Coherent Oscillatory Activity in Monkey Area V4 Predicts Successful Allocation of Attention

Attention serves to select objects from often complex scenes for enhanced processing and perception. In particular, the perception of shape depends critically on attention for integrating the various parts of the selected object into a coherent representation of object shape. To study whether oscillatory neuronal synchrony may serve as a mechanism of attention in shape perception, we introduced a novel shape-tracking task requiring sustained attention to a morphing shape. Attention was found to strongly increase oscillatory currents underlying the recorded field potentials in the \(\gamma\)-frequency range, thus indicating enhanced neuronal synchrony within the population of V4 neurons representing the attended stimulus. Errors indicating a misdirection of attention to the distracter instead of the target were preceded by a corresponding shift of oscillatory activity from the target’s neuronal representation to that of the distracter. No such effect was observed for errors unrelated to attention. Modulations of the attention-dependent enhancement of oscillatory activity occurred in correspondence with changing attentional demands during the course of a trial. The specificity of the effect of attentional errors together with the close coupling between attentional demand and oscillatory activity support the hypothesis that oscillatory neuronal synchrony serves as a mechanism of attention.

Keywords: attention, gamma band, oscillation, shape perception, synchronization, visual cortex

Introduction

Psychophysical investigations have shown that selective attention is an essential prerequisite for shape perception: subjects fail to report the shape of non-attended objects while their individual features such as color or texture may well be recognized (Rock and Gutman, 1981; Rock et al., 1992). In line with these observations, feature integration is known to be a necessary step in shape perception, and to depend on attention (Treisman, 1995, 1998; Wolfe and Bennett, 1997). Different neuronal mechanisms are expected to increase the impact of neuronal responses to attended stimuli and have been proposed to subserve attention. An increase of firing rate for neurons representing the attended stimulus and/or a decrease for non-attended stimuli has been supported by a large number of experimental (Moran and Desimone, 1985; Motter, 1993; Treue and Maunsell, 1996; Luck et al., 1997; McAdams and Maunsell, 1999; Reynolds et al., 1999) and theoretical (Olahs et al., 1993; Hahnloser et al., 1999; Nakahara et al., 2001) studies. An alternative mechanism to enhance common impact is synchronization of neuronal responses to an attended stimulus (Niebur and Koch, 1994; Singer, 1999; Steinmetz et al., 2000; Fries et al., 2001; Keil et al., 2001) that leads to more effective dendritic summation of postsynaptic currents and increases the signal to noise ratio (Segev and Rall, 1998; Usrey et al., 2000; Azouz and Gray, 2003). Precise neuronal synchronization has also been proposed to be particularly instrumental in conjunction neuronal responses related to the same stimulus and to integrate them into a functionally coherent, temporally defined neuronal representation (Singer and Gray, 1995; Kreiter and Singer, 1996a; Singer, 1999; Freiwald et al., 2001). Thus, for a shape-perception task a particularly strong and reliable effect of selective attention on neuronal synchrony is predicted. Consequently, correct behavioral performance is expected to depend on adequate synchronization of the neuronal population processing the attended stimulus.

To test these predictions, we developed a new and demanding shape-tracking task that requires tracking the shape of a morphing object while ignoring a similar distracter. Because of the strict dependence of shape perception on attention (Rock and Gutman, 1981; Rock et al., 1992), successful performance requires allocating selective attention to the behaviorally relevant object. Recordings were taken from area V4, which is known to contain neurons selective for a large variety of form-related features (Desimone et al., 1987; Gallant et al., 1993; Tanaka, 1993; Pasupathy and Connor, 1999, 2001, 2002), indicating its participation in a distributed representation of shape (Pasupathy and Connor, 2002). We used an array of epidural electrodes to record field potentials from an extended part of area V4. Field potentials represent the sum of synchronous currents caused by neuronal activity in a few local columns underneath an electrode (Elul, 1972; Nunez, 1995). The signals in the \(\gamma\)-frequency range reflect the strength of precise synchronization of neurons within the investigated local population (Eckhorn et al., 1993; Singer and Gray, 1995; Livingstone, 1996; Herculano-Houzel et al., 1999; Logothetis et al., 2001; Rolls et al., 2001; Siegel and König, 2003). Recording field potentials with an implanted epidural array provides (i) a measure of synchrony for an entire population of neurons representing the stimulus and (ii) stable and comparable data over multiple recording sessions that allows for compilation of rare, attention-specific error trials.

Our investigations revealed a remarkably strong increase of oscillatory activity in the \(\gamma\)-frequency range, indicating a corresponding increase of local synchrony for attended as compared with non-attended stimuli. In particular, the highly specific modulation preceding the occurrence of attention-related errors indicated a functional role of neuronal synchronization as a mechanism of attention.

Materials and Methods

Behavioral Training and Visual Stimulation

Two male rhesus monkeys (Macaca mulatta) were trained to a novel shape-tracking task. For training and recording sessions the monkeys sat...
in a primate chair with the head restrained. Visual stimuli were presented with a frame rate of 100 Hz on a 21" CRT screen 81 cm in front of the monkeys’ eyes.

