the curves.

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Published online 22 August 2004; doi:10.1038/nn1304

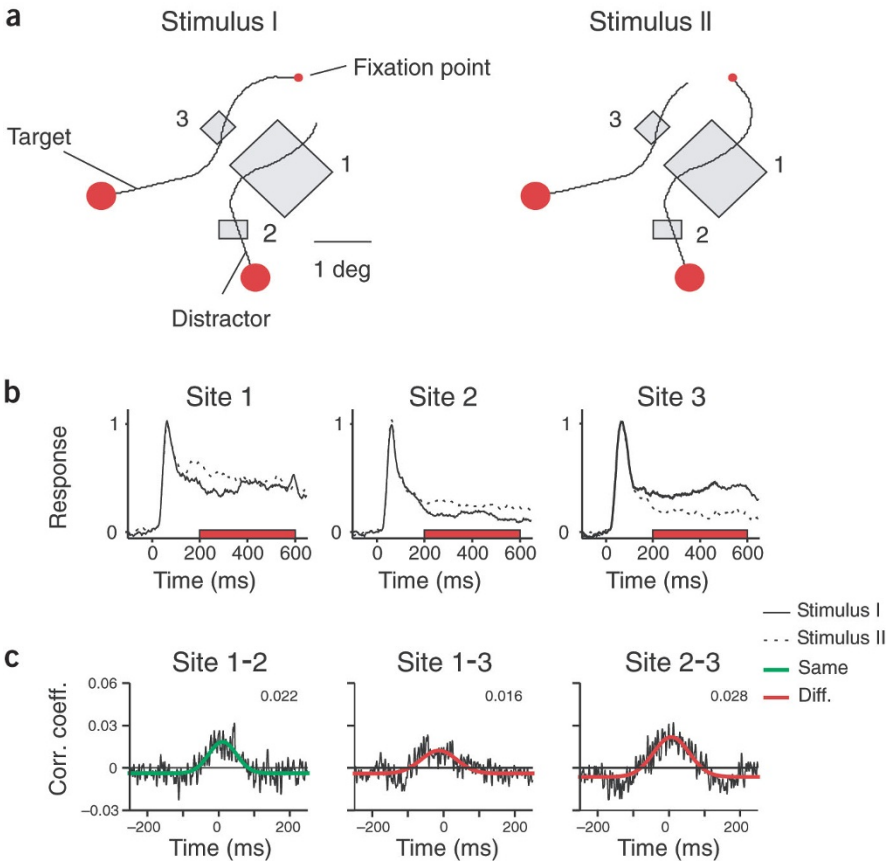

Figure 1 Neuronal synchrony in area V1 during contour grouping. (**a**) Two stimuli. For each stimulus, the monkey had to locate a large red circle at the endpoint of the target curve that was connected to the fixation point (small red circle). Gray rectangles indicate the receptive fields of three multi-unit recording sites in area V1. (**b**) Normalized responses at each of the recording sites. Responses are strongest for sites with a receptive field on the target curve. Stimulus II evoked the strongest response at sites 1 and 2, whereas neurons at site 3 responded more strongly to stimulus I. Red bars indicate the window used for correlation analysis (200–600 ms after stimulus onset). (**c**) Cross-correlation functions between neuronal responses evoked by stimulus I. Green and red traces show fits to correlation functions between neuronal responses to the same and to different curves, respectively. Correlation coefficient (ρ) values are shown at the top-right of each graph.

Secondary task performance was best when the to-be-reported color was located on the target curve. This target superiority effect was observed for all segments of the target curve, implying that attention is directed to the whole curve[18,19]. A correlate of attentional shifts can be observed in area V1 of monkeys that carry out a curve-tracing task, since neuronal responses evoked by the target curve are stronger than responses evoked by the distractor curve[20]. This response enhancement was observed for all segments of the target curve[20]. Here we show that rate covariation in area V1 is mainly caused by trial-to-trial fluctuations in the allocation of attention. Moreover, we demonstrate that the rate covariation is influenced by perceptual organization, since it is strongest between neuronal responses evoked by contour segments that are grouped together in perception.

RESULTS

The curve-tracing task is illustrated in **Figure 1a**. The monkeys first directed their gaze to a fixation point that was at one end of a curve (target curve). The monkeys had to locate a red target circle at the other end of this curve. There also was a distractor curve that was connected to a second red circle, but this curve was not connected to the fixation point. Thus, the monkeys could locate the target circle by grouping all contour segments of the target curve together into a coherent representation. They maintained fixation at the fixation point for 600 ms, and then reported about their percept by making an eye movement to the target circle. A small change close to the fixation point switched the target and distractor curve (compare stimuli I and II in **Fig. 1a**), and these two complementary stimuli were randomly interleaved. When the monkeys had learned the task, electrodes were implanted chronically in area V1, in four hemispheres of three monkeys, to record multi-unit activity (MUA) (**Supplementary Methods** online). The monkeys were proficient on the task: their performance was 99.1% correct, averaged across all recording sessions.

Here we present data from three experiments. Three monkeys were tested in experiment 1, which compares the interactions between neurons with RFs on the same or different curves. Two of these monkeys were also tested in experiments 2 and 3. Experiment 2 investigates whether the interactions change if the stimulus is different. Experiment 3 tests how the interactions depend on task difficulty. For each experiment, we describe first the synchrony of neuronal discharges within trials, and then the covariation of firing rates across trials.

Experiment 1: synchrony and perceptual grouping

To investigate how grouping influences synchrony, we compared the interactions between neurons with RFs on the same and on different curves. Nearby RFs always fell on the same curve, since the target curve did not come close to the distractor curve. We therefore focused our analysis on the paired recordings with RF centers separated by more than 1 degree of visual angle ($n = 235$). Neurons at these cortical distances respond to different parts of the same curve or to different curves. **Figure 1a** shows the RFs of three simultaneously recorded groups of neurons in area V1. The RFs of recording sites 1 and 2 were on one of the curves, and the RF of recording site 3 was on the other curve. The neurons first displayed a transient response, shortly after the stimulus appeared in their RF (time 0 in **Fig. 1b**). This was followed by a more sustained response caused by the continuous presence of a contour in the RF during the 600-ms fixation delay. At each of the three recording sites, the sustained response to the target curve, which was connected to the fixation point, was stronger than the response to the distractor curve (**Fig. 1b**), as has been described previously[20].

To measure synchrony, we computed cross-correlations in a window from 200 to 600 ms after stimulus onset (**Fig. 1c**). Stimulus-locked synchrony was removed (subtraction of shift predictor, see **Supplementary Methods**). The cross-correlation functions have peaks with full-width half-maximum of approximately 100 ms, indicative of coupling at a time scale of several tens of milliseconds.

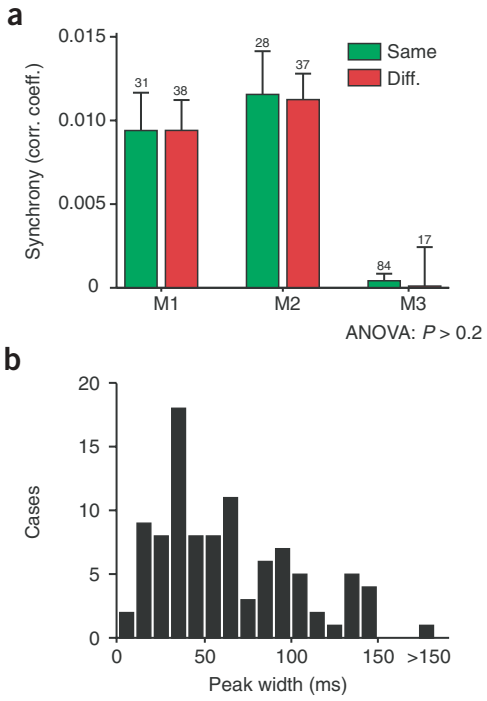

Figure 2 Population analysis of synchrony. (**a**) Strength of synchrony (average correlation coefficient) between neuronal responses to the same (green bars) and different curves (red bars) for each of the monkeys (M1, M2, M3). Error bars represent standard error of the mean (s.e.m.). Number of cases is indicated above the error bars. (**b**) Distribution of the widths of significant peaks (n = 98 out of 235 paired recordings) in the cross-correlation functions.

