

EEG oscillations in the gamma and alpha range respond differently to spatial frequency

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Abstract

Physical properties of visual stimuli affect electrophysiological markers of perception. One important stimulus property is spatial frequency (SF). Therefore, we studied the influence of SF on human alpha (8–13 Hz) and gamma (>30 Hz) electroencephalographic (EEG) responses in a choice reaction task. Since real world images contain multiple SFs, an SF mixture was also examined. Event related potentials were modulated by SF around 80 and 300 ms. Evoked gamma responses were strongest for the low SF and the mixture stimulus; alpha responses were strongest for high SFs. The results link evoked and induced alpha and evoked gamma responses in human EEG to different modes of stimulus processing.

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1. Introduction

Real world images usually consist of a broad spectrum of spatial frequencies. Coarse features are manifest in low spatial frequencies (<5 cycles per degree visual arc, cpd), whereas high spatial frequencies (>5 cpd) contain the details.

Psychophysical results suggest that different spatial frequencies are processed differently (Leonova, Pokorny, & Smith, 2003). On their way from the retina to the cortex, high spatial frequencies are mainly processed by the parvocellular pathway, whereas low spatial frequencies are processed by the magnocellular pathway. In cortical processing, however, such a clear segregation is no longer possible. While processing in the ventral visual pathway seems to depend on both, magnocellular as well as parvo-

cellular input, processing in the dorsal pathway seems to be dominated by magnocellular input (see Merigan & Maunsell, 1993, for review).

Recently, oscillatory phenomena in the gamma frequency range of the EEG (frequencies >40 Hz) have gained considerable interest (Basar-Eroglu, Struber, Schurmann, Stadler, & Basar, 1996; Keil, Gruber, & Müller, 2001; Tallon-Baudry & Bertrand, 1999). These studies revealed two different classes of gamma band responses (GBRs): an early, phase-locked response, usually termed evoked GBR; and a late, nonphase-locked response, usually termed induced GBR (Basar-Eroglu et al., 1996). Due to their strong phase-locking to the stimulus, evoked GBRs can be extracted from the event related potential (ERP, Herrmann, Grigutsch, & Busch, 2005). In contrast, the induced GBR is cancelled out in the ERP. Induced GBRs can, therefore, only be inferred by additionally considering averaged power spectral estimates of gamma band oscillations from single trials (Tallon-Baudry & Bertrand, 1999). Evoked gamma band oscillations have mainly been related to low-level processing of physical stimulus properties

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(Busch, Debener, Kranczioch, Engel, & Herrmann, 2004; Karakaş & Başar, 1998). In addition, recent reports also describe modulations of evoked gamma band oscillations by memory matching (Herrmann, Lenz, Junge, Busch, & Maess, 2004; Morup, Hansen, Herrmann, Parnas, & Arnfred, 2006) and attention (Busch, Schadow, Fründ, & Herrmann, 2006; Tiitinen et al., 1993). Induced gamma band oscillations, on the other hand have been associated with a very wide range of cognitive processes including learning (Axmacher, Mormann, Fernandez, Elger, & Fell, 2006; Gruber, Keil, & Müller, 2001; Gruber & Müller, 2006; Keil, Müller, Gruber, Wienbruch, & Elbert, 2001), perceptual binding (Singer et al., 1997), representation of objects (Lachaux et al., 2005; Tallon-Baudry & Bertrand, 1999; Tallon-Baudry, Bertrand, Hénaff, Isnard, & Fischer, 2005), memory encoding and retrieval (Gruber, Tsivilis, Montaldi, & Müller, 2004; Sederberg, Kahana, Howard, Donner, & Madsen, 2003) and working memory (Howard et al., 2003; Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998). It has been suggested that synchronous oscillations, especially in the gamma range, could group action potentials from different neurons. Such grouping could be used to solve the binding problem (Singer & Gray, 1995), facilitate attentional processing (Fries, Neuenschwander, Engel, Goebel, & Singer, 2001; Fries, Reynolds, Rorie, & Desimone, 2001), or enable hippocampal learning (Axmacher et al., 2006).

Two studies demonstrated a modulation of EEG oscillations in response to patterns of varying spatial frequency and came to contradictory results. Bodis-Wollner, Davis, Tzelepi, and Bezerianos (2001) reported peak responses at high spatial frequencies, while Adjamian et al. (2004) reported peak responses at low and intermediate spatial frequencies. These two studies reported results on induced GBRs. It seems plausible to assume that such an effect of spatial frequency might exist for evoked gamma responses too, since the amplitude of evoked GBRs is modulated by physical stimulus parameters, such as size and eccentricity (Busch et al., 2004). However, to date no study exists that investigates the impact of spatial frequency on evoked GBRs.

Furthermore, the above mentioned experiments used either continuous stimulations (Adjamian et al., 2004) or equidistant interstimulus intervals (ISIs) (Bodis-Wollner et al., 2001), and participants were not required to respond to the stimuli. Since human EEG gamma responses are very sensitive to task difficulty (Senkowski & Herrmann, 2002) and most cognitive experiments require the participants to solve a behavioral task, we asked subjects to perform a choice reaction task. In addition, it has been shown that the expectancy of a predictable stimulus in experiments with fixed ISIs not only leads to contingent negative variation (CNV), but also modulates gamma responses (von Stein, Chiang, & König, 2000). In order to test which of the previous observations can be held under conditions that are typical in behavioral experiments and in order to see how evoked gamma oscillations react, we set out to test

the influence of spatial frequency on human gamma responses in a choice reaction task where stimuli appear unpredictably with randomized ISIs and transient stimulation.

In addition, evoked responses in the alpha band (8–13 Hz) have also been shown to be sensitive to sensory processing (Başar, Schürmann, Başar-Eroglu, & Karakaş, 1997; Schürmann, Başar-Eroglu, & Başar, 1997), although a modulation of alpha by spatial frequency has not been directly investigated yet. An indirect link to spatial frequency tuning in the alpha band is provided by results that indicate a close link between alpha responses and the P1–N1 complex of event related potentials (Klimesch et al., 2004). As the P1–N1 complex is known to be most pronounced at high spatial frequencies (Regan, 1989, p. 407, although this effect is much more pronounced for N1, Ellemberg, Hammarrenger, Lepore, Roy, & Guillemot, 2001), it might be expected that alpha responses increase as a function of spatial frequency.

Nevertheless, alpha responses have also been regarded as reflecting a wide range of cognitive processes (Başar, Başar-Eroglu, Karakaş, & Schürmann, 2001; Klimesch et al., 2004; Klimesch, Vogt, & Doppelmayr, 2000), especially memory. It has even been shown that total alpha responses are modulated in relation to purely internal events even with constant stimulation (Strüber & Herrmann, 2002) or prior to expected stimulation (Başar et al., 1997). Thus, it might be expected that alpha responses do not exclusively depend on spatial frequency.

Sewards and Sewards (1999) argued that alpha oscillations reflect activity of the parvocellular pathway, while gamma responses reflect activity from the magnocellular pathway. Parvocellular activity is regarded to be more strongly modulated by the fine spatial scales of the stimulus, whereas magnocellular activity more strongly responds to coarse spatial scales (Leonova et al., 2003; O'Keefe, Levitt, Kiper, Shapley, & Movshon, 1998). There is considerable evidence that the hypothesis by Sewards and Sewards (1999) does not hold under all circumstances (e.g. gamma responses to static stimuli Gruber & Müller, 2005; Kaiser & Lutzenberger, 2005; Tallon-Baudry et al., 1998). Furthermore, magnocellular and parvocellular streams are mixed at the cortical level (Merigan & Maunsell, 1993). However, we decided to analyze both alpha and gamma responses as a function of spatial frequency.

