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Size matters: effects of stimulus size, duration and eccentricity on the visual gamma-band response☆

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Abstract

Objective: The effects of stimulus size, duration and eccentricity on the visual gamma-band response (GBR) in human EEG were investigated and compared to visual evoked potentials (VEPs) in order to differentiate in future (and past) experiments whether changes in GBRs are due to stimulus-related (exogenous) or cognitive effects.

Methods: EEG was recorded from 23 subjects while they performed a simple choice reaction time task requiring discrimination of squares and circles. In separate blocks stimulus size, duration, and eccentricity were manipulated. EEG was recorded from 64 electrodes. A wavelet transform based on Morlet wavelets was employed for the analysis of gamma-band activity.

Results: Amplitude of the GBR was diminished for small and peripheral stimuli. With short stimulus durations ON and OFF responses of the GBR merged into one peak. In comparison, VEP amplitudes were less susceptible to stimulus features. In contrast to VEP latencies, however, GBR latency did not show a lateralization for eccentric stimuli.

Conclusions: In addition to previous experiments which have shown a modulation of the GBR by various cognitive processes, the present results demonstrate the susceptibility of the GBR in human EEG to exogenous factors, as numerous intracortical recordings in non-human primates have shown before. The results suggest that the human GBR resides in early visual areas.

Significance: The demonstration of the susceptibility of the GBR to stimulus properties implies that studies aimed at exploring the involvement of the GBR in information processing have to be designed carefully. It also constrains the localization of the human GBR.
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Keywords: Gamma-band oscillations; 40 Hz; Exogenous; Size; Duration; Eccentricity

1. Introduction

In recent years there has been a growing interest to complement the classical analysis of EEG and event related potentials (ERPs) with various approaches of analysis in the frequency domain (Engel et al., 2001; Jung et al., 2001; Pfurtscheller and Lopes da Silva, 1999). The EEG frequency spectrum is usually subdivided into different frequency bands. Although the denotation of frequency bands is by no means standardized throughout the EEG literature, the most prevailing terminology distinguishes the delta (<3 Hz), theta (4–8 Hz), alpha (8–12 Hz), beta (13–20 Hz), and gamma (30–80 Hz) bands. Regarding oscillatory activity, it is important to distinguish between evoked and induced oscillations since they are assumed to reflect different processes. Evoked oscillations exhibit a strict phase-locking to the experimental event (e.g. stimulus presentation) across trials. Hence, they can be extracted from the averaged ERP, e.g. by filtering. Induced oscillations, on the other hand, are (by definition) not at all phase-coupled to a stimulus, and show a certain degree of phase-jittering. Therefore, by averaging across trials these oscillations will cancel out completely and hence are only

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detectable by appropriate ways of analysis, e.g. by a single-trial based wavelet analysis with subsequent averaging.

High frequency oscillations in the gamma-band have been investigated in numerous experiments in humans and animals (Keil et al., 2001a; Sannita, 2000; Tallon-Baudry and Bertrand, 1999). Although discovered as early as 1942 (Adrian, 1942) the current interest in gamma oscillations was fostered by experiments on the anesthetized cat in the late 1980s (Eckhorn et al., 1988; Gray et al., 1989). These studies showed that neurons in the cat visual cortex responded strongly synchronized within the 20–80 Hz frequency range when bars were passed across the receptive fields in the same direction compared to bars moving in different directions. The authors concluded that synchronized gamma activity could 'bind together' separate features of an object.

Subsequent studies also found a task-related gamma-band component in human EEG as well as at the intermediate level of electrocorticograms and intracranial recordings in humans and monkeys (Aoki et al., 1999; Lachaux et al., 2000; Menon et al., 1996; Rols et al., 2001). Under visual stimulation a strong increase in evoked oscillations near 40 Hz over posterior areas with a latency of approximately 100 ms and a later increase in induced activity with a latency around 300 ms can be observed. We will refer to both types of these responses as gamma-band responses (GBRs). Such GBRs have been found to be modulated by task variations and hence cognitive processes including visual feature binding (Tallon-Baudry et al., 1997), target detection (Herrmann et al., 1999), voluntary attention (Debener et al., 2003; Gruber et al., 1999; Herrmann and Mecklinger, 2001), memory (Tallon-Baudry et al., 1998), and emotional arousal (Keil et al., 2001b).

However, despite the growing interest in the GBR some authors have been rather critical about the functional role of gamma-band oscillations (Jürgens et al., 1995; Shadlen and Movshon, 1999; Tovee and Rolls, 1992). Numerous attempts to investigate gamma-band oscillations in human EEG have failed to find a GBR at all (Jürgens et al., 1999) and some authors question that gamma oscillations are detectable at the scalp level (Menon et al., 1996). Considering these discrepancies which may, at least in part, result from differences in experimental settings, stimulus design or method of data analysis, it seems important to investigate noncognitive factors that influence the amplitude of the GBR and, hence, its detectability (Lutzenberger et al., 1997).

The influence of visual stimulus properties, for instance size, luminance or spatial frequency, is well known and well examined in the ERP literature (Celesia, 1993). Early ERP components that are strongly influenced by such physical properties of the eliciting stimulus are often called 'exogenous' while the later components, which are more under the influence of cognitive processes, are termed 'endogenous' (Rugg and Coles, 1995). Components that are influenced by both factors are sometimes termed 'mesogenous', a prominent example of which is the N1. While this terminology is commonly used for ERPs it has not been applied to event-related oscillations so far. Nevertheless, some evidence suggests that early event-related oscillations are subject to modulation by rather unspecific factors such as task difficulty (Senkowski and Herrmann, 2002) and subject's age (Böttger et al., 2002). In addition, Rols et al. (2001) showed that stimulus parameters like luminance influence the amplitude of the GBR in electrocortical recordings in the macaque monkey. By using sinusoidal gratings as stimuli Tzelepi et al. (2000) demonstrated an increase in GBR for gratings of higher spatial frequency. Accordingly, early event related oscillations like the GBR could be conceptualized as mesogenous as well.

