

# Time-frequency analysis of target detection reveals an early interface between bottom-up and top-down processes in the gamma-band

Niko A. Busch,\* Jeanette Schadow, Ingo Fründ, and Christoph S. Herrmann

Otto-von-Guericke-University of Magdeburg, Institute of Psychology, Department of Biological Psychology, PO Box 4120, 39016 Magdeburg, Germany

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The early visual gamma-band response is an oscillatory signal evoked approximately 100 ms after stimulation. While some studies have found effects of various cognitive processes on this signal, such effects could not be replicated in other studies. Accordingly, some authors have claimed that evoked gamma-band activity reflects merely sensory functions. To resolve these conflicting positions, we conducted a target detection experiment in which the feature that defined the target could be distributed over a large or a small part of the entire stimulus. Only targets covering a larger area of the entire stimulus evoked stronger gamma-band activity than standards although the over-all stimulus size was identical for all stimuli. This increase in evoked activity resulted from stronger oscillatory power and not exclusively from stronger phase-locking. In contrast, N1 and P3 amplitudes were larger for target stimuli irrespective of the distribution of the relevant stimulus feature. These results are consistent with the notion that early gamma-band activity is generated by feature-selective neural assemblies the activity of which can in fact be modulated by top-down processes. This interaction, however, may be only detectable in scalp-recorded EEG if it affects a sufficient number of neural assemblies.

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## Introduction

### *Gamma-band activity*

Oscillatory processes have been the focus of many recent electrophysiological studies. The so-called gamma-band, i.e. the frequency range from 30–80 Hz, has recently attracted the interest of many researchers (Herrmann et al., 2004b; Kaiser and Lutzenberger, 2003; Sannita, 2000; Tallon-Baudry, 2003). Numerous studies demonstrated that gamma oscillations are involved in

many perceptual and cognitive functions such as feature binding (Tallon-Baudry and Bertrand, 1999), selective attention (Fries et al., 2001b), long-term memory (Gruber et al., 2004; Herrmann et al., 2004a) or speech perception (Crone et al., 2001a,b). This evidence has been obtained using a wide range of recording methods ranging from single cell recordings in animals to electrocorticograms, MEG and scalp-recorded EEG in humans. Moreover, neurologic and psychiatric disorders have been demonstrated to be correlated with gamma-band abnormalities. In epileptic patients, increased gamma-band power can be observed during the inter-ictal phase between two epileptic seizures and just prior to the onset of an epileptic seizure (Willoughby et al., 2003). Schizophrenic patients in general display reduced amplitudes of gamma-band responses as well as reduced gamma-band phase-locking, but abnormalities of these measures are also correlated with the extent of positive or negative symptomatology (Gallinat et al., 2004; Lee et al., 2003; Spencer et al., 2003, 2004). Despite this extensive body of positive results, some authors have been more skeptical about the role of gamma oscillations. Part of the criticism is based on failures to find gamma activity at all (Juergens et al., 1999). It can be speculated that many more negative results have been obtained but have remained unpublished. A second critical argument is focused on the functional role of a certain type of gamma oscillations. It refers to the common distinction between an early phase-locked gamma response (approximately 100 ms after sensory stimulation), and a later non-phase-locked or induced gamma response with a latency of 300 ms or longer (cf. Başar-Eroglu et al., 1996). While most authors agree that the latter is a correlate of various cognitive processes, some have argued explicitly that the early evoked gamma response is merely a reflection of early sensory processes (Karakaş and Başar, 1998) which is “pure of cognition”. Others have consistently found effects of cognition on induced gamma activity but reported no such effects on evoked gamma activity (e.g. Gruber et al., 2004; Tallon-Baudry et al., 1996). In a series of studies, we were able to demonstrate that the strength of gamma oscillations is related to many non-specific factors like subjects’ age (Böttger et al., 2002), task difficulty (Senkowski and Herrmann, 2002) or stimulus properties (Busch et al., 2004). Hence, the failure to find gamma activity, especially in scalp-recorded EEG, does not speak against

\* Corresponding author. Fax: +49 391 6711947.

E-mail address: niko.busch@nat.uni-magdeburg.de (N.A. Busch).

URL: <http://www.uni-magdeburg.de/nbusch> (N.A. Busch).

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the existence of this phenomenon but, instead, may reflect an inappropriate experimental setup (cf. [Lutzenberger et al., 1997](#)). Similarly, one might ask whether (cognitive) condition effects on the early evoked gamma-band response also might be conditional upon a certain experimental setup or stimulation.

#### *Top-down and bottom-up modulations*

Previous studies have revealed that the early gamma-band response is strongly modulated by stimulus features and, hence, is most probably involved in the neural representation of the stimulus. Multi-unit activity and local field potentials in animal studies revealed that gamma oscillations and synchronization are highly dependent on stimulus features such as orientation and direction of movement ([Friedman-Hill et al., 2000](#); [Frien et al., 2000](#); [Siegel and König, 2003](#)). Human EEG studies found gamma-band oscillations to depend on stimulus parameters. Larger gamma-band responses have been obtained for larger stimuli and for central as compared to peripheral stimulation ([Busch et al., 2004](#)). Larger gamma-band responses have been also found for higher spatial frequency ([Tzelepi et al., 2000](#)). Quadrant of stimulation modulates the topography of gamma-band responses similar to ERP topography, with an inverted high-to-low and left-to-right distribution ([Tzelepi et al., 2000](#)). This pattern is similar to ERP topography (although sources were located in different locations) and is compatible with visual system organization. In this respect, the behavior of early gamma-band responses resembles that of so-called “exogenous” ERPs ([Busch et al., 2004](#)). Hence, if cognitive factors do exert an influence on early gamma-band responses, these would most probably result in an interaction between top-down and bottom-up processes. Models of such interactions have been formulated ([Herrmann et al., 2004b](#); [Siegel and König, 2003](#)). One example is the match-and-utilization-model proposed by [Herrmann et al. \(2004b\)](#). The model rests on the observation by [Fries et al. \(2001a\)](#) that ongoing LFP fluctuations (subthreshold oscillations) in the gamma-band in the cat visual cortex are highly coherent for cells with similar but incoherent for cells with different orientation preference. According to [Herrmann et al. \(2004b\)](#), top-down signals which express, for instance, selective attention towards a certain stimulus feature, synchronize subthreshold oscillations of feature-selective assemblies. Other populations that do not code for the expected stimulus would not be primed by means of synchronized subthreshold oscillations, and would therefore have lower amplitude in the EEG after stimulus presentation. Thus, stimuli that meet the “expectancies” (e.g. target stimuli) expressed by coherent states of the network generate more salient responses than non-attended or unexpected stimuli (e.g. standard stimuli). This idea is consistent with findings from animal studies which demonstrated that feature selective attention modulates the sensitivity of feature-selective neurons for orientation ([McAdams and Maunsell, 1999](#)), contrast ([Reynolds et al., 2000](#)) or color ([Motter, 1994](#)). In addition, selective attention enhances oscillatory activity and synchrony towards attended stimuli in monkeys ([Fries et al., 2001b](#); [Taylor et al., 2005](#)) and humans ([Tallon-Baudry et al., 2004](#)). This implies that the more assemblies process an aspect of the stimulus that is subject to top-down influences, the more assemblies will be modulated. EEG measurements at the scalp level do not pick up responses from individual neural assemblies, but instead, average responses of a large number of assemblies. Hence, the wider the attended feature is distributed across the stimulus and the more