The strength of the synchrony was quantified by the correlation coefficient. Recording sites 1 and 2, which had their RFs on the same curve, were coupled with a correlation coefficient (ρ) of 0.022. This is intermediate between the strength of synchrony between sites 1 and 3 (ρ = 0.016) and sites 2 and 3 (ρ = 0.028), which were pairs that responded to different curves (**Fig. 1c**). Thus, in this example, strength of synchrony was unrelated to contour grouping.

To investigate the effect of grouping at the population level, we compared the synchrony between neurons with RFs on the same curve (same-pairs, n = 143) to the synchrony between neurons with RFs on different curves (diff-pairs, n = 92). For the same-pairs, both RFs were on the target curve for one stimulus and on the distractor curve for the complementary stimulus (**Fig. 1a**, sites 1 and 2), and we averaged the correlation coefficient across these two conditions. This is justified because the strength of synchrony evoked by the target and distractor curve was similar (see below). Correlation coefficients were also averaged across two complementary stimuli for the diff-pairs, where one RF always fell on the target and the other on the distractor curve (**Fig. 1a**, sites 1 and 3). Synchrony between responses to different curves was as strong as synchrony between responses to the same curve (**Fig. 2a**) (two-way ANOVA, $F_{1,229} = 0.03$, $P > 0.2$). Overall, the correlation coefficients were rather small, but this was due to the small bin size of the cross-correlation functions (1 ms). Larger correlation coefficients were obtained with larger bin sizes, but even with larger bin sizes, the strength of synchrony did not differ between neuronal responses to the same and different curves. The strength of synchrony did, however, differ between monkeys ($F_{2,229} = 27$, $P < 0.001$), because it was relatively weak in one of them (M3). This indicates that each monkey has its own stereotypical synchronization strength, but the strength of synchrony is unrelated to contour grouping.

We considered the possibility that synchrony reflects grouping just after stimulus appearance, but not at a later point in time during the trial. We therefore repeated our analysis in an earlier time window, from 0–400 ms after stimulus onset. In this window, which included the initial transient response, the strength of synchrony did not differ between neuronal responses to the same and different curves ($F_{1,229} = 2.4$, $P > 0.1$). Thus, synchrony is also unrelated to contour grouping during the initial transient response.

Peaks of the correlation functions had a median width at half-maximum of 64 ms (**Fig. 2b**). This indicates that V1 neurons are relatively loosely coupled in time. Synchrony in previous studies that established a link with binding was temporally more precise, and often associated with oscillations in the gamma-frequency range (30–80 Hz)[3–7]. The incidence of this type of synchrony rapidly decreases with increasing cortical distance[21–24]. When we included only those recording sites with RFs separated by more than 1°, because our focus was on synchrony between responses to spatially separate contour segments, we obtained only one case of gamma synchrony (out of 235 paired recordings, incidence <1%). When we evaluated gamma synchrony for pairs of recording sites with RFs closer than 1°, we observed a significantly higher incidence (8 out of 96 cases; 8%, $\chi^2 = 16.1$, 1 d.f., $P < 10^{-4}$). This indicates that the incidence of gamma synchrony decreases too fast with increasing cortical separation to support perceptual grouping of distant contours, as was required in the curve-tracing task.

Synchrony and attention

Previous studies show that human observers, while performing the contour-grouping task, direct their attention to all contour segments that belong to the target curve[18,19]. We noted that responses evoked by the target curve were stronger than responses to the distractor curve (**Fig. 1b**). A similar enhancement of neuronal responses to the target curve was also evident at the population level (n = 96, $P < 10^{-6}$) (**Fig. 3a**). This suggests that this response enhancement is a correlate of selective attention, which is directed to the target curve[18–20].

A number of recent studies suggest that attention also influences temporal aspects of the neuronal responses. Attended stimuli have been shown to enhance synchronization[25,26] and to increase power in the gamma band (30–80 Hz)[26,27]. Gamma synchrony might increase the saliency of some visual objects over others, a function that differs from the proposed role of synchrony in feature binding. To investigate this possibility in the context of our task, we compared power spectra of neuronal responses evoked by the target and distractor curves. The gray region in **Figure 3b** shows the average power-spectrum across all recording sites (n = 96) in a 300-ms window of spontaneous activity before the stimulus appeared. The visual stimulus increased power in the gamma frequency range (**Fig. 3b**) and decreased power at lower frequencies (5–20 Hz), as compared with frequencies seen in spontaneous activity. These data are in accordance with previous studies[3,4,26,28,29]. The target curve, which was attended, evoked slightly more power than the distractor curve, but this additional power increase was relatively homogeneous across frequencies. Thus, attention does not enhance power in one specific frequency range.

To investigate how attention influences synchrony, we compared the cross-correlation functions between neuronal responses to the target and distractor curves. In this analysis, we included only same-pairs (n = 143 paired recordings). For these cases, stimuli with both RFs on either the attended target curve or on the unattended distractor curve

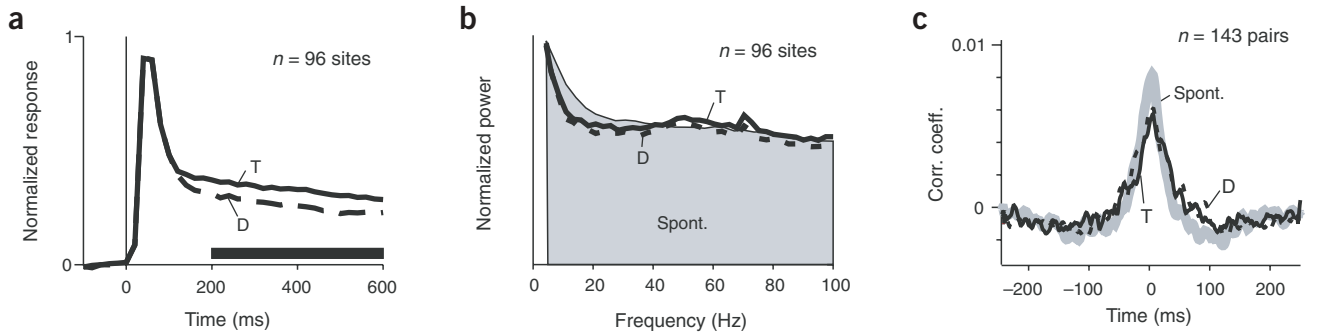

Figure 3 Effects of attention. (**a**) Population response averaged across the 96 recording sites. Continuous trace represents average response to the target curve (T). Dashed trace represents average response to the distractor curve (D). (**b**) Power spectrum averaged across the 96 recording sites. Gray area, normalized power spectrum of spontaneous neuronal activity in a 300-ms window before stimulus appearance. Continuous and dashed traces indicate average power spectra evoked by the target and distractor curve, respectively. (**c**) Average cross-correlation functions across the 143 sites with RFs on the same curve. Gray trace, average cross-correlation function in a 300-ms window of spontaneous activity. Continuous and dashed traces show average correlation functions between responses evoked by the target and distractor curve, respectively.

were randomly interleaved. The appearance of the visual stimulus decreased the peak in the cross-correlation functions, as compared to the spontaneous activity, in accordance with a previous study[30] (**Fig. 3c**). The strength of synchrony between neuronal responses to the target curve did not differ from the strength of synchrony between responses to the distractor curve (paired t test, $t_{142} = -0.7$, $P > 0.3$). Thus, we conclude that selective attention does not influence the strength of synchrony in the curve-tracing task.