It has been suggested that evoked phase-locked gamma responses can be linked to the matching of objects with perceptual memory (Herrmann et al., 2004; Herrmann, Munk, & Engel, 2004; Morup et al., 2006, see Fuster, 2002 for the term perceptual memory). Such matching processes initially seem to rely on low spatial frequencies, while high spatial frequencies are considered later (Bar, 2003; Bar et al., 2006). Since phase-locked gamma responses are evoked as early as 90 ms after stimulus presentation, we expected the evoked GBR to be stronger for stimuli with a strong low spatial frequency content.

Thus, we can summarize three hypotheses:

- we expected (at least evoked) GBRs to be strongest for low spatial frequencies and;
- alpha responses (at least over sensory areas) to peak at high spatial frequencies;
- more specifically we expected (at least the evoked) GBRs to a stimulus with mixed spatial frequencies to be mostly determined by the low spatial frequency component of the stimulus.

2. Materials and methods

2.1. Participants

Seventeen healthy volunteers between 20 and 39 years old (mean age 25.5 ± 5.34 years, 6m, 11f) participated in the study. All participants had normal or corrected to normal vision and reported no current or past neurological or psychiatric disorders. The participants gave informed consent to participate before the experimental session started.

Behavioral data from all participants were analyzed. From the analysis of ERP data, however, two participants were excluded due to strong artifacts. As one participant did not display any gamma response at all, this participant was excluded from the analysis of both alpha and gamma band responses. This resulted in data from the same participants being compared for both EEG frequency bands.

2.2. Stimuli and experimental procedure

Participants watched sine wave gratings of varying spatial frequency on a TFT monitor (width = 34.5 cm, height = 25.9 cm) placed 122 cm in front of the participants. The monitor refresh rate was 75 Hz. The participants' task was to press a button with their right hand in response to horizontal gratings and another button with the left hand in response to vertical gratings. Three different monofrequency achromatic gratings with spatial frequencies of 1, 5.5 and 10 cpd were presented. The 1 cpd stimulus was considered a low spatial frequency, the 5.5 cpd stimulus a high spatial frequency (Tootell, Silverman, Hamilton, Switkes, & De Valois, 1988). In addition, the 10 cpd stimulus was used as a very high spatial frequency. As a fourth stimulus, the algebraic sum of the 1 and the 5.5 cpd stimuli normalized to the same Michelson contrast as the other gratings was presented to evaluate the effects of mixing. The fourth stimulus was derived from the 1 and the 5.5 cpd stimuli instead of the 1 and the 10 cpd stimuli, because we considered the 5.5 cpd stimulus a typical high spatial frequency stimulus, whereas we could not exclude saturation effects beforehand for the 10 cpd stimulus. For all stimuli, the Michelson contrast was 99%. The stimuli were presented as circular displays with a diameter of 12 degrees visual angle and faded to the borders to a medium grey. It has been shown that such large stimuli are well suited to evoke gamma responses (Busch et al., 2004). The participants were instructed to fixate a small light grey dot in the center of the screen during the entire experiment. Stimuli were presented for 1000 ms with ISIs varying randomly between 1500 and 2000 ms. Two example stimuli are presented in Fig. 1. Each stimulus was presented 100 times in horizontal and 100 times in vertical orientation, resulting in a total number of 800 stimuli. The experiment was split into nine blocks. The first block was a practice block and consisted of twenty stimuli. During this phase participants received feedback whether their response was correct or incorrect. Data from the first block was not included in the analysis. Each of the following eight blocks consisted of 100 stimuli that were presented in a pseudorandomized order.

2.3. Measurements

While participants observed the grating patterns, they sat 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 battery operated to avoid line frequency interference (50 Hz in Germany). EEG activity was measured from 31 scalp locations according to the 10–10 system. The nose served as reference. Electrooculographic (EOG) activity was measured from an electrode placed below the orbital rim in order to detect artifacts due to eye movements. Activity was recorded using sintered Ag/AgCl electrodes mounted in an elastic cap (Easycap, Falk Minow Services, Munich) and amplified using a BrainAmp amplifier (Brain Products, Munich). Electrode impedances were kept below 5 k Ω . The EEG was analog filtered between 0.02–200 Hz, digitized at a rate of 500 Hz, and stored on a computer hard-disc for off-line analysis. Digitized EEG data was transferred to a computer outside the recording cabin with a fiber optic cable. The data were digitally high pass filtered offline with a cutoff frequency of 0.5 Hz in order to avoid slow shifts in the baseline. When participants moved their eyes away from the fixation, it was detected by measurements of EOG activity and the trial was discarded. For this purpose, an automatic artifact rejection was computed which excluded trials from further analysis if the standard deviation within a moving 200 ms time window exceeded 40 μ V in one channel. The automatic artifact rejection was supplemented by visual inspection to ensure that only trials without artifacts were included in the subsequent analysis.

2.4. Data analysis

Mean reaction times for each participant were evaluated as trimmed averages containing only a range of three standard deviations from the center of the reaction times distribution. Additionally, the percentage of correct responses was computed. Trials with reaction time outliers or incorrect responses were excluded from the subsequent analysis of behavioral as well as EEG data.

ERPs were computed as the average across all trials of a certain spatial frequency in a time window ranging from 200 ms before stimulation to 800 ms after stimulation onset. The ERPs were corrected for baseline activity that occurred in the 200 ms before stimulation. Grand averages were computed across participants yielding one grand average for each stimulus type.

A wavelet transform was performed on all trials using a complex sinusoidal wavelet (i.e. a modulated Gaussian) with 12 cycles (see Herrmann et al., 2005, for a detailed description of the method), thus obtaining a time–frequency decomposition of the EEG from 200 ms before stimulation to 800 ms after stimulation. Although gamma responses have been observed up to 200 Hz in intracranial recordings (Lachaux et al., 2005), the major part of the gamma response is found below 100 Hz.¹

Response frequencies of alpha (Klimesch, 1999) as well as gamma oscillations (Busch et al., 2004) vary notably between participants (see also Fig. 4). Therefore, instead of simply averaging the time–frequency planes it is more appropriate to average the activity of the participants' individual response frequencies. To achieve responses with the participants' individual frequencies, the different time courses of alpha and gamma responses were computed as convolutions of the raw EEG data and a complex wavelet (i.e. a modulated Gaussian) whose center frequency was adjusted to the individual response frequency in the time–frequency plane. As a decrease in alpha power after visual stimulation is a very prominent phenomenon (Klimesch, 1999), the individual alpha frequency was defined as the frequency between 8 and 13 Hz showing the strongest power decrease between 280 and 800 ms after stimulation onset. The individual response frequency for the evoked gamma response was defined as the local maximum in the time–frequency plane between 30 and 85 Hz and between 60 and 120 ms. For the computation of the time courses alpha responses were analyzed using a wavelet with 6 cycles, gamma responses using a wavelet with 12 cycles. This resulted in a phase space localization of $\sigma_t \approx 300$ ms in time and $\sigma_f \approx 3$ Hz in frequency for gamma responses. Additionally, we investigated induced gamma band responses. As induced gamma band responses are usually cancelled out in the ERP, they were quantified as

¹ For magnetoencephalography, significantly higher frequencies can be observed (e.g. Kaiser & Lutzenberger, 2005).