The present study was conducted to further investigate the impact of visual stimulus properties on the GBR. Such influences are presumably relevant to most experimental paradigms used for the study of relations between cognitive processes and the GBR. In order to properly argue that a difference in amplitude or latency of the GBR between experimental conditions is attributable to cognitive processes it is, first, essential to elicit a significant response at all (which is not as trivial as it may sound). Second, it should be ruled out that differences are simply due to different stimulus properties. Two of such stimulus characteristics are size and eccentricity (i.e. how lateral the stimulus is presented). In addition we varied the presentation duration of the stimuli to investigate whether onset- and offset-related components of the GBR superimpose at short stimulus durations. If ON and OFF responses merge together this could constrain interpretation when comparing experimental conditions with different presentation durations. Our choice of stimulus properties was based on typical stimulus dimensions used in many cognitive ERP experiments (Barcelo et al., 2000; Gomez Gonzalez et al., 1994; Rugg et al., 1985). Exogenous effects on visually evoked potentials have been investigated predominantly using checkerboard stimuli or sinusoidal gratings in a steady-state paradigm (Celesia, 1993). However, studies designed to investigate cognitive processes usually employ figural stimuli, which are presented only once per trial. In order to provide a setting comparable with most cognitive experimental paradigms we used simple geometric shapes as stimuli that were presented transiently in a choice reaction task.

2. Methods

2.1. Subjects

Twenty-three subjects participated in the study (mean age 25; range 20–34 years, 16 female), all were paid for participation. Subjects gave informed consent prior to start of the experiment. All subjects had normal or corrected to

normal vision and were free of current or past neurological or psychiatric disorders.

2.2. Stimuli and procedure

Black circles and squares on a white background were used as stimuli. Subjects were required to press a button with the thumb of one hand if the stimulus was a circle and to press a button with the other hand if it was a square. Response hands were counterbalanced across subjects. Both types of stimuli appeared with equal probability in a pseudo-randomized order. Stimulus presentation was followed by a variable inter-stimulus interval ranging from 1000 to 1400 ms. Stimuli were presented on a computer monitor placed at a distance of 105 cm in front of the subject. Monitor refresh rate was 100 Hz. In 3 separate blocks, we manipulated one of the stimulus parameters size, eccentricity or duration, the order of which was counterbalanced across subjects. In the size-block stimuli had a size of 1.5° (small), 4° (medium) or 8° (large) of visual angle and were presented centrally for a duration of 250 ms. In the duration-block a stimulus with a size of 4° visual angle was presented centrally for 50 ms (short), 150 ms (medium) or 250 ms (long). In the eccentricity-block, a stimulus of 4° visual angle was presented for 250 ms either centrally or with an eccentricity of 4.3° (medium eccentricity) or 8.6° (high eccentricity) to the right side of the fixation cross. Subjects were required to remain always in central fixation. Each block comprised 90 trials per type of stimulus (circles and squares) and level of size, duration or eccentricity, resulting in a total number of 540 trials per block. Two breaks of 1 min duration were given in each block and an additional break occurred between two consecutive blocks.

2.3. Data acquisition

EEG was recorded using a high impedance 64 channel Net Amps 200 system (Electrical Geodesics, Inc. Eugene, Oregon) with Ag/AgCl-electrodes placed in an electrode cap (Easycap, Falk Minow Services, Munich) and a nose-tip reference. Sensor impedances were maintained below 20 kΩ prior data acquisition (Ferree et al., 2001). EEG was analog filtered from 0.1 to 100 Hz, digitized at 500 Hz, and stored on harddisk for off-line analysis. Recordings were made while subjects sat in a dimly lit, sound-attenuated and electrically shielded cabin.

Averaging epochs lasted from 200 ms before to 600 ms after stimulus onset. Baselines were computed in the interval from 200 to 100 ms prior to stimulus onset. An automatic artifact rejection was computed which excluded trials from averaging if the standard deviation within a moving 200 ms time interval exceeded 30 μV. In addition, all epochs were also visually inspected for artifacts and those with remaining artifacts rejected. While data analysis was performed on unfiltered data, ERPs are displayed low-pass filtered digitally at 20 Hz (3 dB edge frequency = 15.05 Hz, steepness of roll-off = 14 dB/octave).

2.4. Data analysis

In order to avoid a loss of statistical power we first computed ERPs and wavelet transforms for the single electrodes and then collapsed selected electrodes into 9 regions of interest (ROIs) for all subsequent analyses (Oken and Chiappa, 1986). ROIs and corresponding electrodes were anterior left (5, 13–15, 23, 24), anterior midline (1, 3, 6–8, 16), anterior right (9, 17–19, 26, 27), central left (22, 30–32, 42, 43), central midline (25, 33–35, 44–46), central right (28, 36–38, 47, 48), posterior left (40, 41, 54, 58, 61), posterior midline (51–53, 55, 56, 59) and posterior right (49, 50, 57, 60, 63). Electrode positions are displayed in Fig. 1. Those electrodes were plotted in the figures at which effects were most pronounced.

For the analysis of the GBR 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)). The main advantage of this approach, compared to the short-term Fourier transform approach (Makeig, 1993), is that the duration of the window of analysis depends on the frequency band: the higher the central frequency, the shorter the window duration and the wider the frequency band. This method thus provides a better compromise between time and frequency resolutions (Sinkkonen et al., 1995). Morlet wavelets can be thought of as 'bandpass filters' having a Gaussian shape both in the time domain and in the frequency domain around their central frequency. The standard deviation σ_t of the Gaussian temporal envelope is reciprocally related to the frequency ($\sigma_t \sim 1/f$). The standard deviation in the frequency domain

