RESEARCH ARTICLE

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EEG gamma-band activity in rapid serial visual presentation

Abstract Evidence is available that oscillatory activity in the gamma frequency range (>30 Hz) might be related to the attentional selection of target items. Rapid serial visual presentation (RSVP) paradigms are instrumental in addressing cognitive functions such as visual attention, and they are increasingly combined with the measurement of electrical brain activity. In the present study, gamma-band responses for target and standard stimuli were investigated in an RSVP oddball paradigm. In a first study, stimuli were presented at a frequency of 10 Hz, the stimulus sequence consisted of rare colored letters (targets) and frequent black letters (standards). In addition, stimulus size was varied across experimental blocks. Significant target modulations were observed for the P3 ERP and induced (i.e., not phase-locked) gamma-band responses. Besides this late activation, no further gamma-band responses were observed. A second study aimed at replicating these findings by employing a reduced stimulus presentation rate of 7.1 Hz. Again, besides the P3 ERP a late increase in induced gamma-band activity was observed. However, as compared to Study 1, this induced response was less pronounced. The induced gamma-band response observed in the present studies might reflect utilization of information derived from previous processing steps for behavioral performance or memory storage as suggested in the 'match-and-utilization-model' of gamma activity.

Keywords Evoked gamma-band activity · Induced gamma-band activity · RSVP · EEG · ERP · Match-and-utilization-model

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Introduction

An increasingly important procedure in the investigation of cognitive processes is the rapid serial visual presentation (RSVP) of series of stimuli such as digits, letters, words, or pictures. RSVP typically refers to the presentation of stimulus series at a fixed location with presentation frequencies ranging from 3 to 20 items per second. Paradigms employing RSVP have been used, for instance, in research on visual awareness (Kranczioch et al. 2005), language processing (Harris and Morris 2001; Rolke et al. 2001), emotion (Junghöfer et al. 2001; Vroomen et al. 2001), and attention (e.g., Raymond et al. 1992; Chun and Potter 1995; Vogel et al. 1998; Müller and Hübner 2002; Kranczioch et al. 2003). In some of these studies, RSVP paradigms have been combined with measuring electrical brain activity. However, a measure that seems of particular interest in this context (Fell et al. 2002), namely, stimulus-related activity in the gamma-frequency range, has not been addressed in RSVP paradigms so far.

Gamma-band responses (GBRs), i.e., stimulus related power changes at frequencies above 30 Hz, have been observed in a wide variety of experiments, including studies on perceptual feature binding, learning, memory, language, and sensory awareness (e.g., Keil et al. 1999; Pulvermüller et al. 1999; Strüber et al. 2000; Gruber et al. 2002). In particular, GBRs have been shown to be modulated by attention. Thus, animal as well as human studies report increased GBRs for attended visual and auditory stimuli (Tiitinen et al. 1993; Sokolov et al. 1999; Fries et al. 2001; Müller and Keil 2004). An increase in gamma activity has also been

found for target stimuli if subjects had to discriminate between target and non-target stimuli (Yordanova et al. 1997; Herrmann and Mecklinger 2000, 2001; Debener et al. 2003). Accordingly, it has been suggested that GBRs may be of functional relevance for attentional selection and identification of stimuli (Engel and Singer 2001; Niebur et al. 2002; Fell et al. 2003). Recently, Fell et al. (2002) have argued that a suppression of the early evoked gamma-band response (EGBR) might cause a phenomenon known as the *attentional blink*. The attentional blink refers to a behaviorally well described transient reduction of attention, which occurs if more than one target has to be processed in a series of stimuli that rapidly succeed one another, i.e., in an RSVP context (Raymond et al. 1992; Shapiro et al. 1997).

In the present study we focused on the investigation of GBRs in an RSVP context. To this end, stimulus material and presentation frequency were chosen to be similar to those usually employed in attentional blink paradigms, yet stimuli were presented in an oddball sequence. In addition, stimulus size was varied as recently it has been shown that the amplitude of the GBR can be particularly susceptible to stimulus size (Busch et al. 2004). An important practical consequence of this finding is that by using stimuli of suboptimal size, particularly the EGBR might remain undetected. By using large and small stimuli we aimed to rule out this possibility for the present study. We, thus, expected an increase in gamma-band activity for target as compared to standard stimuli, as well as an enhancement of early GBRs for big as compared to small stimuli.