assemblies are modulated, the more salient the difference between attended and unattended stimuli (i.e. the target-standard difference) will appear at the scalp.

#### *Present study*

The present study attempts to resolve the question whether evoked gamma oscillations can be influenced by top-down processes and under which conditions these effects can be obtained. Resolving this question would be of both practical and theoretical interest. Previous failures to find top-down influences on gamma-band responses could be explained on the basis of the present study. Moreover, knowing the circumstances under which top-down influences can be optimally observed could guide the effective design of future investigations. This would foster the importance of the gamma-band response as a research and clinical tool. To this end, we analyzed ERPs and gamma activity in a visual target detection (“oddball”) paradigm and hypothesized that target detection modulates early gamma oscillations only if the physical difference between targets and standards is distributed over a large area. In the oddball paradigm, a stream of stimuli is presented and rare target stimuli have to be detected among more frequent irrelevant standard stimuli. Subjects have to respond to the targets, e.g. by pressing a button or counting the occurrence. This task specifically requires target detection the classical electrophysiological correlate of which is the P300, a late positive deflection of the ERP which is larger for targets than for standards ([Herrmann and Knight, 2001](#); [Kok, 2001](#); [Polich and Kok, 1995](#)). Furthermore, phase-locked gamma oscillations have been demonstrated to be similarly modulated by attention directed towards targets approximately 100 ms after stimulation ([Debener et al., 2003](#); [Herrmann et al., 1999](#); [Stefanics et al., 2004](#)). Some studies, however, could not replicate these findings (e.g. [Karakaş and Başar, 1998](#)). We therefore chose the visual oddball paradigm for the purpose of the present study because it is an acknowledged test of top-down cognitive processes and the inconsistent results exemplify the controversy about the functions of gamma oscillations as outlined above. The reasoning of the present study is summarized in [Fig. 1](#). We compared two conditions using the same stimulation but with different instructions. Grating stimuli were presented that consisted of a small part in the center and a large part surrounding the center. The overall stimulus size employed in this study was adopted from [Busch et al. \(2004\)](#) who reported strong gamma-band responses evoked by stimuli subtending 8° visual angle but no gamma responses evoked by small stimuli. Due to cortical magnification, the representation of the foveal part of the visual field is significantly larger than the cortical representation of the periphery ([Covey and Rolls, 1974](#); [Horton and Hoyt, 1991](#)). Therefore, the surrounding part of the stimulus was chosen to be considerably larger than the central part, since for the purpose of the present investigation, it was critical that the cortical representation of the large stimulus part actually recruits a larger cortical area than the small part. Targets and standards were defined by the orientation of the grating patterns. Targets were to be detected either in the small or the large subregion of the stimulus. We hypothesized that target effects on evoked gamma-band activity would only be obtained if targets had to be detected in the large stimulus part. In this condition, the physical feature (grating orientation) defining the target is distributed over a large portion of the stimulus. We assumed that selective attention to this stimulus feature leads to an enhancement of neural activity in response to

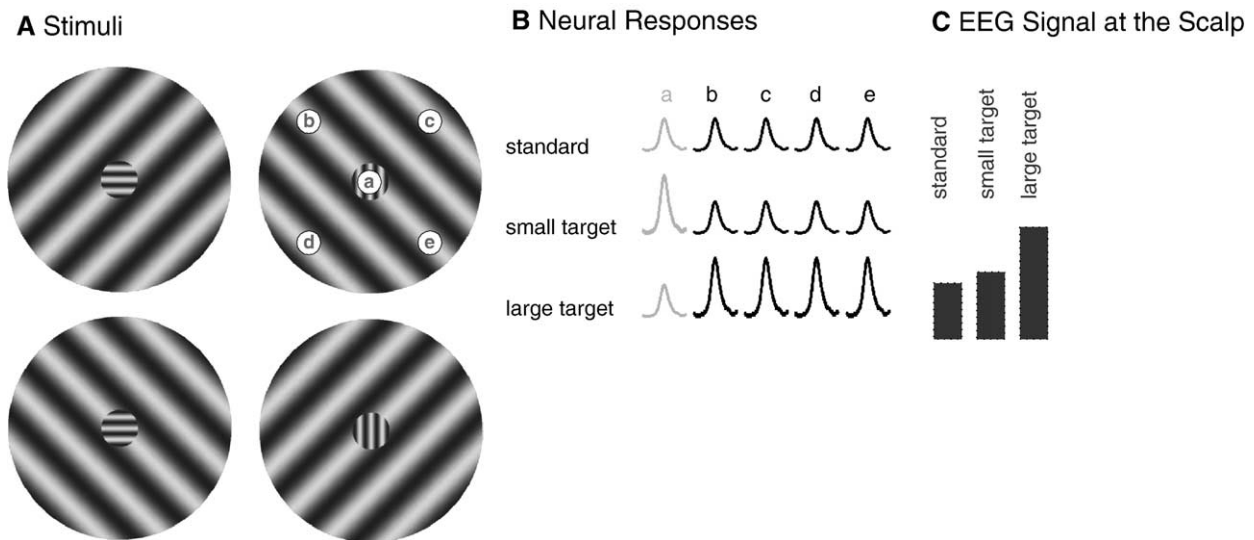


Fig. 1. Schematic depiction of the processes assumed to be involved in the experimental paradigm. (A) Stimuli used in the experiment. In the small-area condition, subjects were instructed to detect one out of two possible grating orientations in the small center of the stimulus. In the large-area condition, subjects had to detect the orientation of the large surrounding grating. Receptive fields of five hypothetical neural assemblies are labeled a–e. (B) Schematic responses of the neural assemblies a–e to standard stimuli, target stimuli with the target feature presented in the small center and target stimuli with the target feature presented in the large surround. Responses of the assembly coding the stimulus' center are depicted gray. Responses to attended features are enhanced. (C) Average response of assemblies a–e as measured at the scalp. A salient difference between target and standard stimuli is visible for large-area targets while effects are minor for small-area targets.

the target stimulus. Thus, in the large-area condition, the activity of a large neuronal assembly would be enhanced upon presentation of the attended stimulus, resulting in a large difference between targets and standards. In contrast, if targets were to be detected in the small part of the stimulus, only a small assembly would be enhanced by target detection and, thus, only a small target effect would be measured at the scalp.