Rate covariation

In addition to synchrony of neuronal discharges within a trial, the firing rates of cortical neurons were also correlated across trials[12–17]. **Figure 4a,b** illustrates the rate covariation between neurons at three recording sites (the same as in **Fig. 1**). If the response strength of neurons at recording site 1 was above average on a particular trial, then the response at recording site 2, evoked by the same curve, also tended to be stronger ($\rho = 0.33$, $P < 0.0005$). The rate covariation between the other two pairs of recording sites with RFs on different curves (1-3 and 2-3) was weaker ($\rho = 0.16$ and 0.17, respectively) than that for pair 1-2. Therefore, in this example, the firing rates of neurons that responded to the same curve were coupled more strongly than the firing rates of neurons that had their RFs on different curves. To investigate whether perceptual grouping also influences rate covariation at the population level, we repeated this analysis for each pair of recording sites. We computed the rate covariation separately for the two complementary stimuli and included the average value in the population statistics. The average rate covariation between neurons with RFs on different curves was 0.16, and that between neurons with RFs on the same curve was 0.24 (44% stronger; ANOVA, $F_{1,229} = 7.3$, $P < 0.01$; **Fig. 4c**).

The stronger rate covariation between same-pairs could be caused by trial-to-trial fluctuations in the attentional enhancement of responses to the target curve, and/or by similar fluctuations in the suppression of responses to the distractor curve (**Fig. 3a**). We considered two possible effects of attention. First, there might be a difference in the strength of the rate covariation induced by the target and distractor curve. We therefore compared the strength of the rate covariation evoked by the target and distractor curve for the 143 same-pairs. The strength of the rate covariation was similar for the two curves ($\rho_{target} = 0.22$, $\rho_{distractor} = 0.22$, paired t test: $t_{142} = -0.16$, $P > 0.2$).

Second, rate covariation might depend on the type of recording site. In our sample, neurons at 56 out of 96 recording sites (58%) had a significantly stronger response to the target curve than to the distractor curve (A sites; sites with an attentional effect that reached statistical significance, $P < 0.025$, U test). Such a response enhancement did not occur at the other 40 sites (42%; N sites; sites with no attentional effect). The lack of an attentional effect at N sites was not associated with reduced visual responsiveness (**Supplementary Fig. 1** online) or weaker orientation tuning. We hypothesized that neurons at A sites might engage in stronger interactions with distant cells than do neurons at N sites. To investigate this possibility, we sorted all paired recordings into three categories: N-N pairs (two N sites, $n = 78$ pairs), N-A pairs (one N site and one A site, $n = 71$ pairs) and A-A pairs (two A sites, $n = 86$ pairs). The covariation of firing rates was strongest ($\rho = 0.39$) for A-A pairs, weaker for N-A pairs ($\rho = 0.21$) and very weak for N-N pairs ($\rho = 0.02$) (**Fig. 4d**). The significance of these effects was evaluated using a three-way ANOVA with the following factors: attention (N-N, N-A or A-A pair), grouping (RFs on the same or different curves) and monkey (M1, M2 or M3). The main effect of attention was highly significant ($F_{2,218} = 176$, $P < 0.001$). Grouping also had a significant main effect ($F_{1,218} = 7.1$, $P < 0.01$), but there was no effect of monkey, which indicates that the rate covariation was relatively similar across monkeys ($F_{2,218} = 1.4$, $P > 0.2$) (**Fig. 4c**).

It should be noted that we computed rate covariation separately for each stimulus before we averaged correlation coefficients across complementary stimuli. This implies that the fluctuations around the enhanced responses evoked by the target curve at A sites are correlated, and that the fluctuations around the depressed responses evoked by the distractor curve are correlated too. We conclude that neurons at A sites are special, because they engage in strong interactions with neurons at other cortical locations. The firing rate of neurons at N sites was only weakly coupled to events in the surrounding cortex, indicating that they may be primarily concerned with the information inside their classical receptive fields.

An unexpected finding was that the average covariation between responses at A sites with RFs on different curves was also large and positive ($\rho = 0.34$) (rightmost red bar in **Fig. 4d**). We sorted recording sites on the basis of an effect of selective attention (significantly stronger response to the target curve), but a large fraction of the rate covariation between A sites was actually unselective, as the effect also occurred between neurons with RFs on different curves. We attribute this unselective rate covariation to general fluctuations in excitability

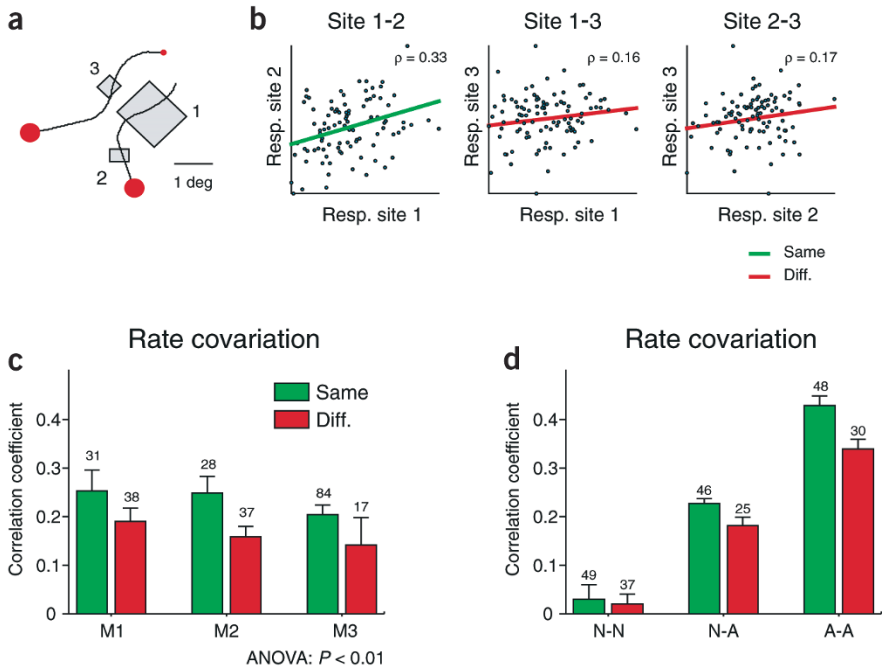

Figure 4 Covariation of firing rates. (**a**) Receptive fields of three recording sites (same sites as in **Fig. 1**). (**b**) Rate covariation between the recording sites. Each point shows the response strength on an individual trial at one recording site as a function of response strength at the other site (total of 101 trials). The axes have been scaled to accommodate the strengths of all single-trial responses (the correlation coefficient ρ is independent of scaling). Green line, linear regression between responses evoked by the same curve. Red lines, linear regressions between responses evoked by different curves. (**c**) Average covariation between the strength of responses evoked by the same (green bars) and different curves (red bars), for each of the monkeys. Error bars show s.e.m. (n = number of cases). (**d**) Average rate covariation between pairs of recording sites without an attentional effect (N-N pairs), pairs where one of the sites had an effect of attention (N-A pairs) and pairs where both sites had an attentional effect (A-A pairs). Green bars, pairs of recording sites with RFs on the same curve. Red bars, pairs with RFs on different curves.

that can be caused, for example, by changes in arousal during the recording sessions. Nevertheless, there was also a fraction of the rate covariation that was curve-specific (difference between red and green bars in **Fig. 4c,d**), which reflects grouping. This fraction may reflect trial-to-trial fluctuations in selective attention, which is directed to the target curve and withdrawn from the distractor curve during the task.