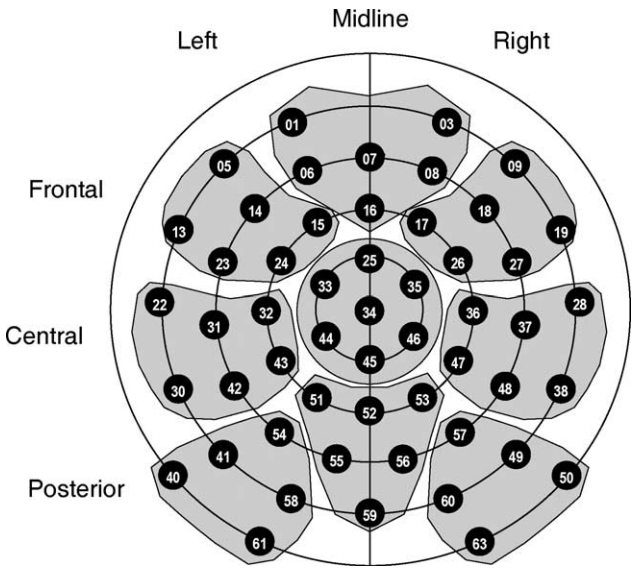

Fig. 1. Channel layout used for statistical analysis. Regions of interest are indicated by grey shaded areas.

is given by $\sigma_f = (2\pi\sigma_t)^{-1}$. The time resolution of this method thus increases with frequency, whereas the frequency resolution decreases. Usually, the characteristics of a wavelet are denoted as $2\sigma_t$ and $2\sigma_f$. Accordingly, a wavelet with a center frequency of 40 Hz employed in the present study had a wavelet duration of $2\sigma_t = 50$ ms and a spectral bandwidth of $2\sigma_f = 12.71$ Hz (Fig. 2).

To reveal the evoked fraction of gamma activity, which is, by definition, strictly phase-locked to the stimulus, the wavelet transform was performed on the averaged evoked potential. In order to analyze also 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 GBR' in order to make explicit that it comprises both the evoked and induced part of the gamma response. However, the same measure has been used previously for the estimation of only the induced part (Tallon-Baudry and Bertrand, 1999). While that may be a legitimate approximation, we prefer to stick to the precise differentiation. The frequency of gamma activity used for the wavelet analysis was individually determined via the time–frequency plane of electrode 34 (equivalent to CZ) in response to the largest stimulus in the size-block (as done before by Senkowski and Herrmann, 2002). This approach assumes that frequencies do not depend on stimulus properties. In fact, it might be speculated that the frequency of the early evoked GBR is dependent on stimulus size, i.e. on the size of the cortical area involved. According to the temporal correlation hypothesis (Singer and Gray, 1995) such a relationship might be expected: "As the rhythm slows down, … binding by synchrony can be achieved over larger distances and between more cells." (Singer, 1993). If assemblies coding bigger stimuli relied on lower frequencies this would broaden the time window during which events can be classified as synchronous. In a first step we tested whether frequencies of evoked GBRs differed between the 3 size conditions. One subject was excluded from this and all further analyses of evoked GBRs because he did not show a significant response in the gamma band (for criteria see below). Although there was a trend towards lower frequencies for bigger stimulus sizes this effect did not reach significance ($F(2, 42) = 3.121$, $P = 0.059$). It might be interesting, however, to further investigate this effect in a separate analysis. In a second step individual maxima of evoked gamma activity were defined as the highest evoked activation peak in the frequency range of 30–80 Hz between 60 and 140 ms. The individual frequencies of total GBRs were defined as the highest total activation peak in the frequency range of 30–90 Hz between 420 and 560 ms. Using this definition the peak frequencies of individually identified evoked GBRs ranged from 32 to 72 Hz (mean 44.09 Hz, SD = 10.04 Hz). The individual peak frequencies of total GBRs were considerably higher with an average frequency of 65.52 Hz (SD = 14.41 Hz) and a range from 39 to 89 Hz. Data from the 4 subjects with the highest and lowest evoked and total gamma-band activity are plotted in Fig. 3.

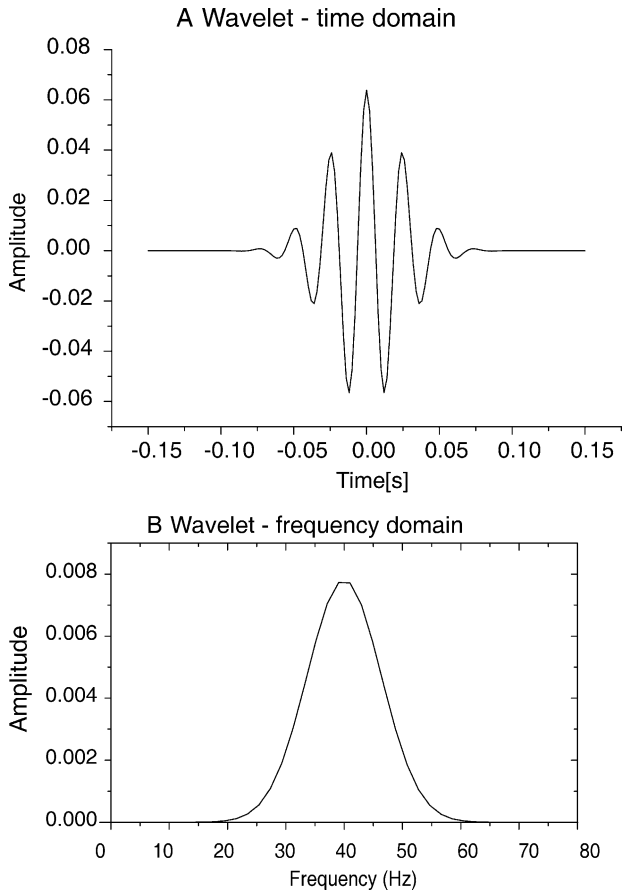

Fig. 2. Characteristics of a 40 Hz wavelet in the temporal (A) and spectral domain (B).

For the statistical analysis of ERP responses we used peak amplitudes in the time intervals between 50 and 130 ms (P1) and 130–200 ms (N1), respectively. P1 and N1 amplitudes and latencies were analyzed for posterior regions only. Statistical analysis of the evoked GBR was performed on peak amplitudes and latencies of the individually adapted wavelet transforms in the time interval between 60 and 140 ms. Analysis of the total GBR in the individually determined frequency was performed using the peak amplitudes and latencies in a time interval of 300–600 ms. The GBR was investigated in all 9 ROIs. All time windows were chosen on the basis of the grand mean average.