Each monkey started a trial (see Fig. 1 and movie in supplemental material) by pressing a lever after the appearance of a central fixation point on the screen. Some 650 ms later, two different stimuli with complex shape appeared at fixed positions in the left and right visual hemifield (S1). To direct attention to the location of the behaviorally relevant stimulus sequence (i.e. the target), it was cued within the first 200 ms of stimulus presentation by green coloring of the stimulus that faded to white within the subsequent 400 ms. After static presentation for 1300 ms, target and distracter underwent a morphing process. During this process each stimulus morphed through a sequence of different shapes, referred to as S2-S6 according to their sequential position. For each trial the required number of different shapes was randomly selected from a set of 10. The respective initial shapes of the target or distracter sequence reappeared at different, randomly selected points in time (S3-S6). Recurrence of the initial shape in the morphing sequence of the initially cued stimulus required the monkey to release the lever to be rewarded with a drop of fruit juice. A reappearance of the initial shape in the morphing sequence of the distracter had to be ignored. If the monkeys broke fixation (rectangular fixation window of $\pm 0.75\degree$), or responded too early or too late, the trial was aborted without reward.

Each stimulus shape was defined by 12 non-visible points interconnected by a smooth Bézier curve, which was 0.5° wide. During a morphing cycle (see Fig. 1), each of the shape-defining points was moved along a straight trajectory from its former position ($P_k$) to its position in the following shape ($P_{k+1}$). The position ($P$) on this trajectory was updated with each frame in 10 ms intervals:

$$P = (P_k - P_{k+1})R_{\text{Pos}} + P_{k+1}$$

$R_{\text{Pos}}$ is the relative position along the trajectory ranging between 0 and 1:

$$R_{\text{Pos}} = (2t - \phi)/\phi^2 + 1/2 \text{ for } t > \phi/2$$

$$R_{\text{Pos}} = -(2t - \phi)/\phi^2 + 1/2 \text{ for } t < \phi/2$$

with time $t$ and the morphing cycle’s duration $\phi$.

This results in a continuous change between slower morphing in the beginning and towards the end of each cycle, and faster morphing inbetween. The response window ranged from 400 ms before the end of a morphing cycle to 750 ms after the beginning of the next cycle. Stimuli were centered 0.9° below the horizontal meridian and 2.9° aside the vertical meridian, and covered a region of $-4° \times 4°$, with the eccentricity ranging from 0.9 to 5.7° and the center at 3°. For an example of the morphing stimulus, see supplemental material.

For a control task (Fig. 8A) used to isolate possible memory-related activity, both morphing stimuli were substituted by sequences of 500 ms static stimuli separated by 900 ms delay intervals. The initial shape was presented for 1550 ms and the target was cued as described above. The monkeys had to respond to the reappearance of the initial stimulus within 1000 ms. Otherwise the task was identical with the main task described above.

In the main task, as well as in the memory-control task, we presented blocks of 60–90 trials with the target stimulus on the same side to support target cueing. Monkey M was tested in addition with the target position chosen randomly for each trial. Analysis of behavioral performance revealed no difference between the two conditions.

For partial retinotopic mapping of the lower visual field representation of V4 on the gyrus prelunatus, small white squares (0.4° × 0.4°) were flashed at different positions in the visual field while monkeys engaged in a fixation task and kept their gaze within $\pm 0.75\degree$ around the fixation point.

**Surgical Preparation**

The monkeys were implanted with a headpost and a thin gold ring placed between the conjunctiva and the sclera of one eye for measurement of gaze direction using the indirect search coil method (Bour et al., 1981). After completion of the subsequent behavioral training, the monkeys were implanted with an epidural array of platinum-iridium electrodes placed over area V4. Based on maps of the monkey brain (Gattass et al., 1981, 1988; Paxinos et al., 2000), the intended position of the array was determined relative to anatomical landmarks. Stereotaxic coordinates of these landmarks were derived from structural magnetic resonance images obtained for each animal from a 4.7 T Bruker Biospec scanner (Ettlingen, Germany). The precise location of the implanted electrode array was estimated postoperatively by the stereotactic coordinates determined during implantation, their comparison with structural magnetic resonance images obtained after implantation and morphological confirmation in one of the monkeys. The localization of the array was further improved and confirmed by the construction of a partial retinotopic map of area V4, based on recordings of $\gamma$-band responses to the small test stimuli described above with the implanted electrode array.