One possible confounding factor that may have contributed to the rate covariation is related to eye movements. Small differences in the accuracy of visual fixation across trials cause systematic shifts of the RFs relative to the curves, and these differences can thereby induce correlated variations in firing rates across trials[31]. We therefore corrected for differences in eye position with a regression analysis. This correction reduced the average rate covariation slightly (from 0.21 to 0.18), but the effects of perceptual grouping and the type of recording site (A or N site) on the rate covariation remained significant (3-way ANOVA: monkey $P > 0.4$; grouping $P < 0.05$; type of recording site $P < 0.001$). We also excluded the possibility that rate covariation is caused by slow drifts in eye position (**Supplementary Methods**).

Experiment 2: switching partners

So far, we have compared interactions between neuronal responses to the same and different curves at recording sites that may not have been matched exactly in their RF properties. In two of the monkeys (M1 and M3) we investigated whether a change in the way contours are grouped perceptually influences synchrony and rate covariation. **Figure 5a** illustrates how an intersection between the two curves changes the contour segments that belong together, while the content of the RFs is held constant. The RFs of recording sites 1 and 2 fall on the same curve for stimuli I and II, but on different curves for stimuli III and IV. If the strength of coupling reflects grouping, it should be highest for stimuli with both RFs on the same curve. Such a within-pair comparison could be made for 59 paired recordings with RFs at different sides of a potential intersection (switching partners). We computed the average strength of synchrony and rate covariation for the two conditions with the RFs on the same curve, and compared it to the average with RFs on different curves. Synchrony between responses to the same curve was not significantly different from synchrony between responses to different curves (**Fig. 5b**) (paired t test, $t_{58} = 1.2$, $P > 0.1$). We estimated the strength of synchrony by fitting a function to the cross-correlation functions. To avoid the fitting of noise, we set the synchronization strength to zero if fits accounted for insufficient variance in the correlation functions[32]. This explains why many cases are superimposed at the origin of **Figure 5b** (for these cases, the fit was not accepted in either condition, $n = 36$). We were concerned that the null effect might be caused by a too stringent criterion for the acceptance of fits, so we repeated the analysis with another method that does not require curve fitting (**Supplementary Methods**). In that additional analysis, the strength of synchrony did not differ between conditions. These results imply that the synchrony between a pair of recording sites remains the same in spite of changes in perceptual grouping.

The strength of the rate covariation, on the other hand, did depend on the stimulus configuration. When RFs were on different curves, the average rate covariation was 0.14. When RFs fell on the same curve, it increased by 38% to an average value of 0.20 (**Fig. 5c**). This difference was significant (paired t test, $t_{58} = 3.6$, $P < 0.0005$). Thus, the rate covariation between V1 neurons is stimulus dependent, as it is strongest when they respond to a single perceptual object.

Experiment 3: task difficulty and errors

We observed that synchrony among spatially separate neurons in area V1 is characterized by relatively broad peaks (**Fig. 2b**), which are suppressed when the stimulus appears (**Fig. 3c**). Previous studies suggested that suppression of broad correlation peaks might be related to the effort that the animal has to put into a visual task[30,33]. To investigate whether synchrony is related to effort, we systematically varied task difficulty for monkeys M1 and M3. For each stimulus shown in **Figure 5a**, we also included a more difficult version to obtain a total of eight stimuli. Difficulty was varied at the location where the two curves came in close proximity[34] (critical zone, green circle in **Fig. 6a**). Narrowing the gap between the two curves increased the difficulty of stimuli with a nonintersection, as this makes the configura-

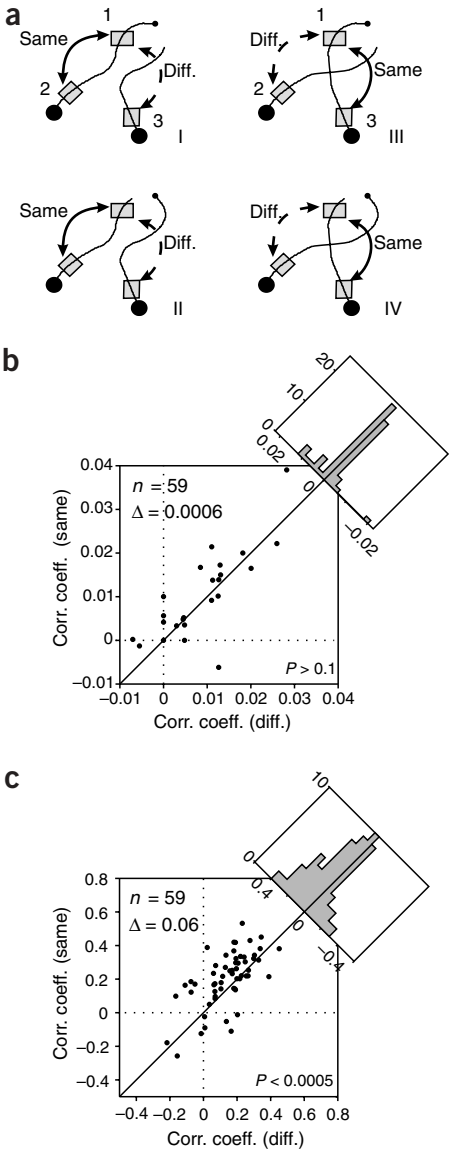

Figure 5 Dependence of synchrony and rate covariation on stimulus configuration. (**a**) An intersection between the two curves changes grouping, but the contours in the RFs remain the same. All stimulus configurations (I–IV) were interleaved within the recording session. (**b**) Strength of synchrony when the RFs (59 pairs) fell on the same curve (ordinate) or on different curves (abscissa). Inset, histogram of the difference in synchronization strength (ρ) between conditions. (**c**) Rate covariation when RFs were on the same curve (ordinate) or on different curves (abscissa). Inset, histogram of differences in rate covariation between conditions. Δ, increase in the average correlation coefficient when RFs fell on the same curve relative to when RFs fell on different curves.

tion more similar to an intersection. Intersections were made more difficult by reducing the angle at which the two curves cross each other, which makes them more similar to nonintersections (intersections with an angle of 0° are identical to nonintersections with a gap of 0). The easy and difficult stimuli were randomly interleaved. As expected, performance with the easy stimuli was better than that with the difficult stimuli (98% vs. 77% correct, on average).

To dissociate the effect of task difficulty from perceptual grouping, we compared the average strength of synchrony evoked by the four easy stimuli to the average synchrony evoked by the four difficult stimuli. This implies that perceptual grouping is on average the same for the easy and difficult stimuli. The difficult stimuli evoked significantly weaker synchrony ($\rho = 0.0029$) than did the easy ones ($\rho = 0.0042$) (paired t test; $t_{115} = 3.9$; $P < 0.0002$) (**Fig. 6b**). This suppression was relatively independent of the RF positions. Suppression of synchrony occurred for the 'switching partner' cases, which had their RFs on different sides of an intersection (*e.g.*, pair 1-2 in **Fig. 6a**; blue symbols in **Fig. 6b**; $n = 41$, $t_{40} = 3.2$, $P < 0.005$). It also occurred for the nonswitching cases that had their RFs always on the same (*e.g.* pair 2-3; green symbols) or always on different curves (pair 2-4; red symbols) ($n = 75$, $t_{74} = 2.9$; $P < 0.01$). We also investigated whether task difficulty influenced rate covariation. Easy and difficult stimuli evoked rate covariation of comparable strength (**Fig. 6c**) ($\rho_{easy} = 0.21$; $\rho_{diff} = 0.20$; paired t test, $t_{115} = 1.2$; $P > 0.2$).

