

# Stimulus intensity affects early sensory processing: Visual contrast modulates evoked gamma-band activity in human EEG

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## Abstract

We studied the effect of different contrast levels on the visual evoked gamma-band response (GBR) in order to investigate whether the GBR is modulated in a similar manner as previously reported for visual evoked potentials.

Previous studies showed that the GBR can be modulated by individual characteristics (age) and experimental conditions (task difficulty, attention). However, stimulus properties, such as size and spatial frequency, also have a large impact on the GBR, which necessitates identification and control of relevant stimulus properties for optimal experimental setups.

Twenty-one healthy participants were investigated during a forced-choice discrimination task. Sinusoidal gratings were presented at three contrast levels with a constant spatial frequency of 5 cycles per degree visual arc (cpd). The present data replicate the results reported for visual evoked potentials and exhibit a contrast dependent modulation of the GBR. Gamma activity is increased for higher contrast levels.

These results demonstrate the importance of stimulus contrast for evoked gamma activity. Thus, it appears meaningful to control the contrast of stimuli in experiments investigating the role of gamma activity in perception and information processing.

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## 1. Introduction

Oscillatory responses of neuronal assemblies in the gamma range (30–80 Hz) have recently been described in the auditory, somatosensory, and especially in the visual modality (Başar et al., 2000). The investigation of modulating factors of gamma activity linked to sensory and cognitive aspects has attracted much interest from numerous research groups (refer to the review of Engel et al., 2001). In general, most studies distinguish between two types of gamma-band responses (GBRs). The early ‘evoked’ gamma-band response is phase-locked to stimulus onset, whereas the later ‘induced’ gamma response jitters in latency from trial to trial and is, therefore, not phase-

locked (Başar-Eroglu et al., 1996). The early gamma activity observed during the first 100 ms after stimulus onset was initially associated with sensory coding processes (Karakas and Başar, 1998). Later, it was shown that early gamma activity might also reflect cognitive processes (Karakas et al., 2001; Senkowski and Herrmann, 2002; Fell et al., 2003; Herrmann et al., 2004a; Busch et al., 2006). For a variety of paradigms, particularly in the visual modality in animals and humans, the late gamma activity around 200–400 ms after stimulus onset is closely related to top-down factors such as attention (Gruber et al., 1999; Müller et al., 2000; Keil et al., 2001; Fries et al., 2001), task complexity (Posada et al., 2003), and perception (Tallon et al., 1995). Moreover, recent studies have highlighted a pivotal role for both types of gamma activity in memory processes (Herrmann et al., 2004a; Gruber et al., 2004). In the ‘match-and-utilization model’, memory is discussed as a global underlying mechanism for early and late GBRs (Herrmann et al., 2004b).

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Several studies investigating gamma oscillations and their potential functional role in animals and humans reported difficulties in either detecting gamma-band activity or gamma modulations (Tovee and Rolls, 1992; Young et al., 1992; Menon et al., 1996; Lamme and Spekreijse, 1998), or pointed out discrepancies in the experimental findings between animals and humans (Menon et al., 1996; Juergens et al., 1999). Juergens et al. (1999) demonstrated a strong stimulus-related increase in gamma oscillations in monkeys, but no related GBR in humans in the same visual paradigm. Furthermore, some research groups failed to replicate former results regarding visual gamma modulations. The group of Roesler (cited in Juergens et al., 1999) tried to replicate the findings of an experiment on visual gamma modulation done by Tallon-Baudry et al. (1996) without success. These inconsistent findings could be attributed to the diverse methodological approaches concerning the analysis of gamma-band activity (Engel et al., 1992). One further possible explanation for the described difficulties in detecting gamma activity or gamma-band modulations might be differences in the experimental design and in the stimulation. Given the strong dependence of the GBR on stimulus properties, it is conceivable that negative results could have been obtained due to inappropriate stimulation.