**Recording**

Field potentials were recorded from a chronically implanted array of epidural electrodes (36 in monkey M and 37 in monkey F) covering area V4. The electrode array consisted of a 0.1-mm-thick sheet of silicone (Goodfellow, Bad Nauheim, Germany), in which Teflon-coated platinum-iridium (90Pt/10Ir) wires (diameter 50 μm, Science Products, Hofheim, Germany) were inserted with a regular spacing of 3 mm. The electrode contact was an uninsulated loop (diameter 210–220 μm) positioned parallel to the dura. Two reference electrodes (platinum-iridium wire, 150 μm diameter) were placed frontally. In monkey F a third reference was attached to the rear side of the electrode array (platinum–iridium foil, diameter 4.5 mm, thickness 0.1 mm). Recordings were referenced to the latter electrode in monkey F and a frontal electrode for monkey M. Signals were amplified (×40 000 in monkey

was 1 for all values of $f_0$ (Tallon-Baudry et al., 1997). This condition requires the normalization constant $A$ to be $(\sigma_2/\pi)^{0.5}$. This results in a flat spectrum estimate of a white noise signal. The central frequency $f_0$ ranged from 5 to 160 Hz according to the scheme of Torrence and Compo (1998), with a ratio $f_0/\sigma_f = 6$. At 10, 60 and 160 Hz, this leads to wavelet durations $(2\tau_f)$ of 194, 52 and 12 ms with a spectral bandwidth $(2\sigma_f)$ of 3.3, 19.7 and 52.6 Hz, respectively. The power spectral density (PSD) with unit $(V/m^2)/Hz$ was computed by taking the square of the observed probability of unspecific false alarms.

Because of the mixed reasons for errors, the average normalized $\gamma$PSD observed for distracter-related false alarms is a composite of the $\gamma$PSD associated with true distracter-related and with unspecific false alarms. The $\gamma$PSD that must have occurred for trials in which the false alarm was truly distracter-related (PSDDisTrue) can be estimated based on PSDDisObs, $\gamma$PSDUnspObs and the $\gamma$PSD observed for the two types of errors (PSDDisObs = $\gamma$PSD observed for distracter-related false alarms; PSDDisUnsp = $\gamma$PSD observed for unspecific false alarms) by using the following relation:

$$\text{PSDDisObs} = \text{PSDDisTrue} + \text{PSDUnspTrue} - (\text{PSDDisTrue} \times \text{PSDUnspTrue})$$

The true probability of distracter-related false alarms can be estimated since $\text{PSDDisObs}$ is observed and $\text{PSDUnspTrue}$ is approximated by $\text{PSDUnspObs}$, the observed probability of unspecific false alarms.

Statistical Analysis
All statistical analysis was done with data taken from the electrode closest to the site of maximum difference between the attended and non-attended condition (see above). The significance of the difference between the $\gamma$PSD observed for the attended and the non-attended condition was tested for the average $\gamma$PSD in a TF window spanning two morphing cycles (3.35–6.15 s after trial start) and a frequency range from 15 to 103 Hz using the Mann–Whitney test. To test the effect of behavioral errors on the attentional modulation of the signal, a two-way analysis of variance (ANOVA) with the factors behavioral relevance (target or distracter) and trial result (hit or error) was performed on $\gamma$PSD values of correct and error trials. These values were first normalized to baseline activity (0.05–0.6 s after trial start) and then subjected to a logarithmic transformation. Normality of distributions and homogeneity of variances were confirmed. The error analysis was confined to responses around the positions S3 and S4 of the shape-tracking task, because only for these positions a sufficient number of error trials were available.

Results
To investigate the effect of selective attention on neuronal synchronization in a demanding perceptual situation, two macaque monkeys were trained to a novel shape-tracking task (Fig. 1, see movie in supplemental material) which requires sustained attention to one of two morphing shapes to identify the reoccurrence of its initial shape. Average performance during recording sessions was estimated over all but the last possible response window in which a response would have always been correct. Disregarding fixation errors, the monkeys
performed correct for 76.9% of the trials (monkey M 81.9%, monkey F 71.8%). The response occurred 127 and 118 ms (median values for monkey M and F, respectively) before the end of the morphing cycle leading again to the shape shown initially (S1). Due to the changing speed of morphing during a morphing cycle, the shape at this time was already very similar to the final shape.

Oscillatory Responses in V4

To estimate a measure of overall synchronization within the population of responding V4 neurons, we recorded field potentials with a rectangular grid of epidural electrodes over area V4 and computed the corresponding CSD. Field potentials and corresponding CSD reflect the time course of the spatially weighted sum of synaptic currents caused by action potentials in the local population of neurons (Llinas and Nicholson, 1974) and are essentially measures of total synchronous activity (Elul, 1972; Nunez, 1995). Such signals can occur either time-locked to the stimulus (evoked activity) or without a fixed phase relation to the stimulus (induced activity). The evoked activity in the field potential (EP) and the CSD (EC) is shown in Figure 2. As expected for the continuously morphing stimulus there was a consistent evoked response with stimulus onset in both monkeys for both measures while evoked components during later parts of the trial were small. Analysis of the oscillatory components of the evoked response revealed only negligible power within the γ-band (see below, Fig. 6). Thus, the oscillations in the γ-band described subsequently are of the induced type, i.e. not phase-locked to the stimulus.