Study 1

Methods

Participants

Participants were recruited at the local university of applied sciences and were paid for participation. The study conformed to the Ethics of the World Medical Association (Declaration of Helsinki) and informed consent was obtained from each participant prior to the start of the experiment. Subjects were required to be free of current or past neurological or psychiatric disorders, to have normal or corrected-to-normal visual acuity, and to have normal color vision. Seventeen subjects participated in the study. Participants were included in the data analysis if they had at least 50 artifact-free trials in each condition. Sixteen subjects (eight female) met this criterion, mean age of these subjects was 24.3 years (SD = 4.1).

Experimental setup

Letter stimuli were presented on a white background for 80 ms with a frequency of 10 Hz. Between two stimuli, the screen remained blank. Target letters ($P = 0.028$) were green, all other letters were black ($P = 0.972$). Two target letters were separated by at least 15 standard or black letters. The stimulus sequence is illustrated in Fig. 1. Subjects were instructed to silently count the targets and to report the count after the end of each block. There were eight blocks in total. In four blocks, stimuli were 1.3° visual angle in height, and 1.0–1.8° visual angle in width (condition small), in the remaining four blocks, stimuli were 4.9° visual angle in height and 3.9–6.8° in width (condition big). The conditions were run in alternating order, and sequence was counterbalanced across participants. In either condition a total of 100 target stimuli (23, 24, 26, or 27 per block) were presented. Experimental blocks lasted between 81 and 100 s, and there was a short break of about 30 s between two blocks.

Electrophysiological recording and data processing

Subjects were seated in an electrically shielded, sound attenuated and dimly lit chamber. The computer monitor used for stimulus presentation was placed outside the chamber, at a distance of about 200 cm in front of the subject. Electroencephalogram (EEG) was recorded using an elastic cap on which 63 Ag–AgCl electrodes were mounted according to an equidistant montage (Easy Cap, FMS Falk Minow Services, Germany). An additional channel was placed below the right eye to monitor eye movements and eye blinks. Nose tip was used as reference, and an electrode positioned below the left mastoid served as ground. EEG was recorded using a high impedance 64 channel NetAmps 200 system (Electrical Geodesics, Eugene, OR, USA). Sensor impedances were kept below 20 kΩ prior to data acquisition. Data were recorded at a sampling rate of 500 Hz with 0.024 μV precision, and analog-filtered from 0.1 to 100 Hz.

Electroencephalogram data processing was performed using EEProbe 3.2 (ANT, Enschede, The Netherlands). Bad channels were linearly interpolated. On an average, less than 0.01% of the channels had to
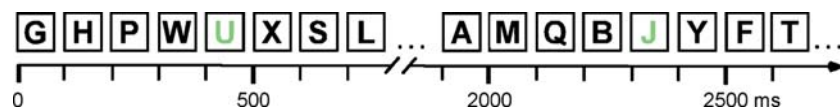

Fig. 1 Example of the stimulus sequence. Rare *green letters* were presented among frequent *black letters*, and stimuli were presented for 80 ms with a frequency of 10 Hz

be replaced. A 631-point notch-filter with −24 dB signal suppression at 50 Hz and −3 dB signal suppression at 48.7 and 51.3 Hz and a 0.5 Hz high-pass filter were applied to remove line-artifacts and slow drifts. Segments of the EEG were marked automatically as artifacts whenever the standard deviation of the signal exceeded 20 μV within a 200 ms interval on the anterior half of the channels. Posterior and occipital channels were not included in the reject algorithm because here, amplitude of the steady-state visual evoked potential (ssVEP) often exceeded the rejection criterion. Results of automatic artifact detection were visually confirmed for all channels. Artifact-free epochs were then derived, lasting from −200 to 800 ms after target onset for analysis of event-related potentials (ERP), and from −300 ms before target onset to 1,000 ms after target onset for wavelet analysis. For either condition, epochs of similar length were also derived for 100 randomly selected standard stimuli. Thus, a total of 100 epochs for target and 100 epochs for standard stimuli could be collected for data analysis.