Busch et al. (2004) demonstrated that stimulus properties such as size and eccentricity significantly influence gamma activity. The largest and most centrally presented stimulus evoked the highest GBR. Similar results for animals have been reported regarding the stimulus size. In recordings from cat retinal ganglion cells, large, but not small, stimuli elicited high-frequency oscillatory potentials (Neuenschwander et al., 1999). The same size dependency was observed in frogs (Ishikane et al., 1999) and rabbits (Ariel et al., 1983). Bodis-Wollner et al. (2001) and Tzelepi et al. (2000) pointed out that the power in the gamma frequency range varies with spatial frequency as a further stimulus characteristic. Tzelepi et al. (2000) reported that responses were larger to grating stimuli with 4 cycles per degree (cpd) than in response to 1 cpd stimuli, whereas Bodis-Wollner et al. (2001) observed the largest power to a spatial frequency of 5.5 cpd. Thus, the occurrence of evoked gamma activity seems to be most sensitive to stimulus properties such as size, eccentricity, and spatial frequency. Accordingly, we hypothesized that contrast, an additional characteristic of a stimulus, may influence the visual evoked gamma-band response. Such a modulation by contrast has already been described in event-related potential (ERP) studies of animals and humans (Tolhurst et al., 1981; Harnois et al., 1984; Campbell and Kulikowski, 1972; Bobak et al., 1987; Vassilev et al., 1994). Harnois et al. (1984) observed a dependence of the transient visual evoked potentials (VEPs) on contrast in rats. The latency of the P1 wave decreased linearly and the amplitude of the P1–N2 component increased with increments of contrast up to 55%. Similar results in visual cortical neurons of the cat were found by Tolhurst et al. (1981). At low contrasts, the response amplitude increased linearly with contrast, but a logarithmic rise might provide a better description for higher contrasts. However, saturation was observed at very high contrast levels above 50%. Human EEG studies confirmed the results described for animals. VEP latency decreased and

amplitude increased as a monotonic function of stimulus contrast (Bobak et al., 1987; Vassilev et al., 1994).

In conclusion, a clear contrast modulation of VEPs was reported in all studies. The aim of the present study was to investigate the influence of contrast on the evoked GBR. We expected to find a similar modulation of gamma amplitude and to replicate results previously reported for VEP amplitudes and latencies.

## 2. Method

### 2.1. Participants

Twenty-one paid subjects (13 females, 8 males, mean age  $26.2 \pm 5$  years) participated in the study. They had normal or corrected-to-normal vision and showed no signs of psychiatric or neurological disorders. All subjects received a written task instruction and gave informed consent to participate. Two subjects were excluded from the data analysis due to numerous eye artifacts. The ethical principles of the Declaration of Helsinki concerning human experimentation were followed.

### 2.2. Stimuli and task

Sinusoidal gratings with a constant spatial frequency of 5 cpd at a size of  $9^\circ$  of visual angle were generated using MATLAB 6.5. They were centrally presented on a TFT computer screen placed 115 cm in front of the subjects. The Michelson contrast of the grating pattern ( $C$ ) is defined as

$$C = \frac{L_{\max} - L_{\min}}{L_{\max} + L_{\min}} * 100$$

where  $L_{\max}$  is the maximum and  $L_{\min}$  the minimum luminance (Bodis-Wollner et al., 1972). Gratings with three varying contrast levels (5%, 20%, and 50%) were created and presented on a grey background with mean luminance  $(L_{\max} + L_{\min})/2$  (see Fig. 1). The present experiment was constructed as a forced-choice discrimination task. The frequent stimulus (80% of presentations) was oriented horizontally, whereas the infrequent stimulus had a vertical orientation. The experimental session consisted of 300 frequent stimuli (100 for each contrast) and 75 infrequent stimuli (25 for each contrast) which were presented in a pseudo-randomized order. Only the frequent stimuli were included in the present analysis. The presentation duration of each stimulus was 1000 ms with an interstimulus interval (ISI) between 1200 and 2000 ms. Participants were instructed to press a button with their right index finger in response to the infrequent stimuli and another button with their left index finger in response to the frequent stimuli. During the entire experimental session, subjects were instructed to fixate a cross in the center of the screen to avoid eye movement artifacts. Two breaks were included. The length of each break was individually determined by the participant.