In a first ANOVA we tested whether the GBR was modulated by stimulus type (circles vs. squares). Since no such effect was observed, for all subsequent analyses data was combined across squares and circles. Thus, the repeated measures ANOVA of ERP effects comprised the factors stimulus (3 levels of size, duration or eccentricity, respectively) and laterality (posterior left, posterior midline, posterior right). The repeated measures ANOVA of the GBR

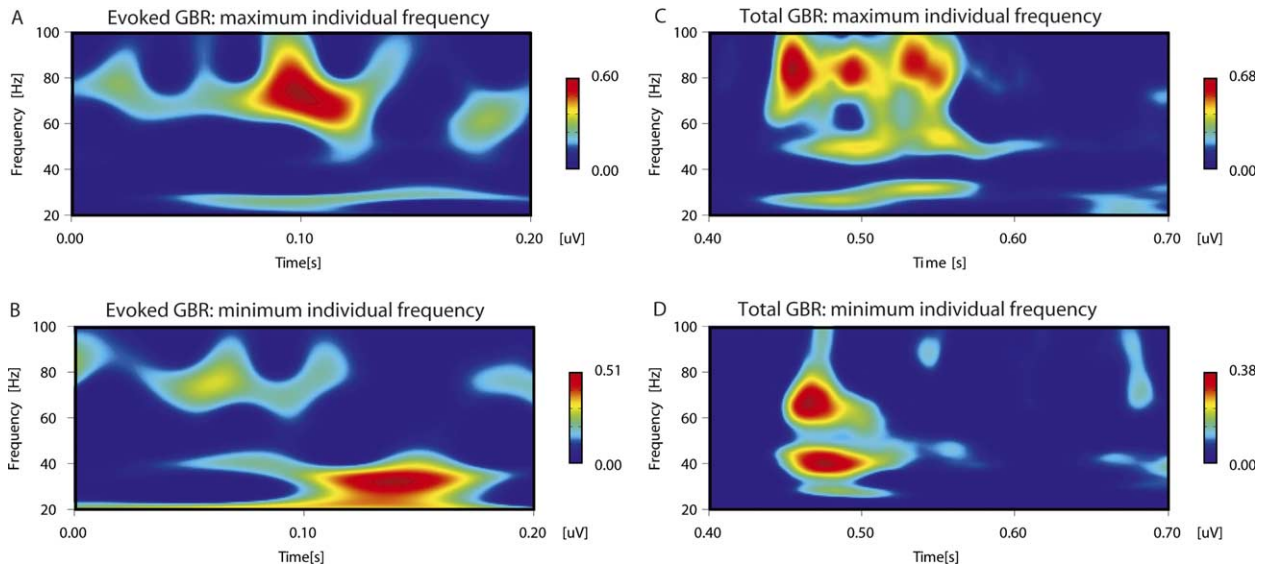

Fig. 3. Time–frequency plots for the single subjects with the maximum and minimum individual evoked GBR (72 and 32 HZ, respectively) and the maximum and minimum individual total GBR (89 and 39 Hz, respectively). Note the different time scales for evoked and total GBRs.

comprised the factors stimulus, laterality (left, midline, right) and caudality (anterior, central and posterior). The repeated measures ANOVA of reaction times comprised the factor stimulus (3 levels of size, duration, or eccentricity, respectively). Greenhouse-Geisser correction was used where appropriate. Uncorrected degrees of freedom and corrected *P* values are reported.

In order to visualize the impact of stimulus manipulations on ERPs and GBRs, we plotted the change in amplitude for medium and large size as well as medium and high eccentricity, relative to the amplitude of small and central stimuli, respectively (Fig. 9). Analysis of amplitude changes rather than a more traditional signal-to-noise computation was chosen in order to yield a measure that allows comparison between ERPs and GBRs. In the figures we plotted those electrodes at which effects were most pronounced.

3. Results

Stimulus presentation evoked a P1 (mean peak latency 100 ms) followed by an N1 (170 ms; Figs. 4A, 6A, 8A). Stimulus disappearance resulted in an OFF response, which was superimposed on a P3. The latency of the OFF responses varied with stimulus duration. However, neither the ERP OFF responses nor the P3 component were the focus of the present study and, hence, were not subjected to further analysis. The analysis of the individually identified GBRs revealed a prominent evoked ON response (mean peak latency 86 ms; Figs. 4B, 6B, 8B). Stimulus offset resulted in an evoked OFF response with a mean latency of 100 ms after stimulus offset. Additionally, stimulus offset resulted in a total GBR, which was observed at an average latency of 232 ms (for stimuli which were presented for 250 ms) after stimulus offset (Fig. 7). This response was not visible in the evoked activity.

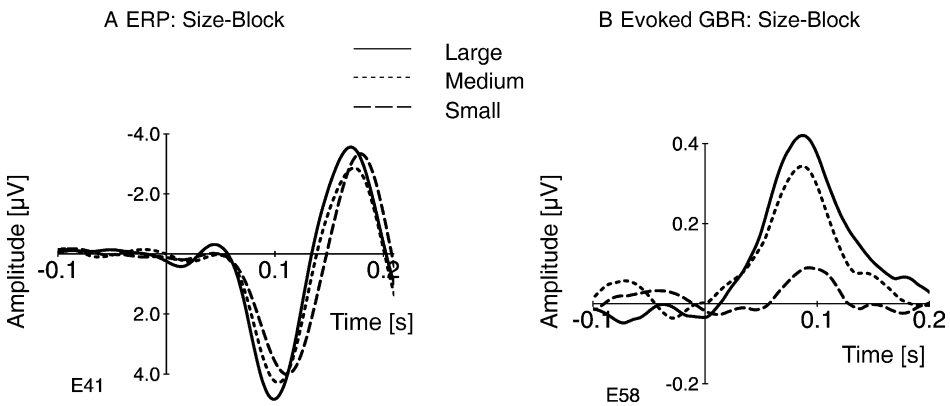

Fig. 4. ERPs and individually defined evoked GBRs in the size-block for large (solid line), medium sized (dotted line) and small stimuli (dashed line) for representative electrodes. Note the considerable effect of stimulus size on the GBR amplitude, which was less clearly observed for the ERPs. Data represent the grand mean average across 23 subjects.