## Materials and methods

### Subjects

16 subjects participated in the study (mean age 23; range 21–35 years, 13 female), all were paid for participation. Subjects gave informed consent prior to the start of the experiment. All subjects had normal or corrected to normal vision and were free of current or past neurological or psychiatric disorders.

### Stimuli and procedure

We presented circular stimuli consisting of two grating patterns, a small one in the center (diameter:  $1.5^\circ$ ; 2 cycles/degree; 40% Michelson contrast; luminance:  $6 \text{ cd/m}^2$ ) superimposed on a larger surrounding pattern (diameter:  $9^\circ$ ; 0.6 cycles/degree; 40% Michelson contrast; luminance:  $6 \text{ cd/m}^2$ ; see Fig. 1A). According to the cortical magnification factor provided by Cowey and Rolls (1974) and Horton and Hoyt (1991), the cortical representation of the large stimulus part in the present study was approximately 3–4 times larger than the representation of the small part, although the area of the large part on the screen was more than 30 times larger than the small center. The grating patterns in the small center part could have either vertical or horizontal orientation whereas the gratings in the larger part had an orientation of either  $45^\circ$  or  $135^\circ$ . Stimuli

were presented on white background (luminance:  $23 \text{ cd/m}^2$ ) on a TFT monitor placed at a distance of 105 cm in front of the subject. Monitor refresh rate was 75 Hz. The experiment consisted of two blocks. In each block, one pattern orientation was defined as target and the other orientation as standard. In the small-area block, subjects were instructed to detect targets in the small central part of the stimulus and disregard the grating in the large surrounding part. Accordingly, in the large-area block, subjects were instructed to detect targets in the large surrounding stimulus part and disregard the grating in the small center. Targets required a speeded button press with the index finger of one hand and standards required button presses with the other hand. Subjects had to fixate a central fixation cross in both blocks. Each block consisted of 100 target and 400 standard stimuli. Stimuli were presented for 1000 ms followed by a variable inter-stimulus interval ranging from 1200 ms to 2800 ms. Target grating orientations in both blocks, block order and response hand were counterbalanced across subjects.

### Data acquisition

The experiments were conducted in an electrically shielded and sound attenuated room. The stimulation monitor was placed outside this cabin behind an electrically shielded window. All devices inside the cabin were operated on batteries to avoid interference of the line frequency (50 Hz in Germany). EEG was recorded with a BrainAmp amplifier (Brain Products, Munich) using 32 sintered Ag/AgCl electrodes mounted in an elastic cap (Easycap, Falk Minow Services, Munich) and placed according to the 10–10 system, with a nose-tip reference and ground electrode between Fz and Cz. Eye movement activity was monitored with an electrode placed supra-orbitally to the right eye and also referenced to the nose. Electrode impedances were below  $10 \text{ k}\Omega$ . Data were sampled at 500 Hz, analog filtered between 0.01 and 200 Hz and stored on a hard disk for off-line analysis. Averaging epochs lasted

from 300 ms before to 800 ms after stimulus onset for ERPs, from –300 ms to 400 ms for early gamma-band responses, and from –300 to 1000 ms for late gamma-band responses. Baselines were computed in the interval from 300 to 100 ms prior stimulus onset and subtracted before averaging. An automatic artifact rejection was computed which excluded trials from averaging if the standard deviation within a moving 200 ms time interval exceeded 40  $\mu$ V. All epochs were also visually inspected for artifacts and rejected in case of eye movements or electrode drifts. While data analysis was performed on unfiltered data, ERPs are displayed low-pass filtered at 20 Hz.

### Data analysis

The statistical analysis of ERPs and gamma-band activity was performed after selected channels were pooled into a region of interest (ROI, see Figs. 4 and 5). Based on inspection of the topographies, those electrodes that displayed a distinct signal were chosen for a ROI. Channels Fp1 and Fp2 were not included in the analysis due to a considerable amount of electrode noise and muscle artifacts. For the analysis of gamma-band activity, a Morlet based wavelet transform with a width of 12 cycles was employed in order to provide a continuous measure of the amplitude of a frequency component (for details refer to Herrmann and Mecklinger, 2000). To reveal the evoked fraction of gamma activity, the wavelet transform was performed on the averaged evoked potential. In order to also analyze activity which is not strictly phase-locked to the stimulus, the wavelet transform was performed for each single trial, and the absolute values of the resulting transforms were averaged. This measure reflects the total activity for a certain frequency range, irrespective of whether it is phase-locked to the stimulus or not. We will refer to this measure as total gamma response in order to make explicit that it comprises both the evoked and induced part of the gamma response (the same measure has been used previously for the estimation of only the induced part; Tallon-Baudry and Bertrand, 1999). The degree of phase-locking was calculated by means of the so-called phase-locking factor. To this end, the phase of the complex wavelet decomposition in each single trial was represented as a point on the unit circle irrespective of amplitude. Averaging these points yields values between 0 for randomly distributed phases and 1 for phases that are strictly phase-locked to stimulus onset across trials. Together, these three measures can shed light on the question of whether stronger evoked gamma-band responses to targets result from stronger phase resetting of ongoing oscillatory activity or, instead, signal increases for target stimuli. Target effects on evoked gamma-responses that are exclusively based on effects on the phase-locking factor but not on total activity would argue for stronger phase resetting to targets. Alternatively, evoked target effects together with stronger total activity would argue for stronger oscillatory activity in response to targets. It should be noted that an increase in phase-locking per se is not informative about the generating mechanism because either phase resetting or additive power can produce an apparent reordering of phases (cf. Jervis et al., 1983; Shah et al., 2004; Yeung et al., 2004). Single trial analysis (a so-called “erpimage”; Makeig et al., 2004) was used to illustrate the phase-locking process in more detail. The erpimage is a colored rectangular image in which each horizontal line represents a single experimental trial and the color values indicate the amplitude at each time point. Single trials were first band-pass filtered around the subject’s individual peak frequency

(see below). Subsequently, a moving average across 10 adjacent single trials was used to highlight trial-to-trial consistency. Furthermore, the single trials were sorted according to the phase of the gamma-band rhythm in the baseline (270 ms before stimulus onset).