### 2.3. Data acquisition

EEG was recorded with a BrainAmp amplifier (Brain Products, Munich), using 32 sintered Ag/AgCl electrodes mounted

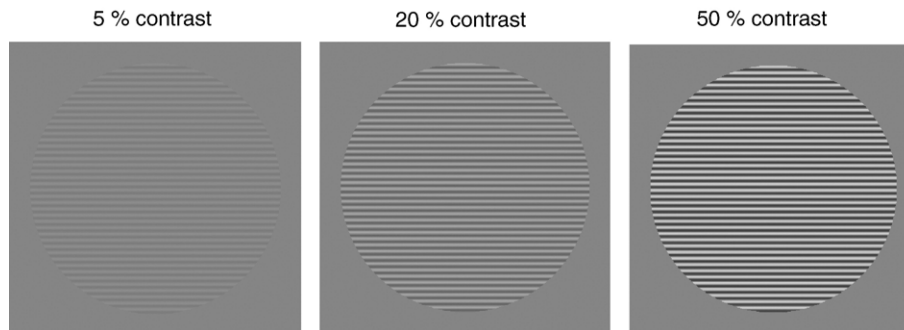


Fig. 1. The horizontally oriented stimuli at three contrast levels.

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 suborbitally to the right eye.

Electrode impedances were always below 5 k $\Omega$ . Data were acquired with a sampling rate of 500 Hz and hardware-filtered between 0.016 and 250 Hz. Stimulus markers and EEG were stored on hard disk for further analysis. The EEG was recorded while subjects sat in an electrically shielded, sound-attenuated room. The 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). Digitized EEG data were transferred to a computer outside the cabin with a fiber-optic cable. Averaging epochs lasted from 200 ms before to 1000 ms after stimulus onset for VEPs and evoked gamma-band responses. Baselines were calculated in the interval from  $-200$  ms to  $-100$  ms 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 when eye movements, electrode drifts, or electromyographic activity occurred. Whereas data analysis was performed on unfiltered data, VEPs are displayed low-pass filtered at 20 Hz.

## 2.4. Data analysis

### 2.4.1. Behavioral data

Only trials with responses given between 200 and 2500 ms after stimulus onset were included in the analysis. False trials were rejected from the behavioral data analysis, as well as trials in which the reaction time (RT) exceeded two standard deviations from the mean.

### 2.4.2. Visual evoked potentials

The statistical analysis of evoked potentials was performed after selected channels were pooled into a posterior region of interest (ROI). Based on the inspection of the topographies, those electrodes that showed a distinct signal were chosen for the ROI (Cp1, Cp5, Cp6, Cp2, P7, P8, P3, P4, Pz, O1, O2). Two VEP components were defined as peak amplitudes in the time

interval of 90 ms to 150 ms (P100) and 160 ms to 230 ms (N200). Amplitudes were analyzed using a repeated measures ANOVA with the factor CONTRAST (3 contrast levels) for each of the two components. Post hoc *t*-tests of specific comparisons of significant ANOVA effects were calculated. The Greenhouse–Geisser correction, an adjustment used in univariate repeated measures when the sphericity assumption is violated, was applied for all ANOVA models. All post hoc *t*-tests were Bonferroni corrected.

### 2.4.3. Early and late gamma-band responses

For the analysis of gamma-band activity, a wavelet transform with a width of 12 cycles based on Morlet wavelets was applied (Herrmann et al., 1999). To analyze the evoked GBR phase-locked to the stimulus, the wavelet transform was applied to the averaged event-related potentials. However, for the non-phase-locked portion of the GBR, each trial was first transformed in the frequency domain and then the resulting wavelet transforms were averaged. This measure represents the total activity, comprising the phase-locked and non-phase-locked part of the GBR. Additionally, the amount of phase-locking across trials was computed. The absolute value yields a number between 0 and 1, determining the degree of phase-locking, where 1 indicates perfect phase alignment across trials and values close to 0 reflect a high phase variability. The frequency used for this wavelet analysis was individually adapted by the time–frequency plane of the O1 electrode. The individual gamma frequency was defined as the highest peak in response to the 50% contrast stimulus in the time interval between 40 and 160 ms (early GBR) as well as 200 and 600 ms (late GBR) after stimulus onset in the gamma frequency range. If no clear GBR peak was visible, a frequency of 40 Hz was chosen for analysis (as done previously, e.g. Herrmann et al., 2004a). For the statistical analysis, early GBRs were defined as the peak amplitude of evoked gamma activity, the phase-locking, and total gamma activity in the time interval between 40 and 160 ms, which turned out to be the peak interval in the time–frequency planes. Thereby, channels were pooled into a ROI comprising the following seven parieto-occipital electrodes which exhibited the strongest responses after visual stimulation: P7, P8, P3, P4, O1, O2, and Pz. Late GBRs were defined as mean amplitude of total gamma activity in the time interval between 200 and 600 ms. A repeated measures ANOVA was calculated for the factor