The higher error rate with difficult stimuli also allowed us to investigate whether synchrony changes when the monkey groups the wrong contours together in perception. Strength of synchrony between neurons changed neither when their RFs fell on contours that were erroneously grouped together, nor when they fell on contours that were erroneously assigned to different curves (**Supplementary Fig. 2** online).

Pitting task difficulty against binding

Our conclusion that synchrony is unrelated to perceptual grouping is based on negative findings, as we did not detect significant differences between the grouped and ungrouped conditions. So far, we cannot exclude the possibility that this negative finding resulted from too few data points. We showed that difficult tasks suppress synchrony, and we can therefore pit this effect against binding. With this objective, we compared synchrony in a condition where it is easy to see that two contours belong to different curves (**Fig. 7a**, left) to synchrony in a condition where it is more difficult to see that they belong to the same curve (**Fig. 7a**, right). The task difficulty effect predicts that synchrony should be strongest in the former condition, whereas the binding-by-synchrony hypothesis predicts that synchrony should be strongest in the latter.

This comparison could be made for 41 paired recordings with RFs on different sides of the critical zone (switching partners). We restricted our analysis to correct trials. Thus, on correct difficult trials, the monkeys indeed reported that the contours in the RFs were part of the same curve, and on correct easy trials they reported that they were part of different curves. Synchrony was weaker in the difficult, grouped condition than in the easy, ungrouped condition (paired t test, $t_{40} = 2.3$, $P < 0.05$; **Fig. 7b**). These results confirm that difficult tasks evoke less synchrony. The results are not in line with binding-by-synchrony, because synchrony was weaker when grouping was stronger.

DISCUSSION

Theories on the neurophysiology of perceptual grouping have posited that neurons encoding features of the same object should share a common 'label,' whereas neurons encoding features of different objects should be labeled differently. Two physiologically plausible labels have been proposed (for review, see ref. 2). The first is synchrony. According to the binding-by-synchrony hypothesis, neurons that respond to features of the same object should fire their action potentials at approximately the same time. The activity of neurons that respond to features of different objects should be uncorrelated. Our data do not support binding-by-synchrony, as synchronization in area V1 was found to be unrelated to the grouping of contours into elongated curves. The second label that has been proposed is an enhancement of neuronal firing

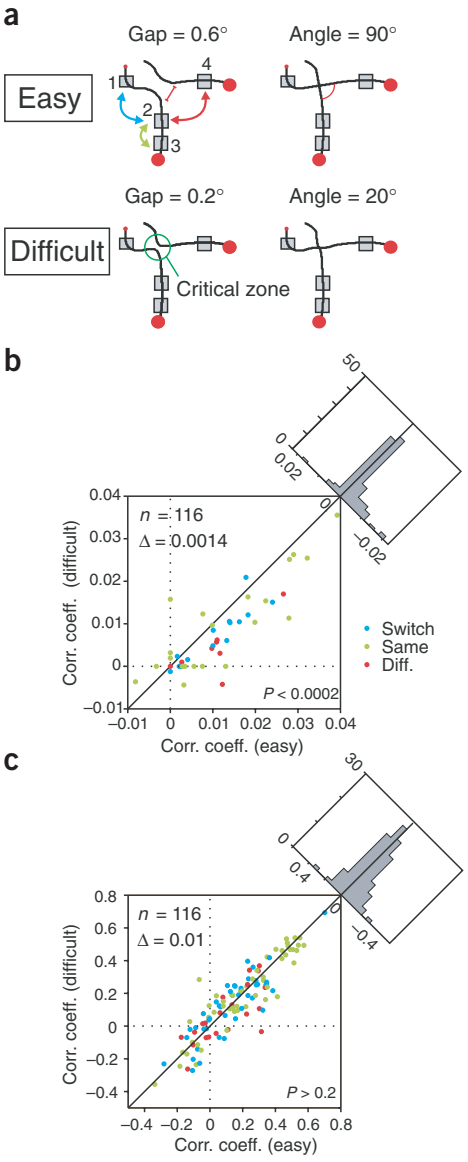

Figure 6 Influence of task difficulty on the interactions between neurons in area V1. (**a**) The stimulus configuration was systematically varied at the location where the two curves came close (critical zone, green circle). On the one hand, nonintersections become more confusable with intersections when the gap between the two curves is narrower. On the other hand, intersections become more confusable with nonintersections if the curves cross at a sharper angle. These four stimuli, and four additional stimuli where the upper curve was connected to the fixation point (interchange of target and distractor curve), were shown in an interleaved sequence. Blue arrow, pair of recording sites where grouping depends on the presence of an intersection (switching partners). Green arrow, pair with RFs always on the same curve. Red arrow, pair with RFs always on different curves. (**b**) Strength of synchrony for easy stimuli (abscissa) and difficult stimuli (ordinate). Inset, histogram of the difference in synchronization strength between conditions. Blue symbols show switching partners, green symbols show pairs with RFs on the same curve, and red symbols show pairs with RFs on different curves. (**c**) Rate covariation for easy and difficult stimuli was similar. Δ, increase in the average correlation coefficient for easy stimuli compared to difficult stimuli.

rates. According to this binding-by–rate enhancement hypothesis, features of a single perceptual object are bound if the neurons encoding them jointly enhance their responses. Our results support this hypothesis, as neuronal responses to contours that were grouped together are indeed simultaneously enhanced in area V1 (refs. 20,35; **Figs. 1b** and **3a**). This rate enhancement therefore labels the neurons that respond to the various contours that belong to the target curve (yellow in **Fig. 8**). Psychophysical results in human subjects indicate that the enhancement of neuronal responses is a correlate of visual attention that is directed to the target curve[18]. At the start of a trial, attention is directed to the initial segments of the target curve, and it then gradually spreads until all segments of the target curve are attended[19]. There is a conceptual link between binding-by–rate enhancement and the feature integration theory originally proposed two decades ago[36]. In the feature integration theory, features of a single object, such as its color and shape, are grouped together by an attentional 'spotlight' that is directed to the object's location. Our results suggest a generalization of this theory to situations in which the features that have to be grouped are spatially separate contours. These contours will not always fit within a single attentional spotlight. A spotlight cannot, for example, selectively shine on a target curve that crosses a distractor curve. In these situations, contours that are labeled by an enhanced response are, at a psychological level of description, grouped together by object-based attention[37]. Previous studies have suggested that attention might also influence temporal aspects of neuronal responses. And it has been shown that attention enhances power in the gamma band and also increases the strength of synchrony[25–27]. In the present contour-grouping task, however, attention influenced neither synchrony nor gamma-power in area V1. Apparently, the effects of attention on the temporal aspects of the neuronal responses do not generalize across tasks and/or across cortical areas.