Since the exact frequency of the gamma-band response varies considerably between subjects, the frequency of gamma activity used for the wavelet analysis was determined individually for every subject. Time-frequency transforms were first computed for every channel. Anterior, central and posterior channels were subsequently averaged to increase the signal-to-noise ratio. From these averaged time-frequency scalograms, individual gamma frequencies were obtained as the maximum response in the frequency range between 30 and 90 Hz in a time window from 60 ms to 120 ms (early gamma-band response), and from 400 ms to 800 ms (late gamma-band response), respectively. One subject who did not exhibit evoked activity in the early time window was excluded from the analysis of early gamma-band activity and four subjects who did not exhibit total activity in the late time window were excluded from analysis of late gamma-band activity. Using this definition, the individual peak frequencies of early evoked gamma-band responses ranged from 30 to 66 Hz (mean 41 Hz, SD = 10.9 Hz) and frequencies of late total gamma responses ranged from 47 to 83 Hz (mean 59 Hz, SD = 11.1 Hz). For the statistical analyses, ERP components were defined as peak amplitudes in the time interval 80 ms to 130 ms (P1), 150 ms to 200 ms (N1), and as mean amplitudes in the time interval from 400 ms to 600 ms (P3). Early gamma-band responses were defined as peak amplitudes of evoked gamma activity, the phase-locking factor and total gamma activity, respectively, in the time window from 50 ms to 120 ms. Late gamma-band responses were defined as the mean amplitude of total gamma-band activity in the time window from 400 ms to 800 ms. Response time (RT) was analyzed for valid responses not exceeding the mean response time by two standard variations after outliers (responses faster than 100 ms or slower than 900 ms) had been removed. Repeated measures ANOVAs of response times, error rates, ERP and gamma-band effects were computed for the factors stimulus-type (targets vs. standards) and target-area (large-area block vs. small-area block). Greenhouse–Geisser corrections were used to adjust for violations of the sphericity assumption for repeated measures factors containing more than two levels (cf. Dien and Santuzzi, 2004). Uncorrected degrees of freedom and corrected *P* values are reported.

We predicted that an interaction between bottom-up and top-down influences on early gamma-band activity would manifest in a statistical interaction between stimulus-type and target-area with larger stimulus-type effects in the large-area block.

## Results

Stimulus presentation evoked a P1 (mean peak latency 106 ms; Fig. 4, top row) followed by an N1 (mean peak latency 170 ms; Fig. 4, middle row) and a late positive deflection we will refer to as P3 (mean peak latency 470 ms; Fig. 4, bottom row). The analysis of the individually identified gamma-band responses revealed a prominent early evoked gamma response (mean peak latency 86 ms; Figs. 2A and 5, top row) that was strongly phase-locked to stimulus onset (Figs. 2B and 5, 2nd row) and was accompanied only by a small increase in total gamma-band power in this early time window (Figs. 2C and 5, 3rd row). The phase-locking process

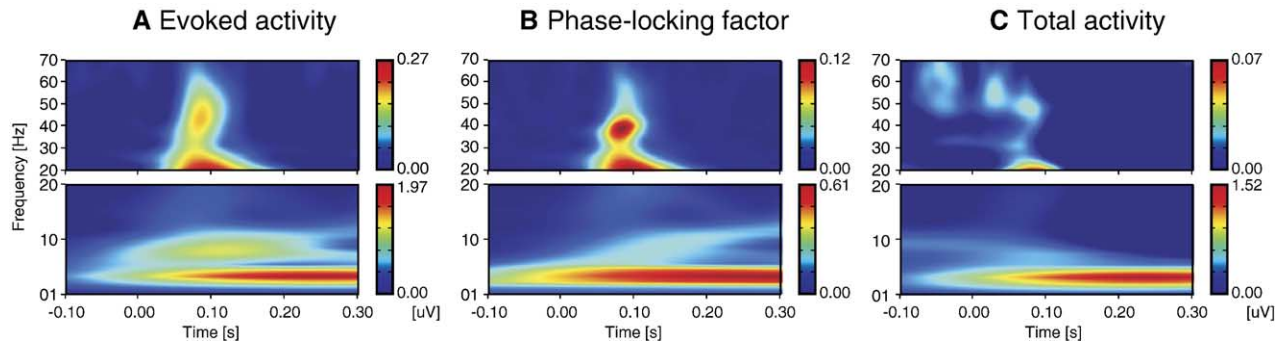


Fig. 2. Time-frequency plots of a representative subject, averaged across all posterior electrodes and averaged across all experimental conditions. High- and low-frequency activity is depicted in separate plots with different amplitudes scales because the low-frequency portion was of considerably higher amplitudes. A distinct signal around 44 Hz is visible in evoked activity (A) and the phase-locking factor (B). In contrast, no equivalent power increase appears in total activity (C).

is further illustrated in Fig. 3. Furthermore, we observed a later gamma-band response in the time window 400–800 ms which resulted solely from an increase in total gamma-band power (Fig. 5, bottom row).

Fig. 3 exemplifies the phase-locking process of the early gamma-band response in more detail. It displays data from the same subject whose time-frequency data are depicted in Fig. 2 from all experimental conditions at electrode O1. Single trials were band-pass filtered around the subject's individual gamma frequency (44 Hz, see Fig. 2). Single trials were sorted according to the phase of the 44 Hz rhythm in the baseline (270 ms before stimulus onset). The vertical lines indicate a time window corresponding approximately to one wavelength of the 44 Hz rhythm centered around  $-270$  ms and time point of maximal phase-locking (90 ms after stimulus onset). The figure reveals trial-to-trial consistencies around 270 ms before and around 90 ms after stimulus onset. The pattern in the baseline time window is a product of the phase sorting procedure. Phase sorting the single trials revealed a random distribution of phases in the baseline which appears as diagonal "stripes" in the erpimage. In contrast, phases were markedly consistent across trials at 90 ms after stimulus onset, resulting in almost vertical "stripes" in that time range. This phase-alignment is reflected also in the band-pass filtered ERP, the phase-locking factor and the evoked gamma activity. Note that amplitudes appear to increase in single trials in these time ranges. This is, however, a result of the moving average which attenuates signals in time ranges that exhibit no consistency across trials. In fact, inspection of total 44 Hz activity revealed only a minor increase of gamma-band power at 90 ms which could not account for the strong increase in evoked phase-locked gamma (see Fig. 2C).