Visual evoked potentials

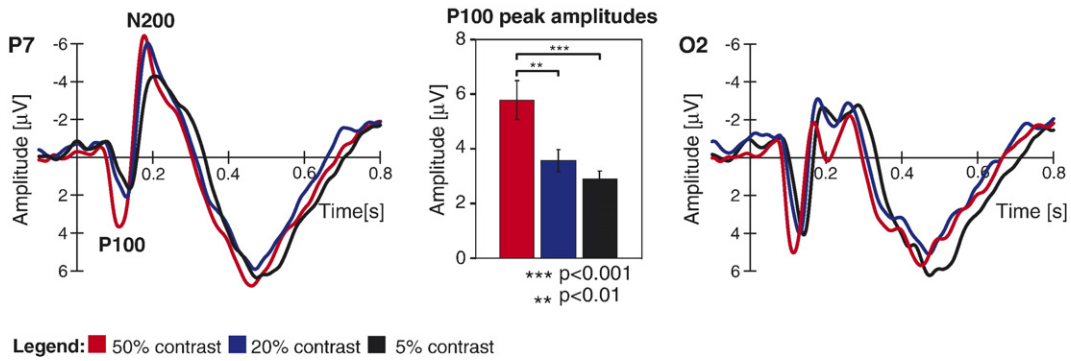


Fig. 2. Grand average VEPs for all frequent contrast stimuli (50%, 20%, and 5%). Left: VEP waveforms at electrode P7. Middle: Peak amplitudes of the P100 and standard error for all electrodes within posterior ROI. Right: VEP waveforms at electrode O2.

CONTRAST (3 contrast levels). Post hoc *t*-tests of specific comparisons of significant ANOVA effects were calculated (50% vs. 20%, 50% vs. 5%, and 20% vs. 5%).

3. Results

3.1. Behavioral data

Participants performed the task with high accuracy (1.3% errors). The ANOVA of the RTs yielded a significant main effect of CONTRAST ( $F[2, 36] = 13.186, p = 0.001$ ). Responses were fastest for stimuli with the highest contrast (50%, mean RT =

488 ms), whereas subjects responded slowest to low contrast stimuli (5%, mean RT = 520 ms). Post hoc tests showed a significant difference between the conditions 50% vs. 5% ( $t[18] = 3.802, p = 0.003$ ) and 20% vs. 5% ( $t[18] = 4.162, p = 0.003$ ).

3.2. Visual evoked potentials

The VEPs of all conditions were characterized by a first positive peak at a latency between 90 and 150 ms (P100) followed by a negative peak between 160 and 230 ms latency (N200, Fig. 2). P100 amplitudes yielded a main effect of CONTRAST ( $F[2,36] = 16.078, p < 0.001$ ), indicating