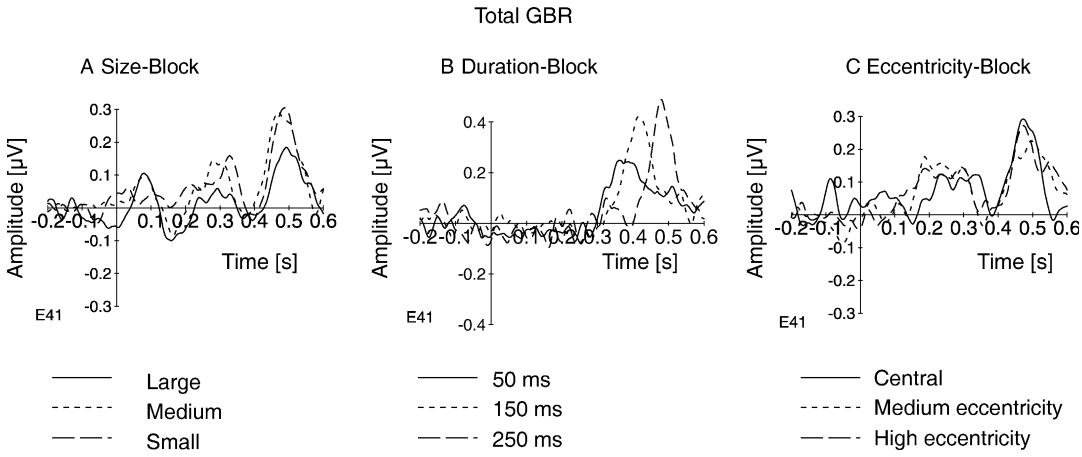

Fig. 5. Individually defined total GBRs in the size-, duration- and eccentricity-block.

3.1. Size-effects

Reaction times showed a main effect of size ($F(2,44) = 9.979$, $P < 0.001$). Responses were fastest to medium sized stimuli (441 ms) while small and big stimuli did not differ significantly in reaction times (457 and 451 ms, respectively; $F(1,22) = 1.70$, $P = 0.206$).

The ANOVA of P1 amplitudes in the size-block yielded a main effect of size ($F(2,44) = 9.856$, $P = 0.001$) with larger amplitudes for bigger stimuli (Fig. 4A). A main effect of laterality ($F(2,44) = 11.816$, $P < 0.001$) indexed smaller P1 amplitudes in the posterior midline ROI than in the lateral ROIs. No interaction of size and laterality effects was observed. P1 latencies showed a main effect of size ($F(2,44) = 18.092$, $P < 0.001$) with longer latencies for smaller stimuli. N1 amplitudes were not modulated by size. A main effect for laterality ($F(2,44) = 5.363$, $P = 0.014$) indicated smaller N1 amplitudes in the posterior midline ROI compared to the lateral ROIs. Analysis of N1 latencies yielded a main effect of size ($F(2,44) = 13.587$, $P < 0.001$) as well as laterality ($F(2,44) = 13.378$, $P < 0.001$), and a significant size × laterality interaction ($F(4,88) = 3.805$, $P = 0.014$) indicating longer latencies for smaller stimuli at lateral ROIs.

For the peak amplitudes of the evoked GBR in the size-block the ANOVA yielded a main effect of size ($F(2,42) = 11.124$, $P < 0.001$; Fig. 4B) with larger amplitudes for bigger stimuli. Peak latencies of the evoked GBR were not influenced by stimulus size. Peak amplitudes of the total GBR were not modulated by size (Fig. 5A). Peak latencies were longer for bigger stimuli ($F(2,44) = 4.522$, $P = 0.016$).

3.2. Duration-effects

Reaction times showed no effect of duration. The values observed were 438 ms for short, 436 ms for medium, and 446 ms for long durations, respectively. Neither P1 nor N1 amplitudes or latencies were affected by stimulus duration (Fig. 6A).

Stimulus offsets elicited an evoked gamma-band OFF response. The latency of the evoked gamma OFF responses were 148 ms for 50 ms stimulus duration, 248 ms for 150 ms stimulus duration, and 350 ms for 250 ms stimulus

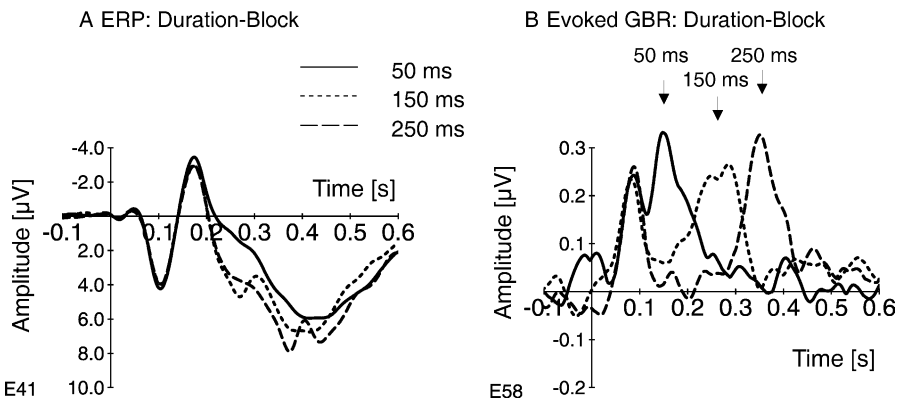

Fig. 6. ERPs and individually defined evoked GBRs in the duration-block for 50 ms (solid line), 150 ms (dotted line) and 250 ms presentation time (dashed line) for representative electrodes. For ERPs the OFF response was superimposed on the prominent P300 and thus no big differences are visible. For the GBR, however, the OFF response was clearly affected by stimulus duration.