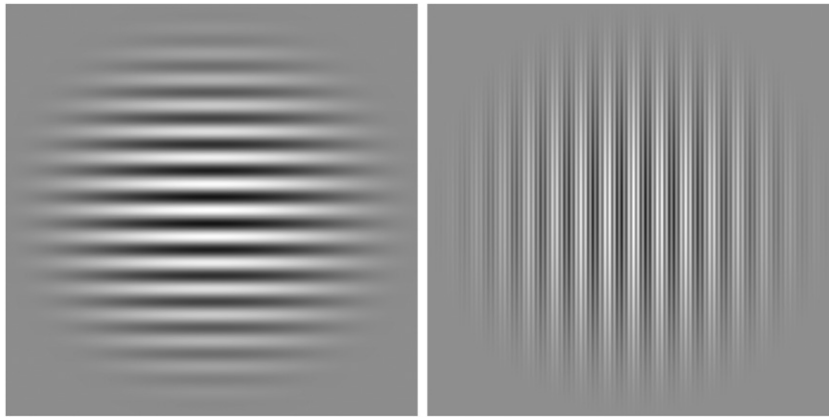


Fig. 1. One of the monofrequency grating patterns (horizontal, 1 cpd, left) and the mixed frequency stimulus (vertical, 1 + 5.5 cpd, right).

total gamma band responses (comprising both evoked and induced oscillations) with the frequency determined from a later time window (500–700 ms) because total gamma responses are often observed at longer latencies (e.g. Busch et al., 2004; Gruber, Müller, & Keil, 2002; Tallon-Baudry et al., 1998). Another approach to quantify induced responses is to subtract the ERP waveform from each trial. The average power derived from the remaining signal should give a measure of induced activity. However, there seems to be practically no difference between these two approaches (Busch, Herrmann, Müller, Lenz, & Gruber, 2006). For alpha responses the phase space localization was $\sigma_t \approx 600$ ms and $\sigma_f \approx 1.5$ Hz. The exact phase space localizations depend on the center frequency of the individual wavelet that has been used for each participant (Louis, Maaß, & Rieder, 1998).

Three measures were computed from the results of the convolution: (i) The time course of *evoked responses* defined as the absolute value of the (complex) result of the convolution of the averaged ERP. Thus, it contains predominantly phase-locked oscillatory activity. (ii) The time course of *total responses*, defined as the average of the absolute values of the convolutions of the single trials. This measure reflects both evoked (phase-locked) and induced (nonphase-locked) responses. (iii) The time course of *phase-locking* reflecting the average of the projections of the single trials on the complex unit circle. The phase-locking values range from 0 to 1. A value of 1 indicates perfect phase alignment across all trials, a value of 0 implies that the trials are not phase-locked in such a way that they cancel out in the evoked potential. The phase-locking values reflect the homogeneity of the instantaneous phase across single trials. If amplitude and phase are independent, the phase-locking value equals the ratio of evoked and total responses. However, as this cannot be guaranteed for the electroencephalogram (Nolte et al., 2004), phase-locking in general yields more information than is contained in evoked and total responses alone. These three measures have been described in more detail elsewhere (Herrmann et al., 2005). Evoked and total responses as well as phase-locking were computed for each spatial frequency and for mixed frequencies separately. The average baseline activity in the time range of 200–100 ms before stimulus onset was subtracted from the evoked and the total time course data. Early gamma band responses (60–120 ms) were characterized by all three measures—evoked, total and phase-locking, while late gamma band responses (500–700 ms) were only characterized by total response time courses.

In the statistical analysis only those channels were included that showed evoked responses. These were CP1, CP2, P3, P4, Pz, O1, and O2 for early gamma and O1, O2, P3, Pz, P4, CP5, CP1, CP2, and CP6 for the alpha band. Late total gamma band responses were analyzed for posterior channels CP1, CP2, P3, Pz, P4, P7, O1, O2, and P8 as was done by Gruber and Müller (2005). In Figs. 6 (gamma) and 8 (alpha) the analyzed channels are marked. Statistical analysis of ERPs was performed on O1 and O2 (early component, SFD80, mean amplitude 60–100 ms) and TP9, TP10, P3, P4, P7, P8, Pz, O1, and O2 for the later components (mean amplitude 130–230 ms as N1 and mean amplitude 280–350 ms as N2).

Effects of the different stimuli on behavioral and electrophysiological measures were analyzed by means of an ANOVA for repeated measurements (factor spatial frequency: 1, 5.5, 10 cpd and “mix”). For statistical analysis of oscillatory responses peak amplitudes in the time window between 60 and 120 ms (gamma responses), and 60 and 280 ms (alpha responses) were used. Total gamma responses were additionally studied as the mean amplitude between 500 and 700 ms. If the ANOVA yielded a significant effect, six *t*-tests (1 vs 5.5 cpd, 1 vs 10 cpd, 1 cpd vs mix, 5.5 vs 10 cpd, 5.5 cpd vs mix and 10 cpd vs mix) were performed to compare the responses to the different stimuli. If a particular participant did not demonstrate any oscillatory response at all in one condition, this response was not considered for the post hoc analysis. These post hoc tests were corrected for multiple comparisons according to Bonferroni’s method. Only corrected *p*-values (the sixfold of the original *p*-values) are reported. Statistical analysis was performed using the statistical software “R” (R Development Core Team, 2004).

3. Results

3.1. Behavioral data

Mean reaction times are displayed in the left panel of Fig. 2. Reaction times significantly increased with spatial frequency ($F_{3,16} = 39.782$, $p < .0001$). Virtually all pairwise comparisons yielded significant differences (see Fig. 2 for details of the post hoc analysis). Only the difference between the mix stimulus and the 1 cpd stimulus was not significant ($t_{16} = 2.272$).

Orientations were correctly identified in more than 90% of the stimuli by all participants. The detection rates are shown in the right panel of Fig. 2. There was a significant effect of spatial frequency ($F_{3,16} = 14.546$, $p < .0001$). Post hoc tests yielded fewer correct responses for the 10 cpd condition compared to all other conditions. Data from single participants did not indicate a speed accuracy trade-off.