Synchrony at various temporal scales

In our task, it was necessary to group contours of a single curve on the basis of their colinearity and connectedness. This is a natural task, given that colinear and connected contours usually belong to the same curve in the natural world[38], and they are readily grouped in perception[39]. Physiologically plausible algorithms for contour grouping therefore suggested that the label, be it synchrony[40] or a rate enhancement[35] should be spread among neurons that respond to colinear and connected contours. Horizontal connections in area V1 can support such a label-spreading process, since they selectively interconnect neurons tuned to colinear contours[41,42]. Horizontal connections have a maximal extent of about 4 mm (ref. 43), which is sufficient for local grouping (**Fig. 8**, black arrows). In our task, however, it is necessary to evaluate the position and orientation of a number of intermediate contour segments before the circle at the end of the target curve can be identified. This implies that the label has to spread across a chain of connections within, but probably also outside of, area V1 (refs. 2,35). Such long chains of connections pose a difficulty for binding by synchrony. Neurons that are separated by many synapses cannot be easily synchronized, because of the accumulation of synaptic and propagation delays in the chain. This implies a trade-off between the temporal precision of the synchrony and the maximal number of synapses between the neurons that can be synchronized[2]. Several studies have shown that neurons separated by larger cortical distances indeed only synchronize their discharges at time scales larger than tens of milliseconds, but not with a precision of a few milliseconds[21,22].

Nevertheless, many earlier studies on perceptual grouping focused on synchrony of millisecond precision[3–7], which is often associated

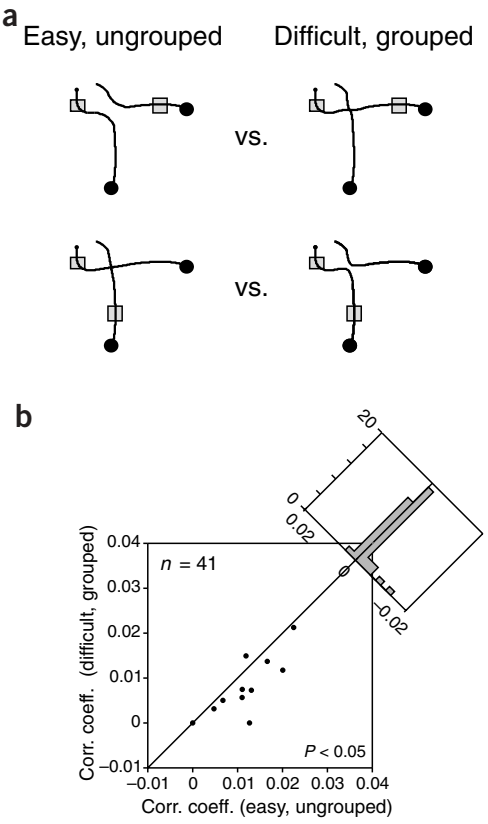

Figure 7 Pitting task difficulty against binding. (**a**) Stimulus configurations where it is easy to see that the contours in the two RFs belong to different curves (left) were compared to conditions where it is more difficult to see that they belong to the same curve (right). (**b**) Synchrony in the easy, ungrouped condition (abscissa) was stronger than synchrony in the difficult, grouped condition. Many pairs did not show significant synchrony for any stimulus. These cases are superimposed on the origin.

with oscillatory activity in the gamma range (30–80 Hz). This type of synchrony only occurs between neurons separated by less than a few millimeters[21–24]. In our data, we rarely (<1%) observed gamma synchrony among neurons with RFs separated by more than 1°. Thus, gamma synchrony is a local process (**Fig. 8**, black arrows) that cannot be used to group spatially separate contour segments in area V1.

Neurons with nonoverlapping RFs also synchronize their discharges, but at a relatively coarse temporal scale. The width of the peaks in the cross-correlation functions was generally between 20 and 150 ms (**Fig. 2b**). Previous studies have demonstrated that task-relevant stimuli decrease the amplitude of these broad peaks[30,33] (as in **Fig. 3c**). Our results extend these findings by showing that difficult tasks cause a stronger suppression of broad peaks. This is in line with electroencephalogram (EEG) studies showing that attention-demanding tasks 'desynchronize' the EEG, that is, they decrease power in the alpha band[44]. Here we used this effect of task difficulty to dissociate synchrony from binding. Synchrony among neuronal responses to grouped features in a difficult task was weaker than synchrony among responses to ungrouped features in an easy task. These results are in accordance with a recent study[11] reporting that synchronization among motion-sensitive neurons in area MT is also unrelated to perceptual grouping. Our findings are also in line with earlier studies that showed that the stimulus specificity of this type of synchrony is low[21–23]. We conclude that longer-range synchrony does not mirror the specificity of cortico-cortical connections[41,42]. One possibility is that these broad correlation peaks reflect fluctuations in the activity of diffuse modulatory systems (blue arrows in **Fig. 8**). This would explain why this synchrony is nonspecific. We showed that there are large differences between monkeys in the strength of these correlations, which makes it unlikely that they have a functional role in perception.

Rate covariation and attention

The final type of coupling occurs at an even coarser time scale: across trials. Previous studies report covariation of firing rates in the primary visual cortex[12–14], in higher visual areas[15,16] and also in areas outside the visual cortex[17]. Our findings shed new light on the origin of rate covariation. First, rate covariation is particularly strong between neurons that exhibit attentional effects (A sites), and it is weak between neurons that do not (N sites). This suggests that rate covariation is caused by trial-to-trial fluctuations in the animal's attentional state. Second, rate covariation depends on perceptual grouping, as it is strongest between neurons that respond to features of the same object (green in **Fig. 8**). The covariation between responses evoked by the target curve can be explained if the spread of the rate enhancement among neurons at A sites is somewhat variable across trials. In this view, the rate covariation would be a by-product of binding-by–rate enhancement. The covariation between responses evoked by the distractor curve can be explained similarly, by trial-to-trial fluctuations in response suppression. It is unlikely that the rate covariation can itself be used as a code for binding, because it can be evaluated only by comparing neuronal responses across different trials.

Third, the strengths of neuronal responses evoked by different curves were also correlated across trials. This nonspecific fraction of the rate covariation is presumably due to a general variability in neu-

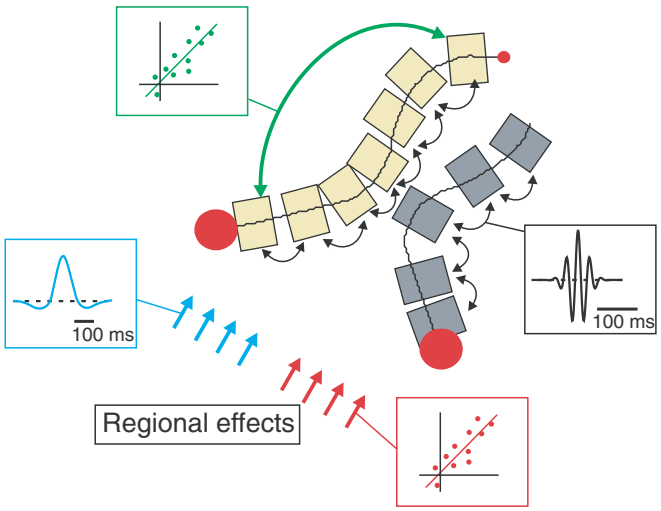

Figure 8 Factors that determine synchrony and rate covariation. Black arrows represent local interactions that can be supported by horizontal connections within area V1. Gamma synchrony has a spatial scale that is similar to the extent of horizontal connections. Blue arrows, global influences on large regions of area V1 cause temporally less precise synchrony (blue). Global grouping is achieved by the spread of a rate enhancement among neurons with RFs on the target curve (yellow RFs). Fluctuations in this process across trials can account for the fraction of the rate covariation that reflects grouping (green arrow). Red arrows represent fluctuations in neuronal excitability across trials, which may be caused by variations in alertness, that lead to a global, nonspecific rate covariation in area V1.