#### Behavioral data

Subjects reacted more slowly (482 ms vs. 414 ms) in response to target stimuli (main effect of stimulus-type:  $F(1,15) = 161.65$ ,  $P < 0.001$ ) and made more errors (77.8% correct vs. 94.1% correct) compared to standard stimuli (main effect of stimulus-type:  $F(1,15) = 71.03$ ,  $P < 0.001$ ). In the large-area block, response times were faster (432 ms vs. 465 ms) than in the small-area block (main effect of target-area:  $F(1,15) = 17.62$ ,  $P = 0.001$ ) and performance was more accurate (87.3% correct vs. 84.5% correct) than in the small-area block (main effect of target-area:  $F(1,15) = 7.86$ ,  $P = 0.013$ ).

#### P1

P1 amplitudes were most pronounced at electrodes O1 and O2 (Fig. 4, top row). No significant effects of stimulus-type or target-area were observed for this component.

#### N1

Parietal electrodes revealed the largest N1 amplitudes (Fig. 4, middle row). N1 was larger for target than for standard stimuli (main effect of stimulus-type:  $F(1,15) = 40.63$ ,  $P < 0.001$ ).

#### P3

P3 topography was widespread with maxima at CZ and PZ (Fig. 4, bottom row). P3 amplitudes were larger for targets than for standards (main effect of stimulus-type:  $F(1,15) = 32.30$ ,  $P < 0.001$ ) and larger in the small-area than in the large-area block (main effect of target-area:  $F(1,15) = 5.77$ ,  $P = 0.03$ ).

#### Early gamma-band activity

Early gamma responses were strongest at parietal and occipital electrodes (Fig. 5, rows 1–3). No main effect of stimulus-type on evoked gamma activity was obtained. Evoked gamma amplitudes were larger in the large-area block than in the small-area block (main effect of target-area:  $F(1,14) = 16.96$ ,  $P = 0.001$ ; Fig. 5, top row). Additionally, target stimuli evoked larger gamma responses than standards in the large-area block, but not in the small-area block (stimulus-type  $\times$  target-area interaction:  $F(1,14) = 8.26$ ,  $P = 0.012$ ). Post hoc tests revealed significant differences between target and standard stimuli in the large-area block ( $F(1,14) = 11.05$ ,  $P = 0.005$ ) but no such differences in the small-area block ( $F(1,14) < 1$ ).

Analysis of the phase-locking factor revealed no differences in phase-locking between stimulus-types but stronger phase-locking in the large-area condition compared to the small-area condition (main effect of target-area:  $F(1,14) = 9.27$ ,  $P = 0.009$ ; Fig. 5, 2nd row).

Early total gamma-band activity was larger on average in response to target stimuli as compared to standards (main effect of stimulus-type:  $F(1,14) = 9.77$ ,  $P = 0.007$ ; Fig. 5, 3rd row), and stronger in the large-area block as compared to the small-area block (main effect of target-area: ( $F(1,14) = 6.31$ ,  $P = 0.025$ ).

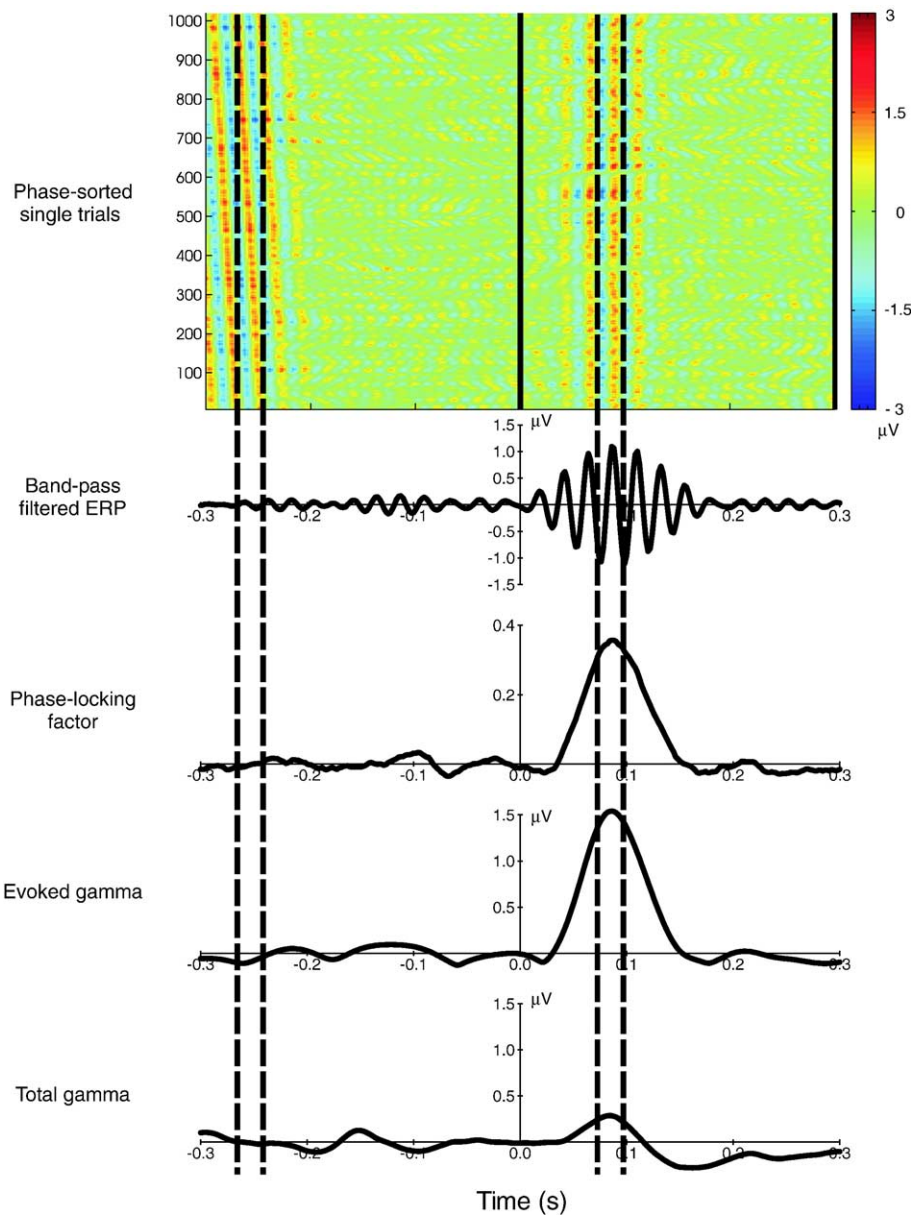


Fig. 3. Single trial analysis (same subject as in Fig. 2, electrode O1) reveals strong phase-locking of gamma-band (44 Hz) activity after stimulus onset. The top part depicts color coded, band-pass filtered single trials from all experimental conditions that were sorted according to the phase of the 44 Hz rhythm in the baseline window. Phases are randomly distributed in the baseline but very consistent across trials around 90 ms post-stimulus. This is reflected in the band-pass filtered averaged ERP, phase-locking factor and evoked gamma-band activity. No equivalent increase in total gamma-band power is observed at the same time.