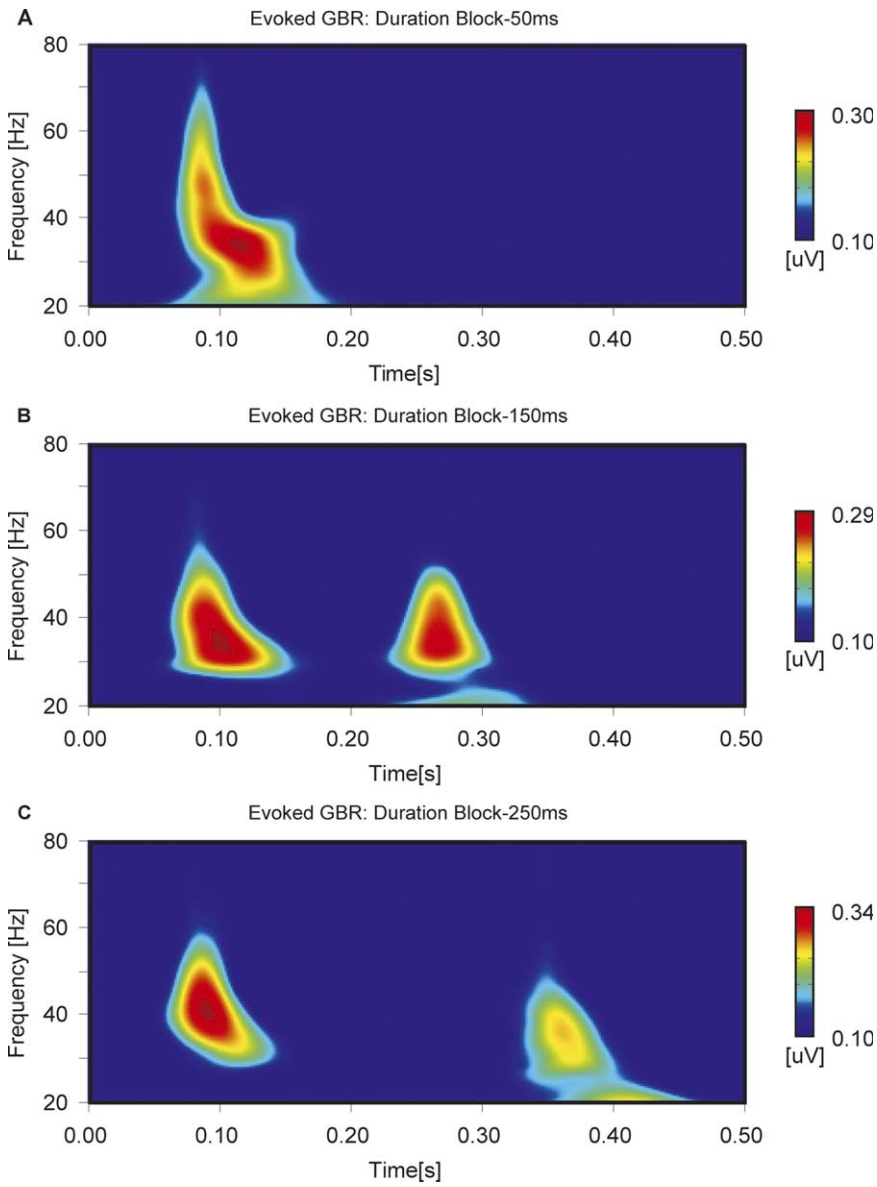

Fig. 7. Time–frequency plots for the 3 different stimulus durations (50, 150 and 250 ms) at electrode E34. For the shortest stimulus ON and OFF responses merged together while in the other conditions a clearly distinguishable OFF response appears approximately 100 ms after stimulus offset.

duration (Fig. 6B), i.e. the evoked OFF response appeared approximately 100 ms after stimulus offset (Fig. 7). For the shortest stimulus duration evoked ON and OFF responses merged together, resulting in a larger evoked OFF response peak. The ANOVA of evoked GBR peak amplitudes yielded a significant caudality × duration interaction ($F(2,44) = 3.756$, $P = 0.020$). Subsequent analysis revealed an effect of stimulus duration at posterior electrodes ($F(2,44) = 6.007$, $P = 0.006$) indicating larger amplitudes for short stimulus durations. This effect probably resultet from a superposition of evoked ON and OFF responses.

Total GBR amplitudes were also modulated by duration with larger amplitudes for longer stimulus durations ($F(2,44) = 6.898$, $P = 0.004$; Fig. 5B). Peak latencies of the total GBR varied with stimulus duration ($F(2,44) = 14.438$, $P = 0.020$) with longer latencies for longer stimulus durations (382 ms for short, 412 ms for medium and 482 ms for long durations).

3.3. Eccentricity-effects

Reaction times showed no effect of eccentricity (454 ms for central, 452 ms for medium, and 457 ms for high eccentricity). P1 amplitudes were modulated by eccentricity ($F(2,44) = 26.069$, $P < 0.001$, Fig. 8A) with larger amplitudes for central stimuli. Amplitudes also varied between ROIs, as was reflected by a main effect of laterality, ($F(2,44) = 12.753$, $P < 0.001$), indicating smaller amplitudes at the posterior midline ROI. Additionally, the analysis yielded an eccentricity × laterality interaction ($F(4,88) = 10.3$, $P < 0.001$) indicating smaller P1 amplitudes for eccentric stimuli on the contralateral (left) side.