Analysis of the spatial distribution of oscillatory γ-band activity within the para-foveal lower field representation of area V4 revealed a strong and localized response to the stimulus. This is shown by the map of oscillatory activity in Figure 3A. It is based on the power spectral density of the CSD in the γ-band (γPSD) between 45 and 76 Hz computed for a time interval containing two consecutive morphing cycles (3.35–6.15 s after

Figure 2. Time course of the averaged evoked potential (A) and the averaged evoked CSD (an analog of the evoked potential) (B) time-locked to stimulus onset. Black lines correspond to signals with the target, gray lines to signals associated with the distracter stimulus. Both measures result in comparable plots. Comparison of the attentional conditions showed no consistent differences.
(trial start). A distinct spot of enhanced \( \gamma \)PSD is confined to a region of \( \sim 7.2 \times 4.3 \) mm (10.6 \( \times \) 4.6 mm in monkey M) and exceeds baseline levels by a factor of 8.8 (3.1 for monkey M). The spot is absent, if no stimulus is present (Fig. 3D) as expected for a signal representing stimulus-related activity. The circumscribed spatial distribution of increased \( \gamma \)PSD induced by the morphing stimulus suggests that it is generated by a local group of responsive neurons in area V4. To compare extent and position of the stimulus in the visual field with the location of enhanced \( \gamma \)PSD in area V4, a retinotopic map was constructed for the region of interest. For this purpose, small bright rectangles (0.4° \( \times \) 0.4°) were flashed at different visual

Figure 3. Spatial distribution of PSD in the gamma band during shape tracking. Maps A-D are based on the PSD of the CSD signals in the gamma band (45-76Hz) computed in a time interval containing two consecutive morphing cycles (3.35-6.15 s after trial start) of the shape-tracking task. Dotted white lines indicate isoeccentricity values within the location of expected stimulus representation in area V4. For the attended condition (A) and the non-attended condition (B) a distinct peak appears at the expected position of the retinotopic map in area V4 that is modulated by attention. (C) The spatial distribution of the difference between the attended and the non-attended condition shows the spatial restriction of the modulatory effect of attention to the region of area V4 engaged in the processing of the stimulus. (D) The map of baseline activity before stimulus onset contains no peak in the expected position of area V4. Map E represents the difference between the first positive and the subsequent negative peak of the evoked response of the CSD signals between 50 and 110 ms after the onset of the initial stimulus. All data were taken from monkey F.
field positions during a fixation task. Based on the spatial location of the maxima of the $\gamma$-PSD, the isoeccentricity lines of the visual field representation were estimated. The area of increased $\gamma$-PSD induced by the morphing stimulus extends from $<1^\circ$ to $~6^\circ$ of eccentricity in area V4 (Fig. 3A). This matches well with the eccentricity of the stimulus in the visual field, ranging from $0.8^\circ$ to $5.8^\circ$, with the center at $3^\circ$. The elongated rather than circular form of the responding part of V4 reflects the distortion expected for a roughly circular stimulus area in a retinotopic map with an overrepresentation of the central visual field. Furthermore, the spatial position of the peak of the $\gamma$-PSD is close to the peak of the evoked current, the CSD-analog of the evoked potential caused by stimulus onset (Fig. 3E). Thus, the enhancement of $\gamma$-PSD, indicating enhanced oscillatory synchrony, is essentially confined to the region of area V4 that is expected to contain neurons responsive to the stimulus.

**The Effect of Changing Selective Attention**

If neuronal mechanisms of selective attention employ synchronized oscillatory patterns of activity, the oscillating current induced in a local group of neurons and thus the corresponding PSD should be larger for processing attended stimuli as compared with processing identical, but non-attended stimuli. The comparison of spatial distributions of $\gamma$-PSD showed indeed a much stronger signal for the stimulus serving as a target of attention (Fig. 3A) as compared with the same stimulus serving as a distractor (Fig. 3B). The spatial extent of this difference (Fig. 3C) was confined to the patch in area V4 where the response occurred.

Spectral composition and time course of oscillatory activity are shown in TF plots (Fig. 4) computed for responses at the location of maximum difference between attentional conditions. This site was virtually identical with the location of the maxima. In both conditions, there was an increase of PSD throughout stimulus presentation which was restricted to the $\gamma$-band and which changed in magnitude in different segments of a trial. The strength of PSD in the $\gamma$-band, observed in response to a target, exceeds the strength obtained for a distractor during the whole trial (Fig. 4C). Averaged over two morphing periods, the $\gamma$-PSD of the response in the range between 45 and 103 Hz increased from the non-attended (distractor) to the attended (target) condition by 43% for monkey F and by 73% for the better performing monkey M. This difference was highly significant in both monkeys (Mann-Whitney U-test, 512/521 and 561/662 trials for the attended/non-attended condition in monkey M and F, respectively, $P < 0.0001$ for both monkeys). At the same time, the normalized PSD in lower frequency bands either decreased or showed only a comparatively small increase (Figs 4C and 5).