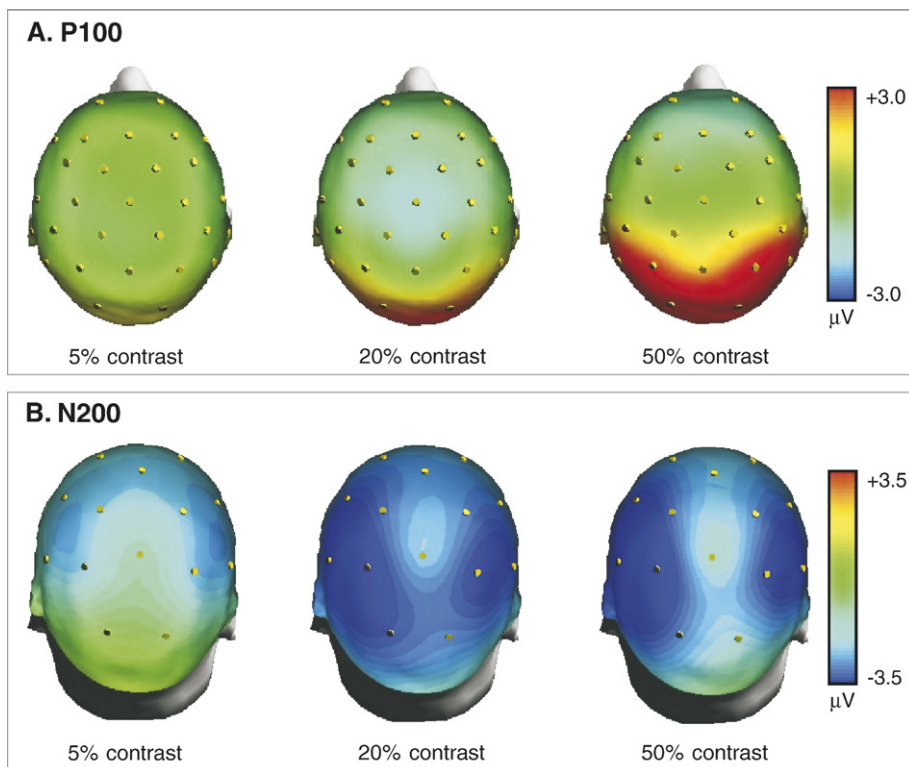
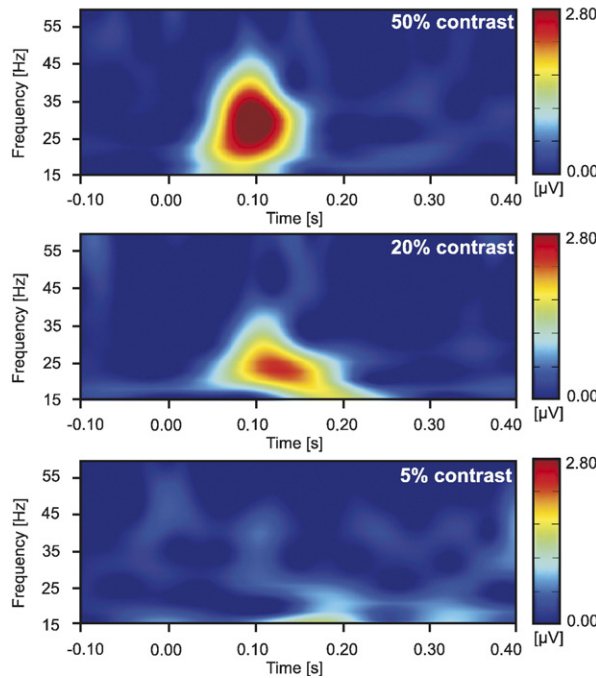


Fig. 3. A. The first row depicts the scalp topographies of the P100 at its peak latency (112 ms) in the top view. B. In the second row scalp topographies of the N200 at the peak latency (170 ms) are displayed in the back view. Both rows represent the grand average of all subjects ( $n = 19$ ) for each contrast (5%, 20%, and 50%).

**Evoked gamma-band responses**

**A. Time-frequency plots of a single subject**



**B. GBR peak amplitudes**

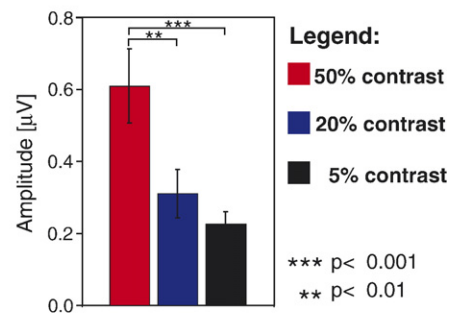


Fig. 4. Evoked GBRs for all contrast stimuli (50%, 20%, and 5%). A. Sample time–frequency plots at electrode O2 for one subject. B. Peak amplitudes of the GBR and standard error for all electrodes within the posterior ROI.