3.2. Event related potentials

Evoked potentials are displayed in Fig. 3. These show different response characteristics to spatial frequency in two time windows. Around 80 ms a strong negative peak was found for high spatial frequencies (5.5 and 10 cpd). For the 1 cpd stimulus as well as for the mixed frequency

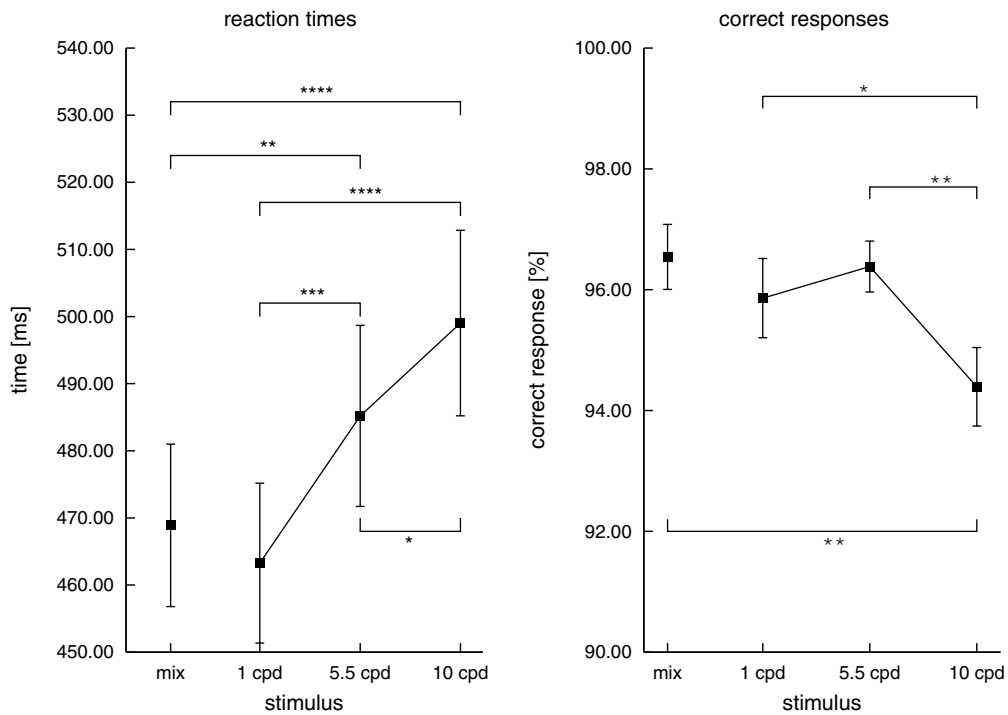


Fig. 2. Behavioral results. Reaction times are shown in the left panel; the percentage of correct responses in the right panel. Mean values are indicated by black squares, standard errors by vertical lines. The brackets above and below the plot indicate significant differences: * indicates $p < .05$, ** indicates $p < .01$, *** indicates $p < .001$, and **** indicates $p < .0001$.

stimulus a positive deflection was observed in the same time window. Both peaks were maximal at posterior locations with the negative peak at high spatial frequencies being more focal and distributed more centrally. Mean amplitudes between 60 and 100 ms showed a significant main effect of spatial frequency ($F_{3,14} = 57.933$, $p < .0001$). This effect was manifested in significant differences between the high spatial frequency stimuli and the low spatial frequency stimulus (1 vs 10 cpd, 1 vs 5.5 cpd,

see Table 1) and between the high spatial frequency stimuli and the mix stimulus (mix vs 10 cpd, mix vs 5.5 cpd, see Table 1).

In the second time window (N1) between 130 and 230 ms, no significant main effect was observed ($F_{3,14} = 2.959$, $p > .1$).

Between 280 and 350 ms, there was a negative deflection that monotonically increased with spatial frequency. The ANOVA yielded a highly significant main effect of spatial

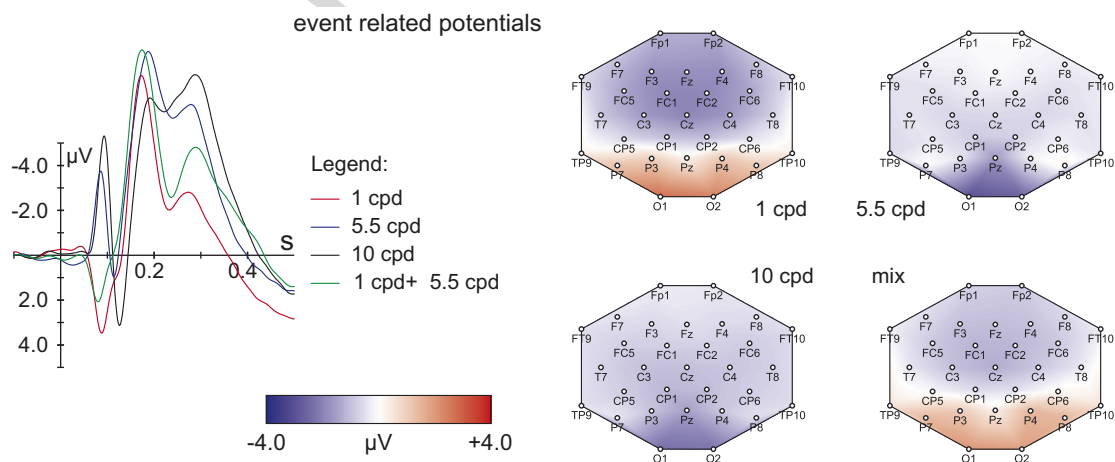


Fig. 3. Evoked potentials after stimulation with gratings of different spatial frequencies averaged across 15 participants. On the left side of the figure the responses at location O1 are displayed. On the right side, maps of average potential between 75 and 85 ms are plotted separately for each stimulus type. Note that the time scale of the ERP display on the left ranges from -100 to 500 ms. For display, the ERP has been low pass filtered with a cutoff frequency of 20 Hz.

Table 1
Results of post hoc comparisons for ERPs

Comparison	<i>df</i>	<i>t</i>	<i>p</i> <	Comparison	<i>df</i>	<i>t</i>	<i>p</i> <
<i>Event related potentials</i>				<i>N2 (280–350 ms)</i>			
SFD80 (60–100 ms)				1 vs 5.5 cpd	14	5.680	.001
1 vs 5.5 cpd	14	5.406	.001	1 vs 10 cpd	14	11.429	.0001
1 vs 10 cpd	14	5.389	.001	5.5 vs 10 cpd	14	4.056	.001
5.5 vs 10 cpd	14	0.810	n.s.	mix vs 1 cpd	14	5.292	.001
mix vs 1 cpd	14	1.511	n.s.	mix vs 5.5 cpd	14	1.715	n.s.
mix vs 5.5 cpd	14	6.990	.0001	mix vs 10 cpd	14	4.664	.01
mix vs 10 cpd	14	6.394	.001				

Reported *p*-levels correspond to Bonferroni corrected values.