The strength of the attention-dependent increase of $\gamma$-PSD varied over time in a manner consistent with changing behavioral demands during the trial. Figure 6 illustrates for both monkeys the time course of the maximum values of normalized $\gamma$-PSD (Fig. 6A) for target and distractor. In addition, the phase-locked component of the $\gamma$-PSD, which represents $\gamma$-band components of the target's evoked response, is plotted (dashed-dotted lines). The very small size of this component confirms the induced, i.e. non-phase-locked, character of the observed signals. The attention-specific relative increase of the maximum values of normalized $\gamma$-PSD is shown in Figure 6B. A first peak reflecting an increase of $\gamma$-PSD by more than 100% was observed in both monkeys between 150 and 650 ms (peaking at 330 ms) after stimulus onset. While it is likely that this effect essentially reflects a difference in attention during examination of the target's initial shape, it cannot be excluded that the difference of color between target and distractor during the cuing period may also have contributed to the first peak. After this initial maximum, the attention-dependent increase of $\gamma$-PSD was comparatively low (around 15% in monkey M and 25% in monkey F) within the remaining time of the static period. Similarly, there was no strong increase of the effect until the subsequent first morphing cycle turned to its end. During these periods the task did not require much attention. The initial shape is expected to be perceived and memorized within the first few hundred milliseconds of the 1300 ms static presentation interval and shape S2 never required a response since it was unavoidably different from the initial shape. The attentional demand increased again with morphing from shape S2 to S3 and to the subsequent shapes, which were possible repetitions of the initial shape and therefore required proper representation and comparison with the memorized initial shape. Within this interval, starting around the presentation of S3 and lasting to the end of the trial, a much larger effect of attention was observed, leading to a peak increase of the $\gamma$-PSD by more than 100% as compared with the non-attended case in both monkeys. In addition to this overall modulation along the major periods of the whole trial, the time course of $\gamma$-PSD and its difference between target and distractor was characterized by a modulation within each morphing cycle (Fig. 6). Factors that contributed to these systematic variations may include changing attentional demands due to the fixed temporal pattern of morphing cycles, the time course of formation and cessation of neuronal representations of individual shapes, as well as the rhythm of stimulus deformation. In summary, the results show that during the whole trial attention was associated with a strong increase of $\gamma$-PSD, indicating a strong increase of oscillatory synchrony that is restricted to the $\gamma$-range in a retinotopically defined region of area V4 that corresponds to the extent of the stimulus in the visual field.

**Neural Correlates of Behavioral Errors**

The hypothesis that oscillatory synchrony serves as a mechanism of attention predicts that a misdirection of attention should be associated with a corresponding relocation of the focus of synchronous oscillations. Behavioral errors, which indicate such a misdirection of attention, are therefore expected to be preceded by periods of decreased oscillatory $\gamma$-band activity for neurons representing the erroneously ignored stimulus. Conversely, oscillatory $\gamma$-band activity for the distractor that was mistakenly attended should have been enhanced. For other behavioral errors, which are not related to attention, no such changes are expected. In the following, we show that our results confirm these predictions.

In the present paradigm, behavioral errors appear either as misses when responses were not correct, or as false alarms when the monkey responded even though it should not have done so. Within the false alarms two groups are distinguished: a distracter-related false alarm (Fig. 7A) is present if the monkey responded to the repetition of the distractor's initial shape within its sequence of morphing shapes. This error suggests a misdirection of selective attention to the distractor. Other false alarms, which do not coincide with the reoccurrence of the distracter's initial shape, are called unspecific false alarms (Fig. 7B). They are thought to be related to reasons that...
are not necessarily related to attention, like a failure in encoding the initial shape or errors in the organization of the motor response. Distracter-related false alarms have been found to occur with a probability 2.15 times higher than unspecific false alarms, suggesting that more than half of these errors are due to a misdirection of selective attention while the rest are not expected to differ from unspecific false alarms. For morphing cycles leading to S3 and S4, a sufficient number of error trials

Figure 4. Time course of oscillatory activity during the shape-tracking task. Time-frequency plots of PSD normalized to baseline activity associated with the target stimulus (A), the distracter stimulus (B) and the difference between both conditions (C). Underneath each plot a schematic time course of the task is shown (for details see Fig. 1). The rectangle depicts the time–frequency window inside which the mean effect of attention was calculated. The γPSD is generally higher for the attended than for the non-attended condition. The attention-dependent increment is not constant over time but modulated with the change from one shape to the next. Note the restriction of the normalized response and also the attention-dependent increase of the response to the γ-band.
Figure 5. Attention-dependent change of normalized PSD in different frequency bands. Each panel shows the change of normalized PSD averaged over the frequency range specified below and within a time interval containing two consecutive morphing cycles (same time interval as the TF window in Fig. 3). Note the strong increment of normalized PSD in the $\gamma$-range, whereas in lower frequency bands normalized PSD either decreases or shows only a small increase.