Furthermore, target-standard differences were larger in the large-area condition (stimulus-type  $\times$  target-area interaction:  $F(1,14) = 6.72$ ,  $P = 0.021$ ). Post hoc tests revealed an increase in total gamma activity in response to target stimuli only in the large-area block ( $F(1,14) = 13.30$ ,  $P = 0.003$ ) but not in the small-area block ( $F(1,14) < 1$ ).

#### Late gamma-band activity

Late total gamma activity had a parieto-occipital topography, similar to early gamma activity (Fig. 5, bottom row). No effects of stimulus-type or target-area were obtained for total gamma-band activity in the late time window.

## Discussion

In the present investigation, we attempted to resolve two issues: under which conditions is early gamma activity modulated by target detection and do such modulations rather involve changes in phase distributions or changes in spectral power.

#### Target detection and the early evoked gamma-band response

Regarding ERPs and behavioral performance, we observed a pattern which is considered typical for target detection experiments: larger P3 amplitudes, slower response times and more errors for infrequent target stimuli (Herrmann and Mecklinger, 2000;

## Event-related potentials

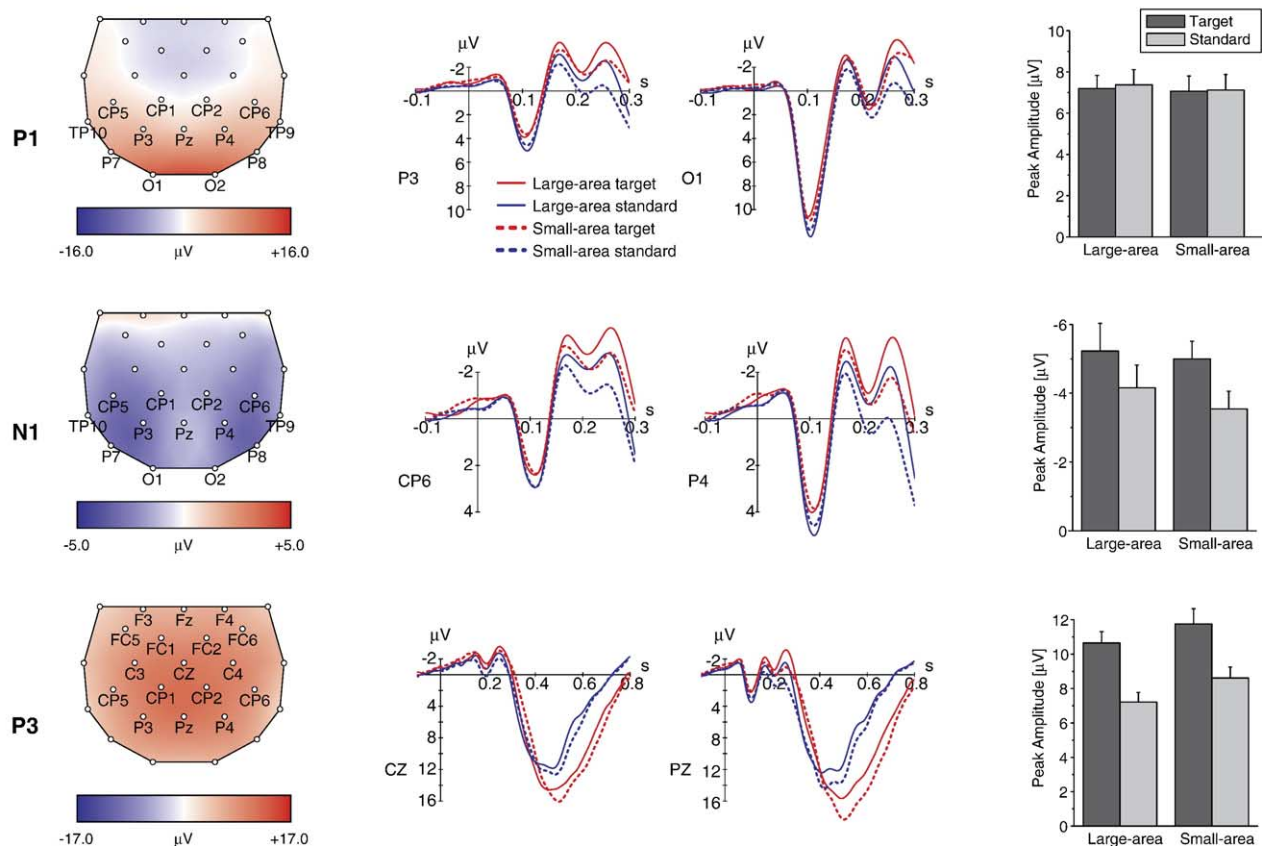


Fig. 4. Left column: scalp topographies of P1, N1 and P3 averaged across all conditions. Electrode names are depicted for those channels that were included in the ROIs. Middle column: time courses of ERPs for selected electrodes. Right column: amplitudes and standard error for all electrodes within the ROI. Electrodes were chosen for display at which components and effects were most pronounced. Note the different time and amplitude scales for P1, N1 and P3, respectively. All plots represent the average across all subjects.

Kok, 2001; Linden et al., 1999; Mecklinger and Ullsperger, 1993). P3 amplitudes were larger for targets than for standards irrespective of the size of the targets and, hence, rather reflected the stimulus category. Previous ERP studies reported larger P3 amplitudes in response to more intense stimuli in the auditory, visual and somatosensory domain (Covington and Polich, 1996; Nakajima and Imamura, 2000). Polich et al. (1996, p. 61) suggested that “stimulus intensity affects P300 because of the increased attention and arousal that can occur with increased levels of stimulation”. While these results suggest that there exists an “exogenous” aspect of the P3 component, no interaction between stimulus factors and top-down factors has been reported. In a somatosensory target detection paradigm for instance, Nakajima and Imamura (2000) varied the physical intensity of both target and standard stimuli. While P3 amplitudes were larger for targets (a top-down factor) as well as for more intense stimuli in general (a bottom-up factor), no interaction between the two factors was observed. Thus, we could confirm and extend previous reports of “endogenous” and “exogenous” contributions to the P3.