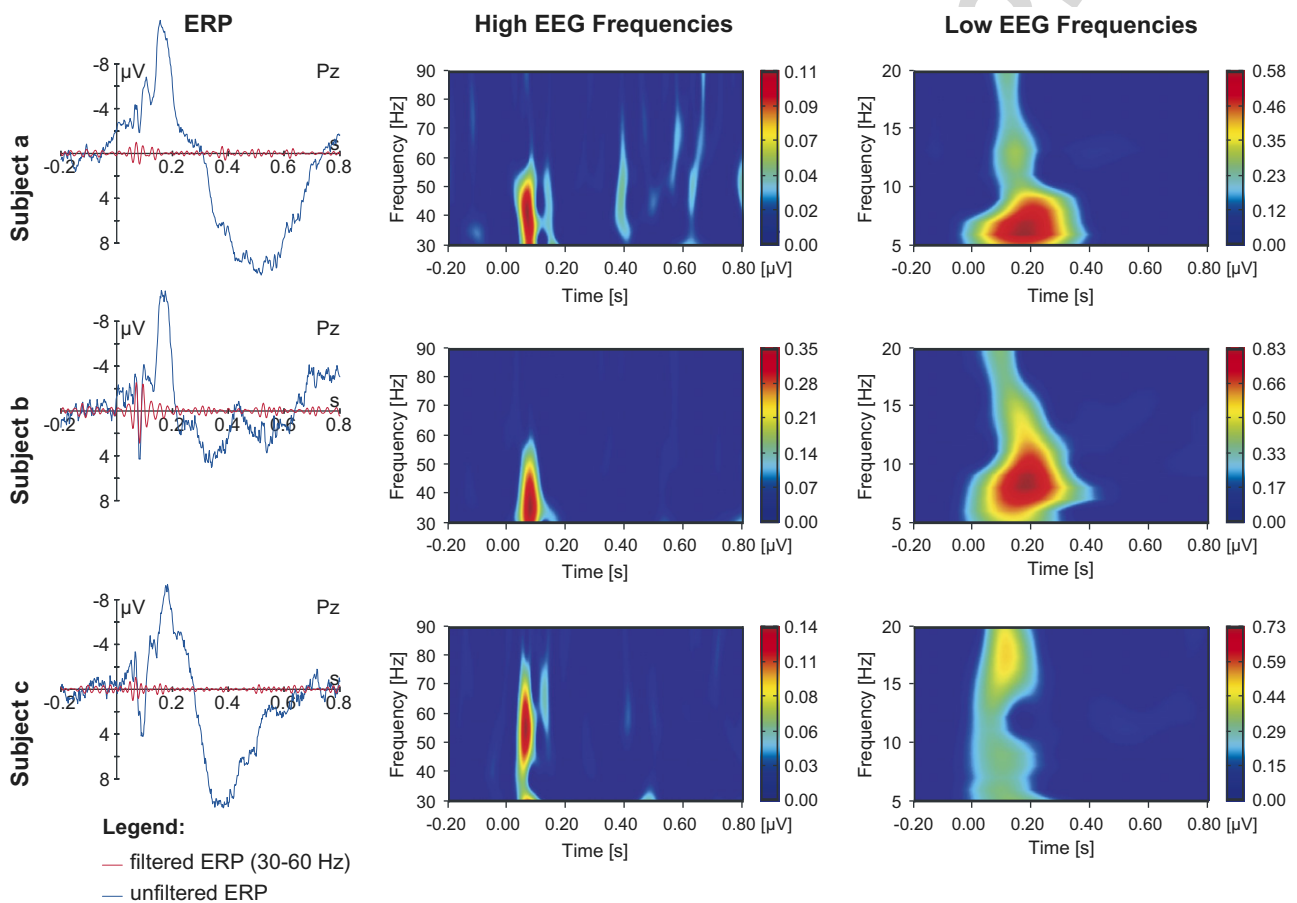


Fig. 4. ERPs and evoked gamma and alpha responses for three randomly chosen participants after stimulation with the 1 cpd stimulus. Left column: unfiltered ERPs (blue line) and bandpass filtered ERPs (30–60 Hz, red line) to emphasize the evoked gamma response. Note that the evoked gamma response is also visible in the unfiltered ERP. Middle column: high frequency (>30 Hz) content of the corresponding ERPs as a time–frequency representation. Note the different response frequencies of the three participants. Right column: low frequency content (5–20 Hz) of the ERPs. All data were taken from electrode Pz.

frequency ($F_{3,14} = 29.875$, $p < .0001$) for the mean amplitude in this time range. Post hoc comparisons revealed significant differences for all pairwise comparisons, except for the comparison of the 5.5 cpd stimulus and the mix stimulus.

3.3. Gamma band

In the ERP display (Fig. 4, left column), unfiltered and band-pass filtered (30–60 Hz) ERP waveforms are shown

in order to separate evoked GBRs and typical ERP results. Note, however, that the evoked GBR is visible in the unfiltered ERP. GBRs were most pronounced at posterior locations. Topographic maps of the evoked gamma responses are displayed in the upper row of Fig. 5. For low spatial frequency (1 cpd), there was a strong evoked GBR. This response clearly decreased with increasing spatial frequency. This was reflected in a highly significant effect of spatial frequency ($F_{3,13} = 12.271$, $p < .0001$). The difference between the 1 cpd and the 10 cpd stimuli was statistically

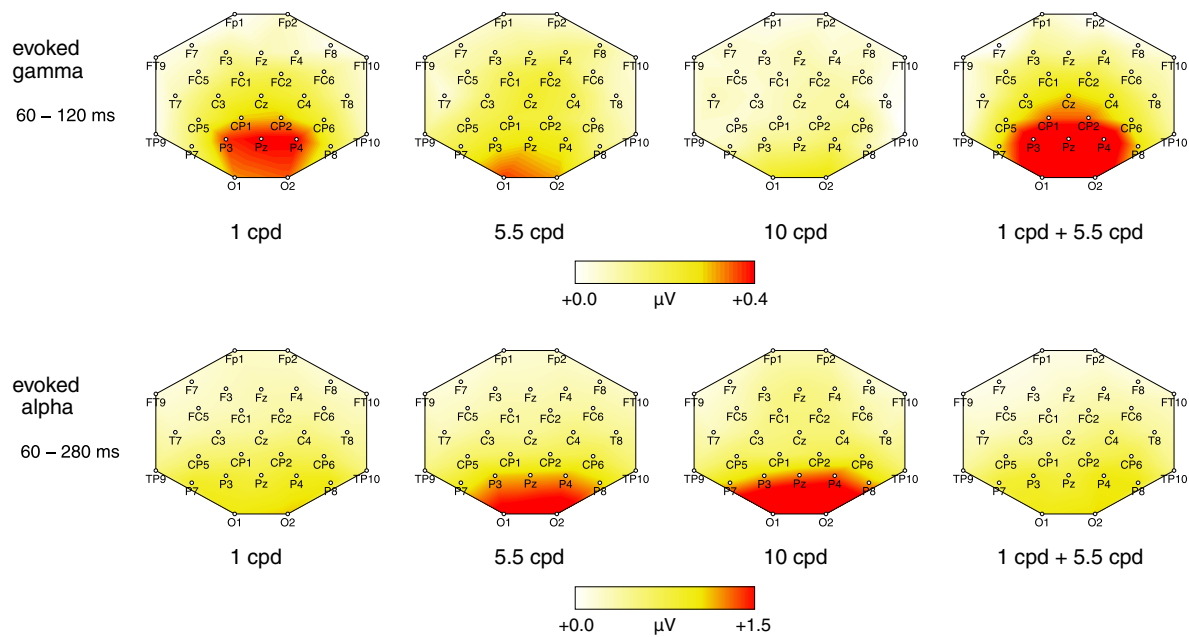


Fig. 5. Topographic maps of evoked gamma (upper row) and alpha (lower row) responses averaged across 14 participants. Each row consists of four maps displaying responses for the different stimuli (from left to right: 1, 5.5, 10 cpd and the mix of 1 and 5.5 cpd). Note the different time windows and color scales for gamma and alpha.

significant (see Table 2 for details about the results of the post hoc tests of oscillatory responses). This was not the case for differences between 1 and 5.5 cpd and between 5.5 and 10 cpd stimuli. The response to the mixed frequency grating (1 + 5.5 cpd) did not significantly differ from that observed for the 1 cpd stimulus. In contrast, differences between mixed stimulus and high spatial frequency stimuli were significant.