Figure 6. Time course of $\gamma$PSD during the shape-tracking task. (A) Solid and dotted lines show the time course of the peak normalized PSD in the $\gamma$-range for the attended and non-attended condition, respectively. Dashed–dotted lines depict the time course of $\gamma$PSD for the evoked current, i.e. the stimulus-locked component of the signal. The plot shows that during the response essentially no stimulus-locked $\gamma$-band activity could be observed. (B) Time course showing the increment of the $\gamma$PSD from the non-attended to the attended condition. Underneath each plot a schematic time course of the task is shown (for details see Fig. 1). The panels show that $\gamma$PSD is generally higher for the attended than for the non-attended condition. This attention-dependent increase is not constant over time but modulated with changing attentional demands in different periods of a trial. In addition, the $\gamma$PSD is modulated with the transition from one shape to the next.
were available to allow for statistical analysis of the relation between error type and strength of γ PSD.

Significant differences in strength of the stimulus-induced increments of γ PSD occurred between distracter-related false alarms and correct responses. The differences were observed predominantly in the last morphing cycle of a trial during which the initial shape of the distracter or the target reoccurred. They were analyzed in a 650 ms time interval preceding the earliest responses, which occurred 400–420 ms before the completion of this final morphing cycle. As expected for correct trials, within this time interval, the γ PSD was higher for attended stimuli than for distracter stimuli (Fig. 7C). In contrast, for distracter-related errors the normalized γ PSD decreased for the target that should have been attended. Conversely, it increased for the distracter, which should have been ignored, but has been attended as indicated by the monkey’s behavior. Two-way ANOVAs confirmed a highly significant dependence between the normalized γ PSD and the interaction of the factors behavioral relevance (target or distracter) and trial result (hit or distracter-related false alarm) in both monkeys for both possible positions of matching shapes S3 and S4 [monkey F, S3: F(3,1595) = 146.68, P < 0.0001; S4: F(3,1548) = 12.85, P < 0.001; monkey M, S3: F(3,1127) = 27.55, P < 0.0001; S4: F(3,1133) = 6.13, P = 0.013]. This result is in line with the expectation that a supposed mechanism of attention should be less active for the representation of stimuli which the animal fails to attend and more for those which it has erroneously attended.

Given this highly significant effect for erroneous redirections of attention, we wanted to test the more advanced prediction of a quantitative reversal of γ PSD that would indicate a reversal of oscillatory synchrony between target and distracter for distracter-related false alarms. The idealized expectation would be that γ PSD rises for the distracter to the level reached by a target in correct trials. Conversely, it should drop for the target down to what is expected for a distracter in a correct trial. For unspecific errors that do not reflect failures of attention, γ PSD associated with the target and the distracter should stay similar to those in correct trials. How does this idealized expectation of a complete reversal of γ PSD between target and distracter compare with the observed data? Errors during the stimulus condition allowing for
distracter-related false alarms do not always reflect such specific misdirections of attention since unspecific errors are also expected to happen at this time (see above). Therefore, the normalized $\gamma$PSD observed in this condition was corrected for contributions from unspecific false alarms (see Materials and Methods). Figure 7C shows this corrected, normalized $\gamma$PSD computed for truly distracter-related false alarms and the normalized $\gamma$PSD observed for correct trials, trials with misses and trials with unspcific false alarms. For correct responses, the strength of the synchronous oscillatory activity was on average 81.6% higher for the target (gray bars) than for the distracter condition (white bars). In contrast, errors based on a misdirection of attention were preceded by an almost reverse pattern of the amount of oscillatory synchronous activity. For these truly distracter-related false alarms, the erroneous inattention to the target was associated with a reduction of 75.1% of the attention-dependent increase observed for targets as compared with distractors in correct trials. Conversely, the $\gamma$PSD increased by 66.2% of the same span for responses to an erroneously attended distracter. No such effect was observed for errors that are not primarily based on a failure of attention. The normalized $\gamma$PSD of targets as well as distracters are much less changed for unspcific false alarms and misses as compared with correct trials. Thus, there is a clear correlation between changes of the strength of oscillatory $\gamma$-band activity and changes of the direction of attention indicated by characteristic behavioral errors.

**Control for Memory-related Activity**

The behavioral paradigm used in this study requires attention to select and enhance the representation of a changing stimulus with complex shape, which needs to be compared with an initial shape presented at the beginning of a trial. Thus, in addition to selective attention, working memory is also expected to occur preferentially for the attended stimulus sequence. We tested whether at least part of the observed task dependent change of the PSD in the $\gamma$-band in area V4 was related to short-term memory. For this purpose, the continuous morphing from one shape to the next was substituted by a sequence of static stimuli flashed for 500 ms and separated by blank delay periods of 900 ms (Fig. 8A), thereby isolating memory-related activity during delay periods. Again, the monkeys were required to respond to the repetition of the target’s initial shape.

During the presentation of the stimuli $\gamma$PSD was somewhat smaller but comparable to the morphing task and larger for the attended than the non-attended condition (Fig. 8B,C). Within the tonic part of the response, which can be compared best with the observations for the morphing stimuli, there was an increase from the non-attended to the attended condition of 46.6 and 30.2% for monkeys M and F, respectively (300 ms window beginning 250 ms after stimulus onset). During the delay periods, $\gamma$PSD decays nearly to baseline levels, with almost no difference between the attended and non-attended conditions. Therefore, $\gamma$PSD that may depend on memory processes is negligible and cannot account for the large difference observed between the two attentional conditions during continuous stimulus presentation. This suggests that the large changes of $\gamma$PSD observed in both tasks depend essentially on the direction of selective attention and cannot be explained by processes, which have to keep information throughout the trial.