increasing amplitudes with increasing stimulus contrast in posterior electrodes (see the scalp topographies for the P100 in Fig. 3A). Post hoc tests yielded significant effects for the 50% vs. 20% ( $t[18] = -4.907, p < 0.001$ ) and for the 50% vs. 5% ( $t[18] = -4.181, p = 0.003$ ) condition. An ANOVA on the P100 latencies revealed a main effect of CONTRAST ( $F [2,36] = 16.491, p < 0.001$ ). This result indicates that P100 latencies increase in posterior electrodes with decreasing stimulus contrast. Post hoc tests showed significant differences between all conditions: 50% vs. 20% ( $t[18] = 2.854, p < 0.05$ ), 50% vs. 5% ( $t[18] = 6.077, p < 0.001$ ), and 20% vs. 5% ( $t[18] = 2.787, p < 0.05$ ). No significant modulation by stimulus contrast was obtained for N200 amplitudes or latencies. The scalp topographies of the N200

show a characteristic pattern after visual stimulation with pronounced activation peaks in more lateral posterior electrodes (see Fig. 3B).

**3.3. Early and late gamma-band responses**

The wavelet analysis revealed that evoked gamma activity increased when stimulus contrast was increased. Fig. 4A depicts sample baseline-corrected time–frequency plots for each contrast condition at electrode O2 for one subject. The GBR showed a clear peak in a time window from 60 to 140 ms after stimulus onset for the 50% contrast stimulus. The ANOVA of the peak amplitudes of the evoked GBR yielded a main effect of

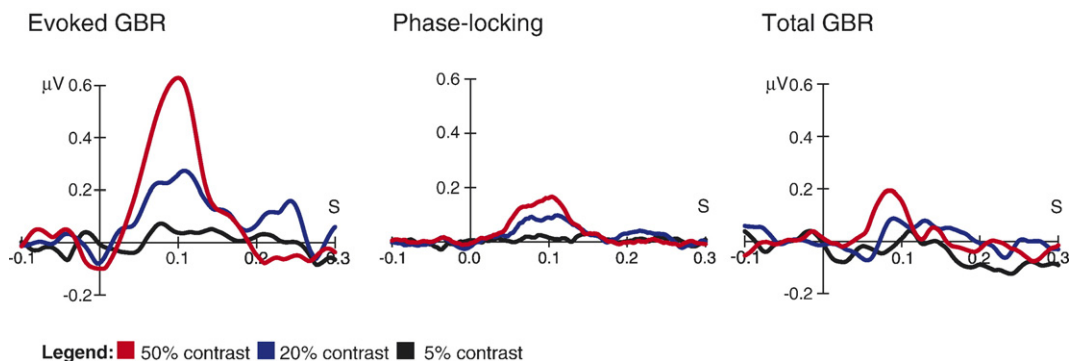


Fig. 5. Time courses for the evoked GBR, phase-locking, and total GBR (containing the phase-locked and non-phase-locked parts of the GBR) at electrode O2 displayed for all contrast stimuli (50%, 20%, and 5%).

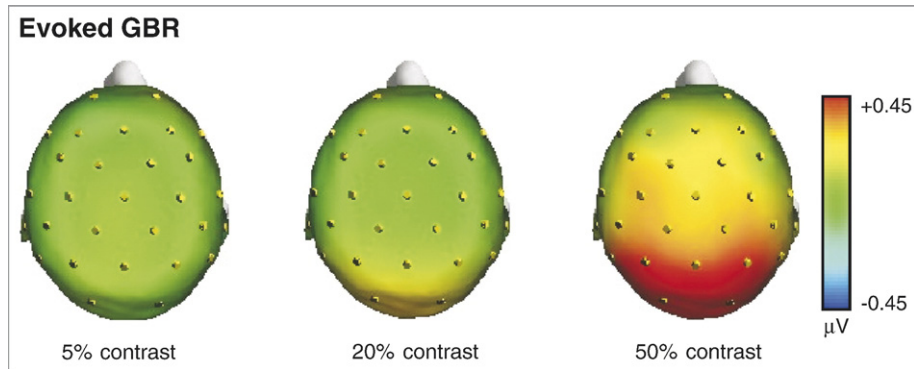


Fig. 6. Grand averaged scalp topographies of the evoked gamma-band activity at the peak latency (98 ms) are displayed for each contrast (5%, 20%, and 50%).