Fig. 6 shows time courses of evoked responses, phase-locking, and total responses for all four conditions at selected electrodes. Above these time courses, topographic maps related to prominent events in the time domain are shown to give an impression of the spatial distribution of the displayed time courses. The same pattern that can be observed for the evoked responses is found for the phase-locking factor. This resulted in a significant main effect of spatial frequency on the phase-locking factor ($F_{3,13} = 15.006$, $p < .001$).

The significance pattern revealed by post hoc testing of the phase-locking factor also yielded similar results for evoked gamma responses and phase-locking. The comparison of the mixed and the 5.5 cpd stimulus was the only comparison that was significant for evoked responses but not for the phase-locking factor. However, the obtained t -value of 2.874 is still relatively high ($p < .1$). The effects of stimulus type on evoked gamma band responses are summarized in Fig. 7 by the filled squares. There was no effect of spatial frequency on total gamma response ($F_{3,13} = 0.63$) in this early time window.²

² Effects on total gamma responses remain insignificant with other ROIs as well as when the same frequencies are analyzed for total and evoked responses.

Fig. 6 also shows a late total gamma response starting at 500 ms and lasting until approximately 700 ms. However, the mean amplitude between 500 and 700 ms, with frequencies adapted to this time window, did not vary significantly with spatial frequency ($F_{3,12} = 0.78$).

3.4. Alpha band

Topographical distributions of evoked alpha responses are shown in the bottom row of Fig. 5. Evoked alpha responses as well as evoked gamma responses were pronounced over posterior leads. However, evoked alpha responses increased with spatial frequency ($F_{1,14} = 10.295$, $p < .001$). This results in a significant difference between the 1 cpd and the 10 cpd stimulus ($t_{14} = 3.652$, $p < .05$).

Fig. 8 shows time courses and topographies of evoked and total alpha responses as well as phase-locking. The time courses reveal increases in both evoked and total alpha responses as well as phase-locking after stimulation. Total alpha responses show a decrease after an initial increase. This decrease has previously been described as event related desynchronization (e.g. Klimesch, 1999). The peaks of evoked and total alpha responses as well as phase-locking in the alpha band increase with increasing spatial frequency. However, the effect of spatial frequency is most prominent for the total response ($F_{3,14} = 12.567$, $p < .001$). For the high spatial frequency gratings, a clear enhancement of alpha amplitudes is visible. This is absent for the low spatial frequency grating as well as for the mixed frequency grating. This is also manifest in the post hoc tests that show significant differences between these two groups but not within. The difference between the 10 cpd and the mix stimulus was not significant

Table 2
Results of post hoc comparisons for oscillatory brain responses

Comparison	df	t	p<	Comparison	df	t	p<
<i>Evoked responses</i>				<i>Alpha band (60–280 ms)</i>			
Gamma band (60–120 ms)				Alpha band (60–280 ms)			
1 vs 5.5 cpd	12	1.155	n.s.	1 vs 5.5 cpd	14	1.751	n.s.
1 vs 10 cpd	13	3.221	.05	1 vs 10 cpd	14	3.652	.05
5.5 vs 10 cpd	12	1.877	n.s.	5.5 vs 10 cpd	14	1.960	n.s.
mix vs 1 cpd	13	1.490	n.s.	mix vs 1 cpd	14	0.307	n.s.
mix vs 5.5 cpd	12	3.463	.05	mix vs 5.5 cpd	14	2.548	n.s.
mix vs 10 cpd	13	3.234	.05	mix vs 10 cpd	14	2.95	n.s.
<i>Total responses</i>				<i>Alpha band (60–280 ms)</i>			
Gamma band				Alpha band (60–280 ms)			
No significant				1 vs 5.5 cpd			
Main effect				1 vs 10 cpd			
In either time window				5.5 vs 10 cpd			
(60–120 ms and 500–700 ms)				mix vs 1 cpd			
				mix vs 5.5 cpd			
				mix vs 10 cpd			
<i>Phase-locking factor</i>				<i>Alpha band (60–280 ms)</i>			
Gamma band (60–120 ms)				Alpha band (60–280 ms)			
1 vs 5.5 cpd	13	1.711	n.s.	1 vs 5.5 cpd	14	1.328	n.s.
1 vs 10 cpd	13	3.213	.05	1 vs 10 cpd	14	2.793	n.s.
5.5 vs 10 cpd	13	1.624	n.s.	5.5 vs 10 cpd	14	2.065	n.s.
mix vs 1 cpd	13	1.890	n.s.	mix vs 1 cpd	14	1.092	n.s.
mix vs 5.5 cpd	13	2.874	n.s.	mix vs 5.5 cpd	14	2.708	n.s.
mix vs 10 cpd	13	3.156	.05	mix vs 10 cpd	14	3.238	.05

Reported p-levels correspond to Bonferroni corrected values.

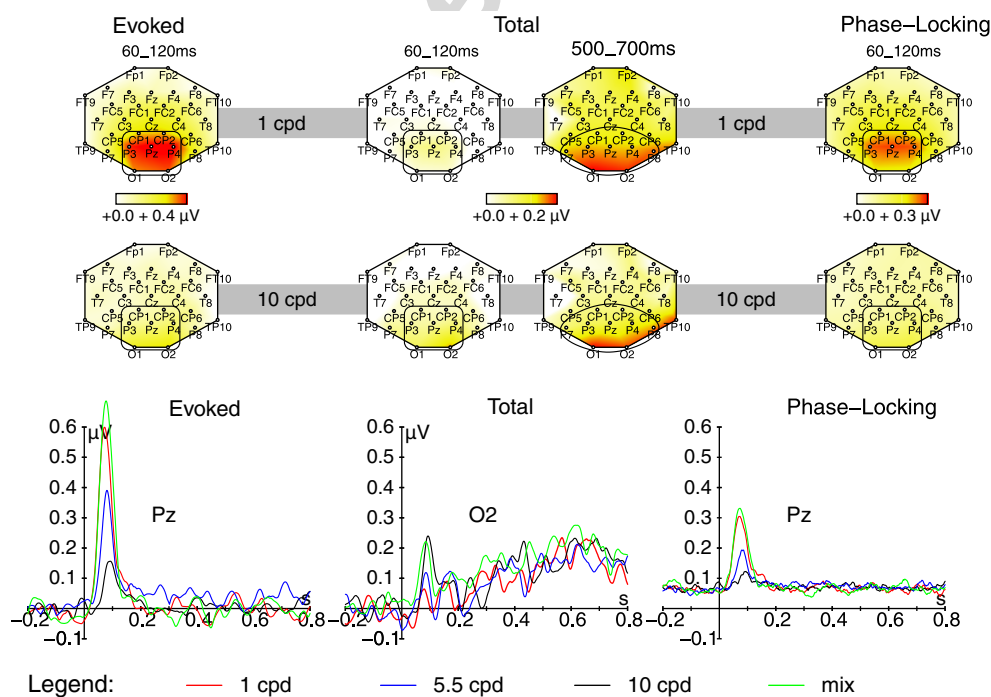


Fig. 6. Evoked and total gamma responses as well as phase-locking in the gamma range. The top row shows (from left to right) maps of early evoked responses (60–120 ms), early total responses (60–120 ms), late total responses (500–700 ms), and early phase-locking (60–120 ms) in the gamma frequency range after stimulation with the lowest spatial frequency grating (1 cpd). The second row shows the same for the 10 cpd grating stimulus. At the bottom, time courses for frequencies adapted to the early time window from single electrodes are displayed. These are (from left to right): evoked activity at Pz, total activity at O2, and phase-locking at Pz. Averages across 14 participants are shown in all displays. Note that averages of evoked and total responses were baseline corrected. Regions of interest are surrounded by black lines.