To address the question of whether there are indications for a change in total neuronal activity due to different states of attention, we computed the evoked potential and its analog, the evoked CSD caused by a stimulus onset (averaged over data for S3 and S4) during the trial. The results obtained for both measures are presented in Figure 9 for both animals. For the major part of the time course of both measures there were no consistent differences between attentional conditions. To the end, a moderate difference in favor of the non-attended stimulus appeared that was restricted to a short period of ~100 ms, peaking ~250 ms after stimulus onset. Another, smaller difference also in favor of the distracter stimulus appears ~350 ms after stimulus onset, lasting for ~100 ms. Attention-dependent changes in firing rate would be expected to occur earlier, to be more persistent and in favor of the attended stimulus.
Therefore, this late and temporally restricted difference provides no evidence for a substantial attention-dependent enhancement of neuronal activity throughout the response.

Discussion

Our novel shape-tracking task revealed a strong correlation between attention drawn to a stimulus and the strength of oscillatory activity in the local population of neurons responding in area V4. This attention-dependent increase reached more than 100%, was present throughout the trial and was confined to the γ-band. Behavioral errors indicating selection and further processing of the distracter instead of the target were associated with a considerable redistribution of oscillatory activity patterns in favor of the distracters’ representation. Much less change was seen for errors not necessarily associated with a failure of attention. Further evidence for a close functional relationship between oscillatory γ-band activity and selective attention is the enhanced γPSD during trial periods requiring more attention as compared with periods with less attentional demand.

Modulation of Oscillatory Activity by Selective Attention

The strong dependence of oscillatory activity on the behavioral relevance of the stimulus indicates that the shape-tracking task effectively challenged cognitive mechanisms that employ oscillatory activity. Since the task required keeping the target’s initial shape in memory, the observed effect may have been related to memory as well as to attention. However, if the considerable difference of γPSD between both behavioral conditions during stimulus presentation would have reflected a change of activity patterns of neurons serving working memory for the behaviorally relevant stimulus, a difference of comparable size should have occurred during the delay period, too. Since the increase of γPSD during delay periods is orders of magnitudes smaller than the difference to be explained during stimulus presentation, this main effect cannot reflect activity patterns of neurons keeping information in memory throughout the trial. This conclusion is further supported by previous investigations which did not find much evidence for substantial delay activity in area V4 (Chelazzi et al., 2001). Furthermore, field potential recordings in monkey temporal cortex revealed memory-related synchronous oscillatory activity for the δ- instead of the γ-band (Tallon-Baudry et al., 2004). We therefore conclude, that the modulation of oscillatory activity in the γ-band is caused by attention selecting the sensory representation of the stimulus in area V4. This does not exclude the possibility that attentional selection of stimulus representations is required to enable interactions with memory processes in addition to its crucial role in form perception.
Behavioral Evidence

The hypothesis of a synchronization mechanism of attention predicts that a misdirection of attention should be associated with a failure of the respective neuronal population to synchronize its activity and hence a reduction of γ-band oscillations. In the shape-tracking task the distracter-related false alarm indicated the execution of a correct matching operation, but this occurred for the distracter instead of the target. For this failure to attend and process the instructed stimulus, γ-PsD stayed rather low for the erroneously ignored target, while it rose for the attended distracter close to the strength expected for a correctly attended target. The pattern of results shows that this reversing effect was not only statistically significant but astonishingly complete, reaching more than two-thirds of the idealized expectation for a complete reversal of synchronization strength between target and distracter. Given that reliability and strength of attention in error trials are not expected to be as good as in correct trials, the observed reversal was remarkably strong and indicates a close relation between selective attention and coherent neuronal oscillations in the γ-band. This conclusion is further supported by the specificity of the diametrical effect for errors of attention. Other errors than distracter-related false alarms may reflect e.g. difficulties to recall or compare the initial shape, or to organize the motor response. Confirming the prediction for errors not reflecting failures of attention, the strength of γ-PsD for these errors remained close to what was found in correct trials. Slight deviations are most likely due to second-order effects, like reduced attention after difficulties to perceive or remember an initial shape, a general decrease of the level of focused attention or a short distraction by external events.

In addition to the specific modulation of γ-band oscillations during attentional errors, the modulation of its time course can be related to variations of attentional demands. Periods during trials that systematically lack behaviorally relevant events are expected to go along with reduced attention (Ghose and Maunsell, 2002). Such a period roughly comprises the second half of initial shape presentation and the first morphing cycle in which no repetition of the initial stimulus can occur. Well in line with a functional role for coherent oscillatory activity in attention, the oscillatory signal was less enhanced for the target during this part of the task that requires less attention. Taken together, the strength of γ-band oscillations is closely related to different states of attention, and it fulfills the predictions for a mechanism of attention in surprising detail and is highly consistent for both animals.