CONTRAST ( $F [2, 36]=12.658, p<0.001$ ; Fig. 4B) with larger amplitudes for stimuli with the highest contrast. Additionally, post hoc tests revealed significant differences between the following conditions: 50% vs. 20% ( $t[18]=4.834, p<0.001$ ) and 50% vs. 5% ( $t[18]=3.777, p=0.003$ ).

Fig. 5 displays the variation in time of the evoked GBR, phase-locking, and total GBR averaged across all subjects at electrode O2. For this figure, peak frequencies of the individually identified evoked GBRs ranged from 25 Hz to 71 Hz (mean 45 Hz,  $SD=14.19$  Hz). A frequency of 40 Hz was chosen for two participants, who showed no clear GBR peak (as done before, e.g. Herrmann et al., 2004a). Similar to the evoked GBR, we found a significant main effect of CONTRAST for the phase-locking ( $F [2, 36]=16.789, p<0.001$ ), whereas the analysis of the total GBR, an index of signal power, revealed no CONTRAST effect ( $F [2, 36]=2.501, p=0.101$ ). Thus, the increase in evoked GBR is most likely based on stronger phase-locking. Although evoked responses for high contrast stimuli occurred slightly earlier (96 ms) than for the middle (104 ms) and low contrast stimuli (98 ms), GBR peak latencies did not differ significantly ( $F [2, 36]=1.187, p=0.314$ ). Fig. 6 represents the topographies of the evoked GBR for each condition. The evoked GBR in response to the highest contrast stimulus shows a characteristic scalp distribution with a maximum at occipital and posterior electrodes, as reported in previous visual experiments (Busch et al., 2006).

For the late gamma-band activity in the time range between 200 and 600 ms after stimulus onset, the time–frequency planes did not reveal any activity that exceeded the noise level. Therefore, no further statistical analyses were calculated.

#### 4. Discussion

The goal of the present study was to investigate whether the visual evoked GBR is modulated by contrast as has been well demonstrated for VEPs. For this purpose, stationary sine wave gratings with three different contrast levels were presented.

##### 4.1. Behavioral data

The behavioral data show that reaction times are significantly affected by contrast variation. Subjects' responses were

shortened as the contrast level increased, which is in accordance with a number of previous experiments (Felipe et al., 1993; Vassilev et al., 2002; Chakor et al., 2005).

##### 4.2. Early gamma-band responses

In the present study, gamma frequency oscillations revealed the strongest responses at occipital electrodes. Our results are consistent with findings showing evoked gamma-band activity in response to visual stimulation in a latency range of about 100 ms (Böttger et al., 2002; Senkowski and Herrmann, 2002; Busch et al., 2006). The data demonstrate that stimulus contrast strongly modulates the visual evoked gamma-band oscillations. High contrast stimulation (50%) enhanced the gamma amplitude, whereas the GBR, elicited by low contrast stimuli (5%), did not differ from noise level. In addition to the evoked GBR, we also analyzed the phase-locking and total response in the same time interval to determine whether the contrast effect on evoked activity is caused by a stronger phase-locking to stimulus onset or by an increase in gamma-band power. In the present study, we observed a stronger phase-locking for high contrast stimuli with no significant effect on the total gamma-band response. This result is in accordance with previous studies (Busch et al., 2004, 2006) which found that changes in bottom-up factors (e.g. stimulus properties such as size or contrast) mainly affected the phase-locking of early evoked GBR, while top-down effects (e.g. attention) on GBR were derived from an increase in gamma-band power.

Our results are in agreement with recent studies in macaque monkeys that investigated the contrast effect in the gamma-band using local field potentials and multiunit activity (Logothetis et al., 2001; Henrie and Shapley, 2005). Whereas a human magnetoencephalographic study reported a linear contrast dependency for the late induced gamma-band amplitude (Hall et al., 2005), the present study only observed effects for the early evoked gamma-band response. This discrepancy might be related to the differences in recording as well as analysis methods, but it is also possible that the discrepancy is attributable to differences in the experimental setup (task, number of stimulus presentations). Whereas in the current experiment 100 stimuli per contrast condition were presented for 1000 ms with randomized ISIs to obtain a good signal-to-noise ratio, Hall et al.