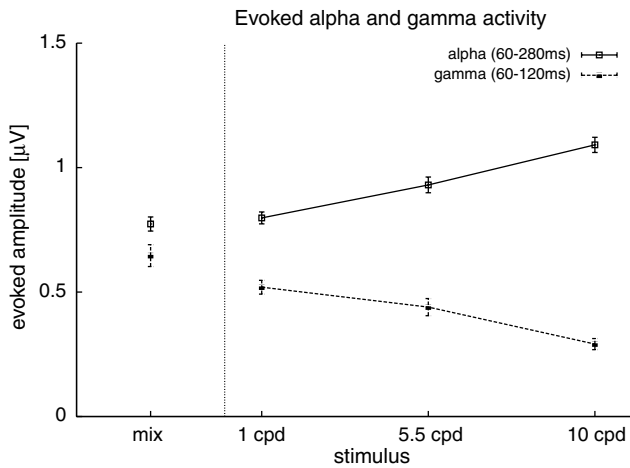


Fig. 7. Evoked alpha and gamma responses as functions of the different stimulations over the corresponding regions of interest. Mean evoked alpha responses are drawn as open squares, mean evoked gamma responses as filled squares. Vertical lines indicate standard errors.

($t_{14} = 2.871$). However, the t -value of this comparison suggests a trend towards significance ($p < .1$). The changes of phase-locking in the alpha band were significant ($F_{3,14} = 11.277, p < .001$). The pattern of post hoc tests is similar to that observed for the evoked alpha response. A significant difference was observed for the comparison of the 10 cpd and the mixed stimulus.

Fig. 7 shows evoked alpha and gamma responses as functions of the different stimuli. Whereas evoked alpha

responses increased with increasing spatial frequency, evoked gamma responses decreased.

4. Discussion

In the current study, we investigated event related potentials and EEG alpha and gamma band responses after stimulation with varying spatial frequencies.

In the ERP, we found a negative deflection after 80 ms for high spatial frequencies. In the same time window, a positive peak could be observed for low spatial frequencies. This phenomenon has been previously reported as spatial-frequency-dependent potential at about 80 ms (SFD80; e.g. Kenemans, Baas, Mangun, Lijffijt, & Verbaten, 2000). Thus, we concluded that our stimuli were suited to evoke different types of spatial frequency processing. Around 300 ms, there was another negative ERP component over posterior areas that showed tuning to spatial frequency. Such a late component has been related to response selection and was observed for responses to spatial frequency and orientation (Kenemans, Kok, & Smulders, 1993). In the study by Kenemans et al. this component only occurred if the participants had to respond to the stimulus and it was stronger for higher spatial frequencies. As participants in the current study had to respond to each stimulus and the component was always visible, our results are in line with the interpretation by Kenemans et al. (1993) that this late negative ERP component may be related to response selection.

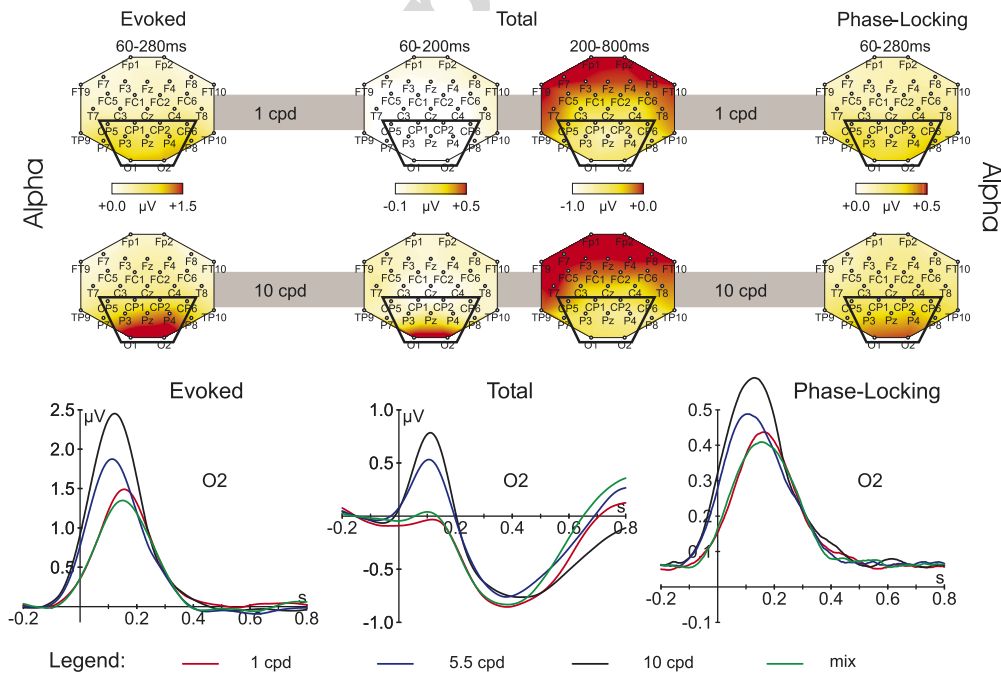


Fig. 8. Evoked and total responses as well as phase-locking in alpha range. The top row shows (from left to right) maps of early evoked responses (60–280 ms), early total responses (60–200 ms), late total responses (200–800 ms), and early phase-locking (60–280 ms) in the alpha frequency range after stimulation with the lowest spatial frequency grating (1 cpd). The second row shows the same for the 10 cpd grating stimulus. The bottom row displays time courses from electrode O2. Averages across 14 participants are shown in all displays. Note that averages of evoked and total responses were baseline corrected. Regions of interest are surrounded by black lines.

Effects of spatial frequency have also been described for the C1 component of the event related potential. This would be expected in a similar time window as the described early potential (Musselwhite & Jeffreys, 1985; Rebaï, Bernard, Lannou, & Jouen, 1998). Based on our current findings, we cannot definitely decide whether this early potential is a C1 or SFD80. Both ERP components respond very early and are assumed to originate from the striate, or the peristriate cortex (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Kenemans et al., 2000). The most salient difference between these two components is that C1 is usually evoked using parafoveal or lateralized stimulation (Andersson, Etard, Denise, & Petit, 2004; Khoe, Mitchell, Reynolds, & Hillyard, 2005; Musselwhite & Jeffreys, 1985) and monotonically increases over a wide range of spatial frequencies (Musselwhite & Jeffreys, 1985; Rebaï et al., 1998). In contrast, SFD80 is usually measured with central stimulation (Baas, Kenemans, & Mangun, 2002; Kenemans et al., 2000, 1993) and changes its polarity from weakly positive at 0.6 cpd to negative at 4.8 cpd (Kenemans et al., 2000). Thus, we believe to have observed a SFD80. However, further research is required to investigate the precise relationship between these two components.