Changing γ-PsD Implies Changing Neuronal Synchrony

The observed increase of oscillatory activity in the γ-band could in principle be due to two different mechanisms: first, it could result from enhancing the total synaptic activity within the population of neurons without changing the probability of synaptic events to lock to the temporal pattern of synchronized oscillatory population activity; or second, it could result from enhancing their synchronization to the common, synchronous oscillatory activity pattern. For the following reasons, the observed strong attention-dependent increase of the γ-PsD can be explained best by an enhancement of precise synchronization within the local population of neurons: (i) the summed extracellular current of a population of neurons determines the amplitude of the field potential and grows almost linearly with the number of neurons contributing synchronous activity, whereas the summed currents of non-synchronized activity changes only in proportion with the square root of the number of contributing neurons. Given the large number of neurons involved, non-synchronized activity therefore provides only a negligible contribution to the field potential as compared with synchronized activity (Elul, 1972; Nunez, 1995). Strong changes in the amplitude of the summed current and the associated field potential are therefore unlikely to occur without changes in synchrony of synaptic events. This conclusion is supported by experimental investigations that found enhanced oscillatory field potentials to be associated with increased synchronization between the contributing neurons (Mitzdorf, 1987; Eckhorn et al., 1989; Gray and Singer, 1989; Murthy and Fetz, 1992; König et al., 1995b; Siegel and König, 2003). A direct dependence between neuronal synchronization and the strength of γ-band activity recorded at the surface of cat visual cortex was demonstrated by Herculano-Houzel et al. (1999). In addition, Fries et al. (2001) observed for a color-change detection paradigm an attention-dependent increase of the local field potential together with an enhanced spike-field coherence. (ii) An increase of the average firing rate without changing the probability of spikes to lock to the pattern of synchronized population activity would at best result in an increase of oscillatory activity proportional to the rate change. However, attention-dependent rate changes in area V4 are small or absent if stimuli do not occupy the same receptive fields (Moran and Desimone, 1985; Luck et al., 1997; Desimone, 1998; Reynolds et al., 1999) and share the same feature domain (McAdams and Maunsell, 1999, 2000) as in the present study. (iii) A general increase of firing rate would raise oscillatory signals in all frequency bands (Shah et al., 2004), whereas the strong increment we observed in the γ-band was instead associated with small changes and even decrements of oscillatory signals in lower frequency ranges. These observed decrements are likely to reflect the redistribution of comparatively large amounts of activity from non- or weakly synchronized patterns to well synchronized activity patterns in the γ-frequency range. Such synchronization requires no change of firing rates since individual neurons do not need to contribute to each cycle of synchronous population activity. (iv) The slightly reduced evoked current in the attended as compared with the non-attended condition does not provide evidence for an enhanced firing rate, which could explain the observed increase of γ-band activity in response to an attended stimulus. In summary, the results suggest that attention specifically increases the amount of synchronous oscillatory activity in the neuronal population processing the attended stimulus, predominantly by increasing neuronal synchrony.

Functional Significance

Psychophysical investigations suggest that the critical contribution of attention to explicit shape perception is the selection of the target’s features and the construction of a structural description (Wolfe and Bennett, 1997). In area V4, the features of an object’s shape are represented by the activity of a subset of neurons responding to a rich variety of stimulus properties (Pasupathy and Connor, 1999, 2001). Attention needs first to select this population for further conjoint processing. The modulation of synchrony in cortical networks is a very efficient way to selectively increase the common impact of activity from a specific subpopulation of neurons (Segev and Rall, 1998; Usrey et al., 2000; Azouz and Gray, 2003). Synchronized output from
the selected population (e.g. a population of V4 cells) will summate particularly well in target cells (e.g. a population of IT cells) and will therefore be more effective than other, non-synchronized input. Theoretical work (Niebur and Koch, 1994) suggests that attention-dependent synchronization in V4 would thereby contribute to the selective responses of inferotemporal neurons to attended stimuli and to the suppression of responses to non-attended stimuli being present simultaneously within their large receptive fields.

After stimulus selection the construction of a structural description, defining the overall shape of the target, requires specification of the relations between its features (Wolfe and Bennett, 1997). It has been demonstrated that relations between feature selective neurons can be expressed by the synchrony of their responses (Engel et al., 1991a,b; Freiwald et al., 1995; König et al., 1995a; Kreiter and Singer, 1996b). Thus, the putative neuronal mechanisms for attentional selection could also serve to represent the structural relations defining overall shape.

In summary, the results show that oscillatory synchronization exhibits important properties expected for a mechanism of attention: it increases strongly within the neuronal representation of the attended object whereas it is weaker elsewhere, and it changes in close correspondence with patterns of attention-specific behavioral errors. This indicates a functional role of oscillatory synchronization as a mechanism of attention, which in shape perception may serve both required functions: stimulus selection and construction of structural descriptions for objects with complex shape.

Notes
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