Table 1 Factors that dissociate synchrony and rate covariation

Synchrony	Rate-covariation
Differs between monkeys	Similar across monkeys
Suppression by difficult tasks	Independent of task-difficulty
Unrelated to grouping	Depends on grouping
Similar for A and N sites	Strongest among A sites

ronal excitability across trials (red in **Fig. 8**). General excitability changes, which may be caused by changes in alertness, predominantly influenced neurons at A sites and had weak effects at N sites. This was unexpected because A sites and N sites were distinguished on the basis of an effect of selective attention, that is, a difference between the responses evoked by the target and distractor curve. It has been suggested[45] that there are independent attentional networks for alerting and for stimulus selection. Our results indicate, however, that these two attentional systems modulate the same circuits within area V1 (neurons at A sites).

The correlations across trials can also be measured with positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) in humans, where they are used to estimate the 'functional connectivity' among cortical areas[46,47]. Neurons that are influenced by attention (as well as neurons that are not) are found in many, if not all, areas of the cerebral cortex[48]. If the difference between N sites and A sites also holds up for interareal interactions, then the present results imply that functional connectivity that is measured in imaging studies actually reflects the coupling between neurons that exhibit attentional effects.

Rate covariation and synchrony have independent sources

It has been suggested that synchrony might also be responsible for the correlations in response strength across trials[16]. However, we uncovered several factors that dissociate synchrony and rate covariation (**Table 1**). First, strength of synchrony differs between monkeys, whereas rate covariation is similar across individuals (**Figs. 2** and **4**). Second, difficult tasks suppress synchrony, without an effect on the rate covariation (**Fig. 6**). Third, rate covariation depends on grouping of distant contours, but synchrony does not (**Figs. 2**, **4** and **5**). Fourth, rate covariation is strongest among A sites and weakest among N sites (**Fig. 4**), but synchrony does not show this dependence (**Supplementary Methods**). These dissociations imply that synchrony and rate covariation have largely separate sources. It is therefore essential to use distinct methods for the quantification of synchrony and rate covariation, as is discussed in **Supplementary Methods** online.

Implications for decision making

Finally, our results have implications for models of decision making. These models usually assume that sensory neurons are noisy, but that the accuracy of a perceptual decision can be improved by pooling signals across neurons, to average out this noise. In some[15] (but not all[49]) of these models, rate covariation impairs noise suppression, because common noise cannot be averaged out. The present results demonstrate that perceptual grouping increases rate covariation. Perceptual grouping should thereby reduce the benefit of pooling. This prediction is supported by a psychophysical study[50], in which subjects were asked to estimate the speed of moving grating patches. Accuracy improved when there were multiple grating patches moving at the same speed, suggesting that pooling across multiple speed detectors improved the subjects' accuracy. Remarkably, this improvement did not occur when the grating patches were connected to each other to give the appearance of a single elongated grating. We conjecture that in this previous experiment, perceptual grouping caused an increase in the rate covariation between neuronal responses to separate grating patches, thereby decreasing the accuracy of the perceptual decision.

METHODS

Behavioral task. Three macaque monkeys were trained in a contour-grouping task. Each trial started as soon as the monkey's eye position was within a 1° 1° square window centered on a 0.3° red fixation point. The stimulus appeared after 300 ms of visual fixation (**Fig. 1a**). The monkey had to locate a red circle that was connected to the fixation point by a curve (target curve). After an additional 600 ms, the fixation point disappeared and the monkey made a saccade to this circle. There also was a distractor curve that could be ignored. On average, 88 trials (range 33–199) were obtained for each of the stimuli, which were randomly interleaved.

Experimental procedures. Recordings were made using standard procedures that have been described elsewhere (ref. 20). In brief, a head holder was implanted in a first operation, and a gold ring was inserted under the conjunctiva of one eye for the measurement of eye position. Multi-unit recordings were obtained from electrodes that were chronically implanted in area V1 (4 hemispheres of 3 monkeys) in a separate operation (40–65 Teflon- or polyimide-coated platinum-iridium wires per hemisphere), and positioned 1–2 mm below the cortical surface. Operations were performed under aseptic conditions and general anesthesia, which was induced with ketamine (15 mg/kg intramuscularly), and maintained after intubation by ventilating with a mixture of 70% N_2O and 30% O_2, supplemented with 0.8% isoflurane, fentanyl (0.005 mg/kg body weight, injected intravenously) and midazolam (0.5 mg/kg per hour, injected intravenously). The animals recovered for at least 21 d before training resumed. All procedures complied with the US National Institutes of Health Guide for the Care and Use of Laboratory Animals and were approved by the institutional animal care and use committee of the Royal Netherlands Academy of Arts and Sciences. The method used to record multi-unit activity is illustrated in **Supplementary Fig. 3** online , and the cross-correlation method is explained in **Supplementary Methods**.

Note: Supplementary information is available on the Nature Neuroscience website.

ACKNOWLEDGMENTS

We thank J.C. de Feiter and K. Brandsma for technical assistance. We thank P. König and C. van der Togt for comments on an earlier version of the manuscript. This work was supported by a grant from the McDonnell Pew Program in Cognitive Neuroscience, and a grant of the Human Frontier Science Program.

COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

Received 26 February; accepted 14 July 2004
Published online at http://www.nature.com/natureneuroscience/

1. von der Malsburg, C. The what and why of binding: the modeler's perspective. *Neuron* **24**, 95–104 (1999).
2. Roelfsema, P.R. & Singer, W. Detecting connectedness. *Cereb. Cortex* **8**, 385–396 (1998).
3. Gray, C.M., König, P., Engel, A.K. & Singer, W. Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature* **338**, 334–337 (1989).
4. Singer, W. & Gray, C.M. Visual feature integration and the temporal correlation hypothesis. *Annu. Rev. Neurosci.* **18**, 555–586 (1995).
5. Castelo-Branco, M., Goebel, R., Neuenschwander, S. & Singer, W. Neural synchrony correlates with surface segregation rules. *Nature* **405**, 685–689 (2000).
6. Brosch, M., Bauer, R. & Eckhorn, R. Stimulus-dependent modulation of correlated high-frequency oscillations in cat visual cortex. *Cereb. Cortex* **7**, 70–76 (1997).
7. Gail, A., Brinksmeyer, H.J. & Eckhorn, R. Contour decouples gamma activity across texture representation in monkey striate cortex. *Cereb. Cortex* **10**, 840–850 (2000).
8. Kreiter, A.K. & Singer, W. Stimulus-dependent synchronization of neuronal responses in the visual cortex of the awake macaque monkey. *J. Neurosci.* **16**, 2381–2396 (1996).
9. Lamme, V.A.F. & Spekreijse, H. Neuronal synchrony does not represent texture segregation. *Nature* **396**, 362–366 (1998).
10. Shadlen, M.N. & Movshon, J.A. Synchrony unbound: a critical evaluation of the temporal binding hypothesis. *Neuron* **24**, 67–77 (1999).