Most importantly, we were able to demonstrate that early gamma activity is, in fact, larger for targets than for standard stimuli. However, the pattern of results observed for early gamma-band responses differed from those of the P3 in one important aspect. Target effects on gamma activity were found only for large targets, i.e. when the stimulus feature defining the

target was distributed over a large area of the stimulus. This finding is relevant both for theoretical and practical reasons. The interaction of stimulus category and area occupied by the target defining feature suggests that modulations of early gamma-band activity reflect an interaction of bottom-up and top-down processes. At stimulus presentation, a stimulus is processed by neural assemblies some of which are feature-selective. The strength of activation of these assemblies depends largely on the extent to which the preferred feature is present in the stimulus (bottom-up). Target detection involves the expectation of a stimulus defined by specific stimulus features, e.g. orientation (top-down). In the present experiment, a grating in the large surround of the stimulus activates a larger orientation selective network than the grating in the small center. We argue that top-down influences enhance activity in these feature-selective networks. In case of a larger feature distribution (such as in the large-area condition), top-down influences lead to modulation of a larger network. This interaction leads to a larger gamma amplitude measured at the scalp and, thus, to the target effect we observed. Accordingly, in the case of a smaller distribution of the target defining feature (such as in the small-area condition), the difference between targets and standards is less pronounced and, therefore, harder to be detected reliably at the scalp. Thus, our results confirm and extend previous studies that found the evoked gamma-band response to be under the

### Gamma-band activity

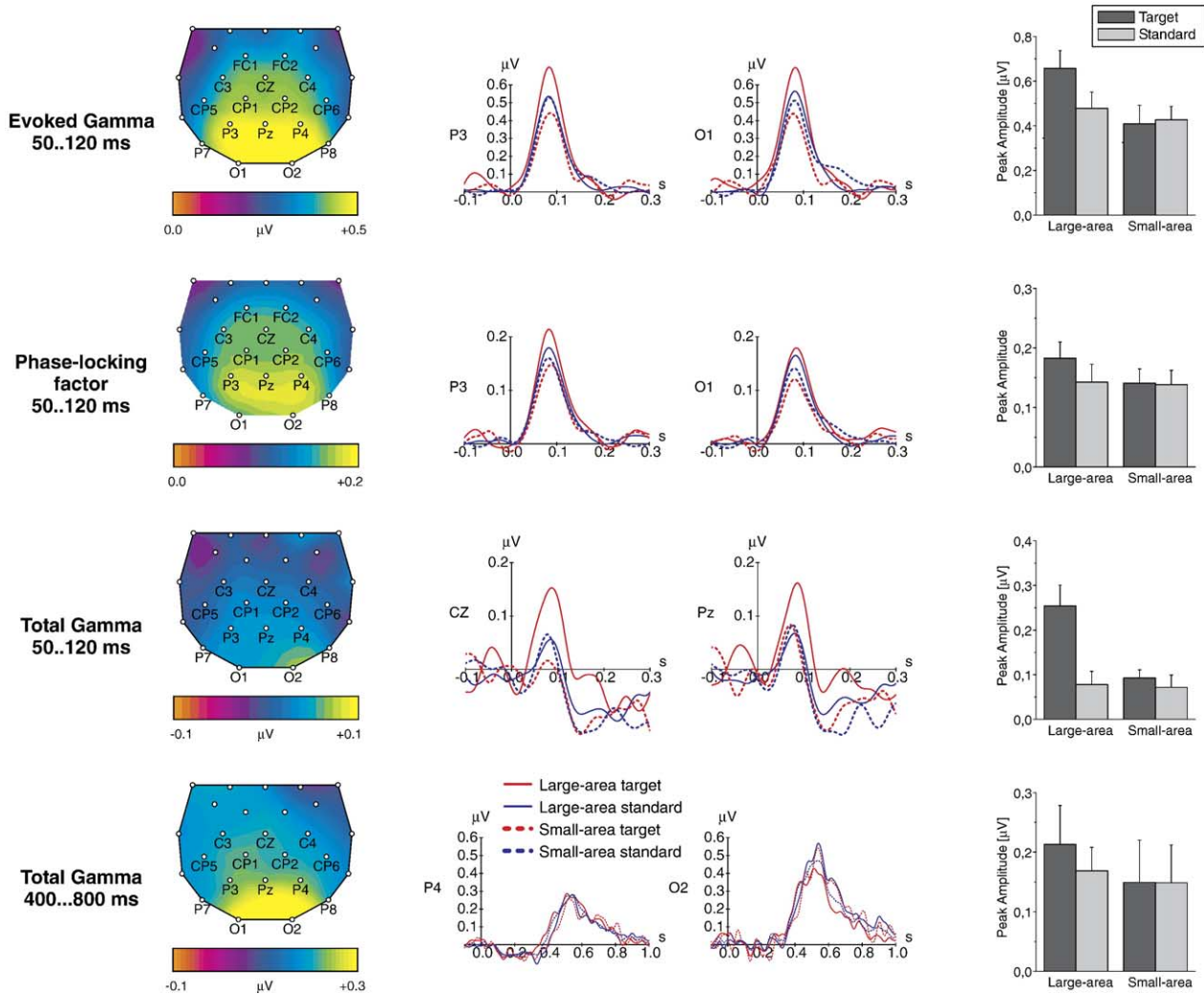


Fig. 5. Left column: scalp topographies of early evoked gamma-band activity, phase-locking factor, total gamma-band activity and of late total gamma-band activity averaged across all conditions. Electrode names are depicted for those channels that were included in the ROIs. Middle column: time courses for selected electrodes. Right column: amplitudes and standard error for all electrodes within the ROI. Target effects occurred only in the large-area condition. Electrodes were chosen for display at which components and effects were most pronounced. Note the different time and amplitude scales. Also note that different frequencies were analyzed for early and late gamma-band responses. All plots represent the average across all subjects.

influence of top-down cognitive mechanisms. Such a property may not be commonly associated with early visual processing. Recent models of the primate visual system, however, assume that visual processing relies on the interaction of feed-back and feed-forward connections already at a very early stage (Bullier, 2001; Lamme and Roelfsema, 2000). In an ERP experiment, Foxe and Simpson (2002), for instance, reported occipital activation after 56 ms and frontal activation as early as 80 ms after visual stimulation. Thus, this framework of early visual processing makes it plausible how a signal as early as the evoked gamma-band response can be modulated by bottom-up as well as top-down factors simultaneously.