(2005) presented 25 stimuli per condition in an on–off mode at a frequency of 0.5 Hz where subjects were not required to respond to the stimuli. The employed task in our study required active involvement by the participants, ensuring active processing of the grating stimuli. Since gamma-band oscillations depend on active stimulus processing (Senkowski and Herrmann, 2002; Marshall et al., 1996), this might be one explanation for the differing findings of the two studies. The early gamma-band response phase-locked to the stimulus is regarded as being most sensitive to processing demands (Yordanova et al., 1997). Moreover, we chose randomized ISIs to avoid task expectancy as a confounding parameter because it has been demonstrated that the state of anticipation enhances the gamma-band power (Lee, 2003; Fitzgibbon et al., 2004).

In addition to the contrast dependency, human studies have reported that oscillatory activity in the gamma range is modulated by changes along a variety of stimulus dimensions in the visual system. The size, eccentricity, luminance, and spatial frequency of a stimulus verifiably affect the magnitude of gamma activity (Busch et al., 2004; Rols et al., 2001; Tzelepi et al., 2000). To date it is still unclear, however, why some research groups failed to find gamma-band activity or gamma-band modulations (Menon et al., 1996; Juergens et al., 1999) and some did not. These conflicting results in the literature may be due to experimental designs in which variables like the aforementioned stimulus features are confounded with the independent variable. Stimulus contrast as one visual parameter is required to integrate stimulus features to form a global percept and segregate such a percept from its background or other elements. A large contrast appears as a very salient cue for segregation and indicates object borders. Hence, future visual studies that analyze early evoked GBRs should choose an appropriate stimulus contrast and control it across different conditions.

#### 4.3. Visual evoked potentials

The strongest effects of stimulus contrast for the P100, elicited by grating stimuli, were found at posterior electrodes. As described in the Results section, the first positive deflection showed the expected contrast dependency in amplitudes and latencies. While the P100 amplitudes exhibited an increase, the latencies decreased as a function of contrast. These findings are in accordance with both animal (Tolhurst et al., 1981; Harnois et al., 1984) and human studies (Campbell and Kulikowski, 1972; Spekreijse et al., 1973; Wright and Johnston, 1982; Bobak et al., 1987; Vassilev et al., 1994). However, most of these experiments applied a pattern reversal, an onset–offset presentation, or a moving stimulation. Despite different stimulation settings, contrast variations yield a similar modulation of the visual evoked potentials, namely a monotonic increase of VEP amplitude with an increase in grating contrast. In particular, at low contrast levels Tolhurst et al. (1981) and Wright and Johnston (1982) postulated a linear amplitude increase with contrast, whereas a logarithmic function seems to provide a better explanation for the increased VEP amplitudes at higher contrasts. Regarding the negative component in the later time window between 160 and 230 ms, no significant contrast effect

on amplitude and latency was observed. This result is in line with recent studies that reported a stronger contrast dependency on the P100, while the N200 is rather involved in, and modulated by, motion and form perception (Müller and Göpfert, 1988; Bach and Ullrich, 1997; Göpfert et al., 1998).

The different scalp distributions of the P100 and the N200 after visual stimulation indicated different underlying generators in the cortex (Herrmann and Knight, 2001). The P100 with an occipital topography is probably generated within the ventral part of the occipitotemporal cortex (Heinze et al., 1994; Yamazaki et al., 2000; Martinez et al., 2001; Di Russo et al., 2002). The subsequent negativity (N200) revealed a more distributed topography compared to the P100. Previous studies assumed that this negativity arises from activity in multiple brain areas within the extrastriate occipital and parietal cortex (Gomez Gonzalez et al., 1994; Di Russo et al., 2005).

#### 5. Conclusion

The present study shows that visual contrast modulates the early evoked gamma-band activity and that the increase in evoked activity is mainly caused by stronger phase-locking. High contrast stimuli appear to be most suitable to elicit a strong response in the human scalp recorded EEG. Therefore, cognitive studies employing visual stimulus material should carefully match low level attributes of their stimulus material to avoid confounding GBR modulations.

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