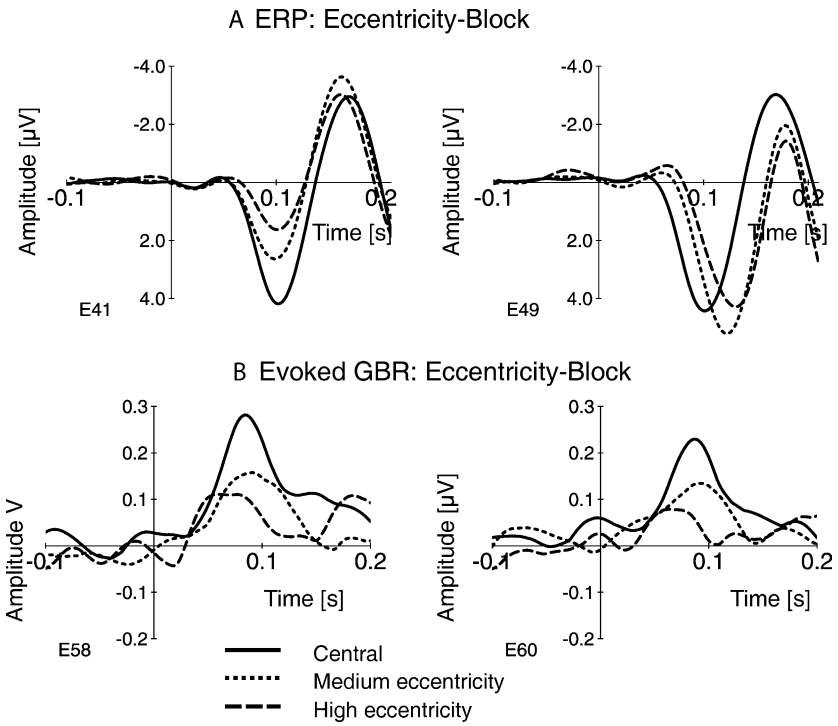

Fig. 8. ERPs and individually defined evoked GBRs in the eccentricity-block for central (solid line), medium eccentric (dotted line) and highly eccentric stimuli (dashed line) for representative electrodes (E41 and E58: contralateral; E49 and E60: ipsilateral).

P1 latencies were also influenced by eccentricity ($F(2,44) = 6.102$, $P = 0.012$) and laterality ($F(2,44) = 11.966$, $P < 0.001$). An eccentricity × laterality interaction ($F(4,88) = 7.281, P < 0.001$) indicated longer P1 latencies for eccentric stimuli at the ipsilateral (posterior right) ROI but shorter latencies for eccentric stimuli at the contralateral (posterior left) and the posterior midline ROI. The analysis of N1 amplitudes yielded a main effect for laterality ($F(2,44) = 5.239$, $P = 0.009$) with smaller amplitudes at the posterior midline ROI. N1 latencies also varied with laterality ($F(2,44) = 18.0$, $P < 0.001$) with shorter latencies at the posterior midline ROI. An eccentricity × laterality interaction ($F(4,88) = 6.595$, $P < 0.001$) indicated longer N1 latencies for eccentric stimuli on the ipsilateral (right) side.

In the eccentricity-block the evoked GBR was modulated by eccentricity ($F(2,44) = 4.692$, $P = 0.025$; Fig. 8B) with bigger amplitudes for central stimuli. The analysis also yielded a main effect of caudality ($F(2,44) = 3.752$, $P = 0.044$) and a significant caudality × laterality interaction ($F(4,88) = 3.349$, $P = 0.025$), indicating larger amplitudes in the central midline ROI. GBR latencies were not influenced by eccentricity. Neither peak amplitudes nor latencies of the total GBR were modulated by eccentricity

3.4. Relative amplitude changes

ERPs and evoked GBRs were differently influenced by stimulus size and eccentricity (Fig. 9). While P1 and N1 amplitudes were only moderately modulated by stimulus size, evoked GBR amplitudes were more than doubled for large compared to small stimuli. In the eccentricity block P1 and evoked GBR amplitudes moderately decreased with stimulus eccentricity, while again N1 amplitudes were almost unaffected.

4. Discussion

The present study investigated effects of stimulus properties on event-related potentials and oscillations in

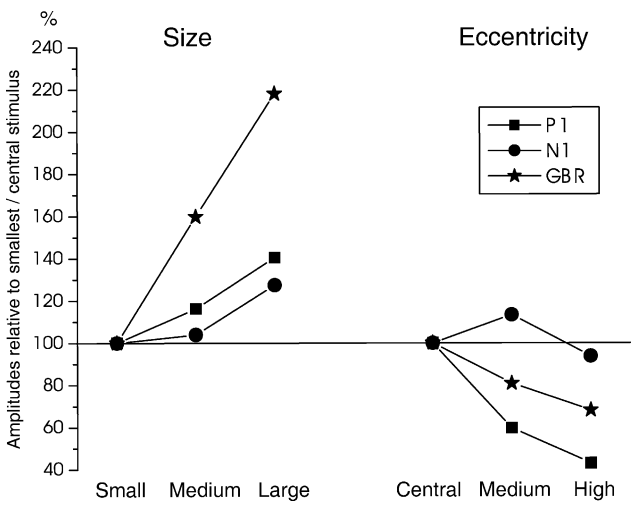

Fig. 9. Amplitudes of P1, N1 and evoked GBR expressed as percentage of amplitudes elicited by the small and central stimulus, respectively.

the gamma-band. ERPs revealed the expected modulation of P1 and N1 with stimulus properties, i.e. larger ON responses for larger and central stimuli. In addition, it was obvious that P1 and N1 OFF responses were evoked by stimulus offset, which appeared superimposed on late ERP components (P3). Therefore, it seems advisable to present stimuli longer than the largest latency of any ERP component which shall be analyzed. Otherwise a superposition of P1 and N1 could affect the quantification of later ERP components.

The GBR has been used as a tool to study a large variety of cognitive processes and has proven to be a valuable complement to traditional ERPs (Keil et al., 2001a; Sannita, 2000; Tallon-Baudry and Bertrand, 1999). It has become a common practice to differentiate between early versus late gamma responses. Within this framework, early gamma responses are usually evoked by a stimulus while late ones are induced. Numerous previous experiments have focused on demonstrating top-down modulations of both the evoked and induced GBR. Our results show that both fractions of the GBR can be also strongly modulated in a bottom-up fashion by stimulus properties.

4.1. Influence of stimulus properties on evoked GBRs

The amplitude of the evoked GBR seems to be directly related to the size of the stimulus, which probably results from bigger stimuli activating larger cortical areas in retinotopic visual cortices than smaller ones. For small and peripheral stimuli the amplitude of the evoked GBR hardly exceeded the noise level (Figs. 4B and 6B). The present data also show that the eccentricity of visual stimuli modulates the amplitude of the evoked GBR. While the central visual field is represented in the calcarine fissure near the occipital pole, the periphery is represented more anteriorly (Engel et al., 1997). Thus, peripheral stimuli evoke responses in neural tissue which is more distant from the scalp electrodes. If the early evoked GBR is generated in early visual areas and follows a retinotopic mapping, this could explain the observed eccentricity effect. Electrocorticogram recordings in monkey V1 (Rols et al., 2001) did not reveal effects of eccentricity on the GBR. This may, however, be due to the subdural recording methodology and to the fact that a large part of V1 in macaque monkeys is represented on the lateral surface of the occipital pole. Therefore, in the study by Rols et al. (2001), the electrodes were always close to the signal-generating sites for all investigated eccentricities.