These results also bear practical implications for the design of stimuli and experiments destined for the investigation of cognitive effects on early gamma-band activity. In a previous study, we were able to demonstrate that only strong stimulation will lead to a measurable gamma-band response in scalp EEG (Busch et al., 2004). In combination with the present data, it seems advisable that

experimental conditions which differ in some cognitive parameter (e.g. targets vs. standards) be not different with respect to physical stimulus features which are known to modulate gamma-band activity (e.g. different size, contrast or spatial frequency). The difference that defines the cognitive conditions should be distributed over a large area of the stimulus in order to modulate the activity of a larger neuronal assembly. Furthermore, more salient effects might be achieved employing a salient perceptual difference between conditions (e.g. a difference in line orientation of 90° instead of, say, 10°).

#### Power increase vs. phase resetting

A second concern of this study was to determine the origin of the target effect on evoked gamma-band activity. The early evoked gamma-band response has so far been mainly described as being accompanied by strong phase-locking to stimulus onset with little or no increase in gamma-band power (e.g. Busch et

al., 2004; Sannita et al., 2001). Therefore, one might argue that this type of gamma oscillations reflects a phase reorganization of ongoing gamma activity due to sensory stimulation without an increase in signal power (Fell et al., 1997). In contrast, other EEG signals such as ERPs or induced gamma oscillations are believed to be generated by an increase in (oscillatory) activity, although the generation of ERPs is still an issue of ongoing debate (e.g. Makeig et al., 2004; Shah et al., 2004; Yeung et al., 2004). Two alternative (but not necessarily exclusive) mechanisms have been proposed. On the one hand, sensory stimulation may induce “phase resetting” of ongoing electroencephalographic (EEG) rhythms in each trial (but no other neural response additional to background activity) and averaging these phase-coherent rhythms produces the ERP. The alternative view proposes that the stimulus elicits an additive, neural-population response in each trial and that averaging these evoked responses produces the ERP. Although early evoked gamma-band responses as such appear to result from the first aforementioned mechanism (see Fig. 3), it is so far unclear whether task differences in evoked gamma activity are caused by a different degree of phase-locking or a difference in signal power. Most previous studies which investigated phase resetting phenomena focused on data from a single experimental condition. It might be possible, however, that the two proposed mechanisms are involved in different modes of processing. For instance, Busch et al. (2004) found that changes in stimulus properties (bottom-up factors) affected mainly the phase-locking of the early gamma-band response with little effect on total gamma-band power. On the other hand, studies employing auditory oddball and choice reaction tasks (involving top-down processes) found target stimuli to elicit stronger early evoked gamma-band activity than standards (Debener et al., 2003; Yordanova et al., 1997) which was not caused by an increase in phase-locking as in studies manipulating stimulus properties, but instead stemmed from an increase in gamma-band power. In the present study, we observed stronger evoked (i.e. phase-locked) gamma activity for large targets. Although we observed strong phase-locking in the gamma-band (cf. Fig. 3), the degree of phase-locking was not influenced by stimulus-type. In contrast, early total gamma-band activity, an index of signal power, was increased for large targets at the same time. In fact, total gamma-band responses were almost absent in the other conditions. We therefore suggest that the early evoked gamma-band response is a combination of phase-locking across trials due to bottom-up processing of stimulus features plus additional signal power due to top-down processing. Our results thus seem to concur with the notion that event-related brain responses are not completely independent of ongoing activity (Arieli et al., 1996; Makeig et al., 2004). Interactions between spontaneous and event-related activity have recently received a lot of interest, but to date, no conclusive account of the functional significance of phase-locking of ongoing activity in the gamma-band has been given. An increase of phase-locking in the absence of larger power changes indicates that the timing of stimulus processing exhibits less intertrial variability. It could well be that all neuronal assemblies relevant for the generation of the early gamma response are located at such an early stage of visual processing that they are activated at the same time in every trial because the distances from the retina (in terms of the number of intermediate synapses) do not vary across trials and no other processes are located in between that may introduce

additional time jitter. Neurons seem to fire in the gamma-band before as well as after presentation of a stimulus as indicated by the absence of a change in total gamma activity (cf. Fig. 3). However, the presentation of a stimulus forces a large number of neurons to fire at a certain latency after stimulus onset. This latency is determined by the number of synapses between the retina and these particular neurons and remains more or less stable across trials. This represents a synchronization to the stimulus leading to the observed increase in evoked EEG gamma activity. At the same time, cortical subthreshold oscillations exhibit different phases for neurons responding to different regions in the visual field (VanRullen and Thorpe, 2002). Therefore, each neuron responds at the same latency in every trial but within one trial, multiple neurons respond at different latencies resulting in no increase of total gamma activity. Such an increase of evoked activity without a simultaneous increase of total activity is considered a phase reset. We argue that the early evoked gamma activity is generated by such a mechanism. This is consistent with existing models of cortical computation that rely on timing of neural events (Körner et al., 1999; VanRullen and Thorpe, 2002). The increase of the early evoked gamma activity in response to targets as compared to standards, however, is not due to phase resetting but to an increase in total power. It should be noted that scalp EEG reflects the activity of large patches of cortex. Hence, an increase of total gamma-band activity in scalp-recorded EEG could, in principle, be generated by two different underlying mechanisms. On the one hand, changes in spectral gamma power could be caused either by more neurons oscillating in the gamma-band range, i.e. by changing firing rates or dendritic current fluctuations from low frequencies to gamma frequencies. On the other hand, stronger synchronization between neural assemblies without a change in the number of assemblies oscillating with that frequency would also lead to more gamma-band power at the scalp. As suggested by Engel et al. (2001, Fig. 4, part d), expectancy can influence the phase of subthreshold oscillations. If a certain target is expected, those neurons which code for features of that target exhibit subthreshold oscillations which are in phase to each other. Those neurons that code other features exhibit subthreshold oscillations with random phases. If, now, those neurons that code features of the target receive input from the retina, they will fire synchronously, because their firing thresholds are all reached at the same time due to their subthreshold oscillations being in phase. This leads to increased total gamma power at the scalp. Early evoked gamma-band activity then might be a combination of such power increases and phase resetting effects. If, however, neurons that code for features of the standard stimulus receive input from the retina, they will fire asynchronously due to their subthreshold oscillations being out of phase. In this case, no total power is added to the early gamma activity and thus results in the smaller response to standards.

### Conclusion

Our results suggest that early evoked gamma-band activity in scalp-recorded EEG is modulated by target detection if enough neural assemblies process the target defining stimulus feature. Furthermore, we propose that sensory stimulation as a bottom-up process results in a phase-locking of evoked gamma-band activity while target detection as a top-down influence increases the power

of gamma-band activity in the same neural assemblies that are activated by stimulation.

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