11. Thiele, A. & Stoner, G.R. Neuronal synchrony does not correlate with motion coherence in cortical area MT. *Nature* **421**, 366–370 (2003).
12. van Kan, P.L.E., Scobey, R.P. & Gabor, A.J. Response covariance in cat visual cortex. *Exp.Brain Res.* **60**, 559–563 (1985).
13. Gawne, T.J., Kjaer, T.W., Hertz, J.A. & Richmond, B.J. Adjacent visual complex cells share about 20% of their stimulus-related information. *Cereb. Cortex* **6**, 482–489 (1996).
14. Leopold, D.A., Murayama, Y. & Logothetis, N.K. Very slow activity fluctuations in monkey visual cortex: implications for functional brain imaging. *Cereb. Cortex* **13**, 422–433 (2003).
15. Shadlen, M.N., Britten, K.H., Newsome, W.T. & Movshon, J.A. A computational analysis of the relationship between neuronal and behavioral responses to visual motion. *J. Neurosci.* **16**, 1486–1510 (1996).
16. Bair, W., Zohary, E. & Newsome, W.T. Correlated firing in macaque visual area MT: time scales and relationship to behavior. *J. Neurosci.* **21**, 1676–1697 (2001).
17. Lee, D., Port, N.L., Kruse, W. & Georgopoulos, A.P. Variability and correlated noise in the discharge of neurons in motor and parietal areas of the primate cortex. *J. Neurosci.* **18**, 1161–1170 (1998).
18. Scholte, H.S., Spekreijse, H. & Roelfsema, P.R. The spatial profile of visual attention in mental curve tracing. *Vision Res.* **41**, 2569–2580 (2001).
19. Houtkamp, R., Spekreijse, H. & Roelfsema, P.R. The cause of delays in contour integration. *Percept. Psychophys.* **65**, 1136–1144 (2003).
20. Roelfsema, P.R., Lamme, V.A.F. & Spekreijse, H. Object-based attention in the primary visual cortex of the macaque monkey. *Nature* **395**, 376–381 (1998).
21. Nelson, J.I., Salin, P.A., Munk, M.H.J., Arzi, M. & Bullier, J. Spatial and temporal coherence in cortico-cortical connections: a cross-correlation study in areas 17 and 18 in the cat. *Vis. Neurosci.* **9**, 21–37 (1992).
22. Nowak, L.G., Munk, M.H.J., Nelson, J.I., James, A.C. & Bullier, J. Structural basis of cortical synchronization. I. Three types of interhemispheric coupling. *J. Neurophysiol.* **74**, 2379–2400 (1995).
23. Frien, A. & Eckhorn, R. Functional coupling shows stronger stimulus dependency for fast oscillations than for low-frequency components in striate cortex of awake monkey. *Eur. J. Neurosci.* **12**, 1466–1478 (2000).
24. Maldonado, P.E., Friedman-Hill, S. & Gray, C.M. Dynamics of striate cortical activity in the alert macaque: II. Fast time scale synchronization. *Cereb. Cortex* **10**, 1117–1131 (2000).
25. Steinmetz, P.M. *et al.* Attention modulates synchronized neuronal firing in primate somatosensory cortex. *Nature* **404**, 187–190 (2000).
26. Fries, P., Reynolds, J.H., Rorie, A.E. & Desimone, R. Modulation of oscillatory neuronal synchronization by selective visual attention. *Science* **291**, 1560–1563 (2001).
27. Tiitinen, H. *et al.* Selective attention enhances the auditory 40-Hz transient response in humans. *Nature* **364**, 59–60 (1993).
28. Frien, A., Eckhorn, R., Bauer, R., Woelbern, T. & Kehr, H. Stimulus-specific fast oscillations at zero phase between visual areas V1 and V2 of awake monkey. *Neuroreport* **5**, 2273–2277 (1994).
29. Friedman-Hill, S., Maldonado, P.E. & Gray, C.M. Dynamics of striate cortical activity in the alert macaque: I. incidence and stimulus dependence of gamma-band neuronal oscillations. *Cereb. Cortex* **10**, 1105–1116 (2000).
30. Supèr, H., van der Togt, C., Spekreijse, H. & Lamme, V. A. F. Internal state of monkey primary visual cortex (V1) predicts figure–ground perception. *J. Neurosci.* **23**, 3407–3414 (2003).
31. Gur, M. & Snodderly, D.M. Studying striate cortex neurons in behaving monkeys: benefits of image stabilization. *Vision Res.* **27**, 2081–2087 (1987).
32. König, P. A method for the quantification of synchrony and oscillatory properties of neuronal activity *J. Neurosci. Meth.* **54**, 31–37 (1994).
33. Roelfsema, P.R., Engel, A.K., König, P. & Singer, W. Visuomotor integration is associated with zero time-lag synchronization among cortical areas. *Nature* **385**, 157–161 (1997).
34. Roelfsema, P.R. & Spekreijse, H. The representation of erroneously perceived stimuli in the primary visual cortex. *Neuron* **31**, 853–863 (2001).
35. Roelfsema, P.R., Lamme, V.A.F. & Spekreijse, H. The implementation of visual routines. *Vision Res.* **40**, 1385–1411 (2000).
36. Treisman, A.M. & Gelade, G. A feature-integration theory of attention. *Cogn. Psychol.* **12**, 97–136 (1980).
37. Duncan, J. Selective attention and the organization of visual information. *J. Exp. Psychol. Gen.* **113**, 501–517 (1984).
38. Sigman, M., Cecchi, G.A., Gilbert, C.D. & Magnasco, M.O. On a common circle: natural scenes and Gestalt rules. *Proc. Natl. Acad. Sci. USA* **98**, 1935–1940 (2001).
39. Kellman, P.J. & Shipley, T.F. A theory of visual interpolation in object perception. *Cogn. Psychol.* **23**, 141–221 (1991).
40. Sporns, O., Gally, J.A., Reeke, G.N., Jr. & Edelman, G.M. Reentrant signaling among simulated neuronal groups leads to coherency in their oscillatory activity. *Proc. Natl. Acad. Sci. USA* **86**, 7265–7269 (1989).
41. Bosking, W.H., Zhang, Y., Schofield, B. & Fitzpatrick, D. Orientation selectivity and the arrangement of horizontal connections in tree shrew striate cortex. *J. Neurosci.* **15**, 2112–2127 (1997).
42. Schmidt, K.E., Goebel, R., Löwel, S. & Singer, W. The perceptual grouping criterion of colinearity is reflected by anisotropies of connections in the primary visual cortex. *Eur. J. Neurosci.* **9**, 1083–1089 (1997).
43. Angelucci, A. *et al.* Circuits for local and global signal integration in primary visual cortex. *J. Neurosci.* **22**, 8633–8646 (2002).
44. Worden, M.S., Foxe, J.J., Wang, N. & Simpson, G.V. Anticipatory biasing of visuospatial attention indexed by retinotopically specific α-band electroencephalography increases over occipital cortex. *J. Neurosci.* **20**, RC63:1–6 (2000).
45. Posner, M.I. & Petersen, S.E. The attentional system of the human brain. *Annu. Rev. Neurosci.* **13**, 25–42 (1990).
46. Büchel, C. & Friston, K. Assessing interactions among neuronal systems using functional imaging. *Neural Net.* **13**, 871–882 (2000).
47. McIntosh, A.R., Rajah, M.N. & Lobaugh, N.J. Interactions of prefrontal cortex in relation to awareness in sensory learning. *Science* **284**, 1531–1533 (1999).
48. Lamme, V.A.F. & Roelfsema, P.R. The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci.* **23**, 571–579 (2000).
49. Oram, M.W., Földiák, P., Perrett, D.I. & Sengpiel, F. The 'ideal homunculus': decoding neural population signals. *Trends Neurosci.* **21**, 259–265 (1998).
50. Verghese, P. & Stone, L.S. Perceived visual speed constrained by image segmentation. *Nature* **381**, 161–163 (1996).