4.2. Influence of stimulus properties on induced GBRs

In addition to the early evoked GBR we found a later gamma response, which was only present in the total GBR and must therefore reflect induced activity. The latency of this response varied with presentation duration and, hence, was probably related to the stimulus offset. Such an induced offset response has been described before by Tallon-Baudry et al. (1998). It seems noteworthy that both in their as well as in our experiment the latency of the induced OFF response was markedly later than the evoked OFF response in our experiment (350 ms for evoked and 480 ms for induced GBRs for a stimulus with 250 ms duration). Previous experiments revealed that the late induced gamma response in human EEG can be modulated by top-down processes such as memory (Tallon-Baudry et al., 1998), attention (Gruber et al., 1999) and object recognition (Rodriguez et al., 1999). These findings are supported by studies investigating local field potentials in monkeys (Fries et al., 2001; Woelbern et al., 2002). However, our present study clearly demonstrates that also bottom-up factors like the duration of a stimulus modulate induced GBRs.

4.3. Differences between ERPs and GBRs

Our data revealed an interesting difference regarding the impact of stimulus eccentricity on ERPs and evoked GBRs. ERP latencies were found to covary with eccentricity on the side ipsilateral to stimulus presentation. This delay for eccentric stimuli at ipsilateral sites has been observed before and was explained with interhemispheric transfer (Rugg et al., 1985). According to this hypothesis, information from the peripheral visual field needs to be relayed across the corpus callosum while no such transfer is necessary for central stimuli. Thus, latency differences between central and eccentric stimuli at electrodes ipsilateral to stimulus presentation may reveal the transfer time between the two cortical hemispheres. Interestingly, we found no such latency difference for the evoked GBR. In two previous studies Basar-Eroglu and colleagues reported a reduced time for interhemispheric transfer from the contralateral to the ipsilateral hemisphere for beta frequencies compared to alpha and theta frequencies and ERPs (Nalcaci et al., 1999a, b). The authors hypothesized that transfer of different frequency bands relies on callosal fibers with different conduction velocities (Aboitiz et al., 1992). The present data might indicate a similar effect for the gamma-band.

4.4. Origin of the evoked GBR

Our results raise the question of where in the hierarchy of visual processing the generators for the early evoked GBR reside. Early ERPs like P1 and N1 are known to be modulated by stimulus properties as well as cognitive factors like spatial attention. Their sources have been located in occipito-temporal and occipito-parietal areas (Di Russo et al., 2002; Gomez Gonzalez et al., 1994). In our study the mean peak latency of the early evoked GBR was shorter than P1 latency (86 and 102 ms, respectively) suggesting that the source of the evoked GBR is located earlier in the visual hierarchy. This interpretation is supported by the fact that the early evoked GBR was even stronger influenced by stimulus properties than early ERPs.

Findings from animal studies investigating local field potentials and multi unit activity corroborate this view (Eckhorn et al., 1993; Engel et al., 1991; Frien et al., 1994). These investigators found synchronous oscillations in early visual areas of cats and monkeys. The factor exerting the strongest impact was stimulus size, but stimulus eccentricity also led to modulations in the evoked GBR, suggesting an involvement of sources located in primary visual cortex. Due to the differential effects of experimental manipulations on latency and amplitude of ERPs and the early evoked GBR, these two measures might reflect partly different neuronal processes. Despite its short latency and its probable generation early in the visual hierarchy, the evoked GBR has shown to be also under the influence of top-down cognitive mechanisms, a property that is not commonly associated with early visual processing. Recent models of the visual system, however, assume that visual processing relies on the interaction of feedback and feedforward connections already at a very early stage (Bullier, 2001; Lamme and Roelfsema, 2000; Taylor, 2002). In an ERP experiment Foxe and Simpson (2002), for instance, showed 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 GBR can be modulated by bottom-up as well as top-down factors simultaneously.

4.5. Implications for GBR studies

It should be emphasized that even the smallest stimulus size and the highest stimulus eccentricity employed in the present study are common in and sufficient for ERP experiments. The susceptibility of evoked GBRs to extrinsic influences might explain why other researchers failed to observe an evoked GBR in their experiments. Therefore, the present findings are of practical importance for the design of experiments on gamma-band oscillations. First, since for small and peripheral stimuli the amplitude of the GBR is diminished, stimuli should expand over at least 4–5° visual angle and should not be presented too peripheral in order to elicit a significant GBR at all. Second, interpretation of cognitive effects on the GBR is difficult if conditions employed stimuli of different size or eccentricity. Also, for short stimulus durations one may not be able to distinguish between ON and OFF responses. If such a short stimulus duration was employed in only one condition, one might mistake the superposition of onset and offset response as a larger amplitude due to the experimental manipulation. One would run the risk of confounding task effects with stimulus effects. Also, given the small amplitude of the GBR compared to ongoing noise one should take care about technical issues during data recording and analysis (Lutzenberger et al., 1997). For instance, it seems advisable to use a high amplifier gain and ensure a sufficient electrical shielding of the recording environment.

5. Conclusion

It is well known that early ERPs are susceptible to stimulus properties like stimulus size or eccentricity. Here we were able to demonstrate that fast oscillatory EEG activity is even more susceptible to these parameters.

While previous studies showed that evoked as well as induced GBRs are modulated by top-down influences our data demonstrated that both types of GBRs are also modulated by bottom-up influences. While evoked GBRs were modulated by stimulus size, eccentricity and duration, induced GBRs were influenced by stimulus duration only.

The fact that the evoked GBR was significantly modulated by the size of stimuli indicates that it is generated by a retinotopic brain area, i.e. early visual cortex.

Since the present study employed a rather simple choice reaction task, subsequent studies should investigate the interaction of both bottom-up and top-down influences on the GBR. An interesting question would be, for instance, to what extend modulation of the evoked GBR by stimulus size and by top-down attention interact. Also, the bottom-up effects on total gamma-band activity should be investigated more closely using longer stimulus durations.

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