In our study, EEG alpha and evoked gamma band responses were shown to vary as a function of spatial frequency. Evoked GBRs decreased with spatial frequency, whereas alpha responses increased. This resembles the observed frequency tuning in magnocellular and parvocellular layers of the lateral geniculate nucleus (LGN) and visual cortex in animals (O'Keefe et al., 1998; Tootell et al., 1988). Thus, it seems tempting to associate alpha and evoked gamma band responses with activity that originates from these structures. Indeed, Sowards and Sowards (1999) argue that gamma responses might be generated predominantly by the dorsal visual pathway (which mainly receives input from the magnocellular layers of the LGN, Merigan & Maunsell, 1993), since it can be found in animal experiments when moving stimuli are used. They further argue that alpha responses might be generated more by the ventral pathway (which receives input from both the magnocellular and the parvocellular layers Merigan & Maunsell, 1993), since it is also found in response to static stimuli. This would imply that stronger alpha responses should be measured over occipito-temporal regions of the ventral visual pathway, whereas gamma responses should be found over more parietal regions belonging to the dorsal visual pathway. Our topographies, however, cannot support this claim due to the limited spatial resolution of scalp recorded EEG. In addition, intracranial recordings have also found gamma responses in other cortical and subcortical locations, such as the temporal cortex or hippocampus (Cantero, Atienza, Madsen, & Stickgold, 2004; Lachaux et al., 2000). Evoked alpha responses can be measured from a wide variety of brain regions including the thalamus, reticular formation, hippocampus and cortex (Başar et al., 1997; Schürmann, Demiralp, Başar, & Başar-Eroglu, 2000). Furthermore, it should be noted that magnocellular

as well as parvocellular responses display a rather broad tuning to spatial frequency. A direct association of alpha and evoked gamma band responses to visual pathways should thus be considered with caution. The current results rather imply that different dynamical patterns are triggered by different spatial frequencies, the anatomical origin of which yet has to be identified. It could be possible, that large scale brain oscillations measured with EEG constitute a mechanism to structure the interplay between different brain areas (Chen & Herrmann, 2001; Engel, Fries, & Singer, 2001; Singer & Gray, 1995; von Stein & Sarntheim, 2000). In this case, neither of the studied oscillatory responses needs to be restricted to a single anatomical pathway.

Evoked GBR and SFD80 occur within a similar time window. It might, thus, be argued that the evoked gamma band responses are only an epiphenomenon of the SFD80. This seems unreasonable given the current results, since the evoked gamma response can be observed in the unfiltered ERP of single participants even before the SFD80 (see Fig. 4). While SFD80 is nearly exclusively observable in occipital electrodes, the evoked GBR peaks over parietal electrodes. In addition, these two components react differently in response to the different spatial frequencies: the prominent feature of the SFD80 is a change in polarity. In contrast, a change in phase-locking is the most salient effect in the gamma range. Kenemans et al. (2000) observed different dipole locations for the SFD80 in response to high vs. low spatial frequencies. The source of the SFD80 in response to high spatial frequencies was located in V1 (area 17) or adjacent V2, whereas for the SFD80 in response to low spatial frequencies they found a more radial orientation and a location which they interpreted as indication for a source in area 18 or 19. Thus, it might be speculated that the changes of the SFD80 ERP component are due to a change in the *location* of processing rather than a change in the *dynamics* of processing. In contrast, the topography of the evoked GBR did not vary considerably. We propose that the evoked GBR could be modulated by the number of neurons engaged in a local network and their temporal organization.

Previous studies which investigated gamma responses as a function of spatial frequency observed an increase in spatial frequency (Bodis-Wollner et al., 2001; von Stein & Sarntheim, 2000). In those studies participants were not required to perform a behavioral task and the results focussed on gamma power after stimulation, i.e. total responses. The studies mentioned above did not report results on phase-locked gamma responses. In the current study, phase-locked gamma responses were strongly modulated by spatial frequency, whereas no significant modulations of total responses were found. From previous results, it is known that phase-locked gamma responses are stronger if the participants are required to perform a behavioral task (Senkowski & Herrmann, 2002). Thus, it seems reasonable that the effects that were described in the current study could not be observed in previous experiments

because the evoked gamma response was not sufficiently large due to the lack of a behavioral task. Previously described modulations of total responses by spatial frequency (Adjamian et al., 2004; Bodis-Wollner et al., 2001) could not be replicated. (This is at least the formulation from the last revision.) Note, however, that these studies differ from the current one in other aspects, too. Adjamian et al. (2004) used continuous stimulation and Bodis-Wollner et al. (2001) used regular stimulation with fixed interstimulus intervals. This is in contrast to the transient stimulation procedure used in the current experiment where ISIs were randomized. Furthermore, another study, which investigated the impact of physical stimulus parameters on gamma responses with a similar experimental setup, did not find effects on total gamma either (Busch et al., 2004).

The latency of the total gamma response is relatively late compared to results by other authors (Gruber & Müller, 2006; Tallon-Baudry et al., 1998). Gruber and Müller (2005) demonstrated that induced changes in the gamma range between 200 and 400 ms are modulated by the semantic content of a stimulus. Although studies using simple stimuli like gratings or large uniform squares and circles did not find modulations of the total gamma band response by stimulus features, these studies found total gamma band responses 500–700 ms after stimulus onset (Busch et al., 2004; Busch, Schadow, et al., 2006). Thus, we argue that our total responses are similar to those of Busch et al. (2004) but not to those of Gruber and Müller (2006) or Tallon-Baudry et al. (1998).

The increase in reaction times might be interpreted as indicating an increasing difficulty to detect the correct orientation with increasing spatial frequency. However, similar or even higher increases in reaction time with increasing spatial frequency have been previously observed in experiments where the participants did not have to discriminate different orientations (Gish, Shulman, Sheehy, & Leibowitz, 1986; Musselwhite & Jeffreys, 1985; Plainis & Murray, 2000; Vassilev, Mihaylova, & Bonnet, 2002). It has been shown that these differences can mainly be explained as differences in neural processing time (Parker & Dutch, 1987) that are generated in extrastriate cortical areas (Musselwhite & Jeffreys, 1985). Furthermore, Burr and Wijesundra (1991) were able to show that for high contrast gratings such as the ones used in the current study, orientation discrimination depends on spatial frequency only for spatial frequencies below 0.2 cpd. We therefore conclude that orientation discrimination is a suitable task to investigate the modification of oscillatory EEG activity under conditions that resemble those that are employed in more cognitive experiments.

Our results indicate the importance of controlling spatial frequencies in such experiments, if visually evoked EEG oscillations are to be studied. In order to create stimuli with equivalent contents of spatial frequencies, Sadr and Sinha (2004) suggest averaging the amplitude spectra of all stimuli and only varying the phase spectrum.

For both alpha and gamma, the 1 cpd component seemed to dominate in the mix stimulus. This may be due to the fact that, for the task in our experiment, it was sufficient to discriminate the orientation of the low spatial frequency component gratings of the mix stimulus since the orientations of the component gratings were always identical. It is conceivable that the results for the mix stimulus change if participants have to selectively attend to one of the two spatial frequencies.

In conclusion, this study shows different response characteristics of oscillatory alpha and evoked, but not total gamma responses to spatial frequency under task requirements. Further investigations should explore the interactions between these oscillatory responses and higher cognitive processes.

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