Analysis of gamma-band activity

Gamma-band activity was quantified by means of wavelet analysis using custom software tools (Max-Planck-Institute of Cognitive Neuroscience, Leipzig, Germany). For mathematical details of the wavelet approach applied here see Herrmann et al. (1999) and Herrmann and Mecklinger (2000). The epoch between −250 and −100 ms before stimulus onset served as prestimulus baseline. Generally, there is a distinction between evoked and induced activity (Tallon-Baudry and Bertrand 1999). The former is, by definition, strictly phase-locked to the stimulus onset, whereas latency of the latter jitters and leads to random phases from trial to trial. For obtaining evoked gamma-band responses (EGBRs), wavelet transform was applied to the averaged potential. To get a measure of induced gamma-band responses (IGBRs), wavelet transform was applied to each single trial. Absolute values were then averaged, which gave a representation of total gamma activity, comprising both evoked and induced gamma-frequency components. By subtracting the evoked activity (wavelet transform of the mean of single trials) from the total gamma activity (mean of single trial wavelet transforms), induced gamma activity was derived.

Grand-mean time–frequency representations of evoked and induced activity were computed using multiple wavelets in frequency steps of 1.253 Hz. For statistical analysis of potential EGBRs, the averaged signal was convolved with a 12-cycle 40 Hz Morlet wavelet ($2\sigma_f$ = 12.7 Hz). This frequency was chosen because the evoked gamma response is usually found to center around 40 Hz (Tallon-Baudry and Bertrand 1999). For statistical analysis of the IGBRs, gamma activity with a center frequency of 70 Hz was extracted, since visual inspection of the time–frequency representations clearly indicated maximum effects in this frequency range. Evoked 70 Hz activity was subtracted from total 70 Hz activity to derive the IGBR. Wavelet analysis with a 12-cycle 70 Hz Morlet wavelet ($2\sigma_f$ = 22.3 Hz) revealed two distinct peaks in activity. For the IGBRs, mean values were derived, time windows ranging between 470–530 ms (time window 1) and 590–650 ms (time window 2), respectively.

IGBRs were statistically analyzed by means of repeated measures ANOVAs. In order to avoid a loss of statistical power (Oken and Chiappa 1986), electrodes were combined into 12 regions of interest (ROI). ROIs were defined as left anterior (LA), central anterior (CA), right anterior (RA), left anterior middle (LAM), central anterior middle (CAM), right anterior middle (RAM), left posterior middle (LPM), central posterior middle (CPM), right posterior middle (RPM), left posterior (LP), central posterior (CP), right posterior (RP). Electrode clusters belonging to each ROI are depicted in Fig. 2. Within factors of the ANOVA were TIME WINDOW (1, 2), SIZE (small, big), STIMULUS (target, standard), LATERALITY (left, central, right), and CAUDALITY (anterior, anterior middle, posterior middle, posterior). For all analyses, Huynh-Feldt correction was applied when necessary (Huynh and Feldt 1976). Corrected P-values are reported with uncorrected degrees of freedom and the epsilon value.

A possible relation between P3 ERP and IGBR was explored by correlating peak amplitudes of the two measures. For the ERP, the 200 ms before stimulus onset were defined as the prestimulus baseline and corrected to 0 μV signal average. For P3, peak amplitude was determined within the 300–550 ms post target onset. For the IGBR, the maximum was determined in a single time window between 400 and 750 ms comprising both ANOVA time windows and allowing for an additional
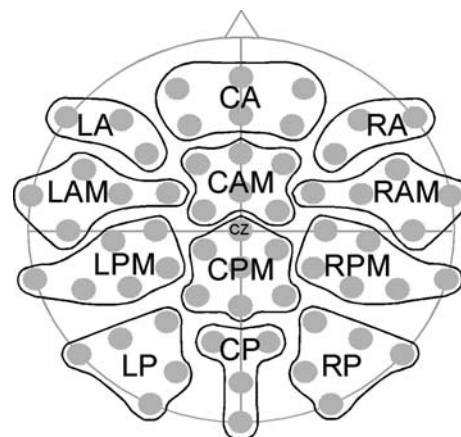

Fig. 2 Electrode clusters formed to define the regions of interest (ROI) used for statistical analysis. ROI labels: *LA* left anterior, *CA* central anterior, *RA* right anterior, *LAM* left anterior middle, *CAM* central anterior middle, *RAM* right anterior middle, *LPM* left posterior middle, *CPM* central posterior middle, *RPM* right posterior middle, *LP* left posterior, *CP* central posterior, *RP* right posterior
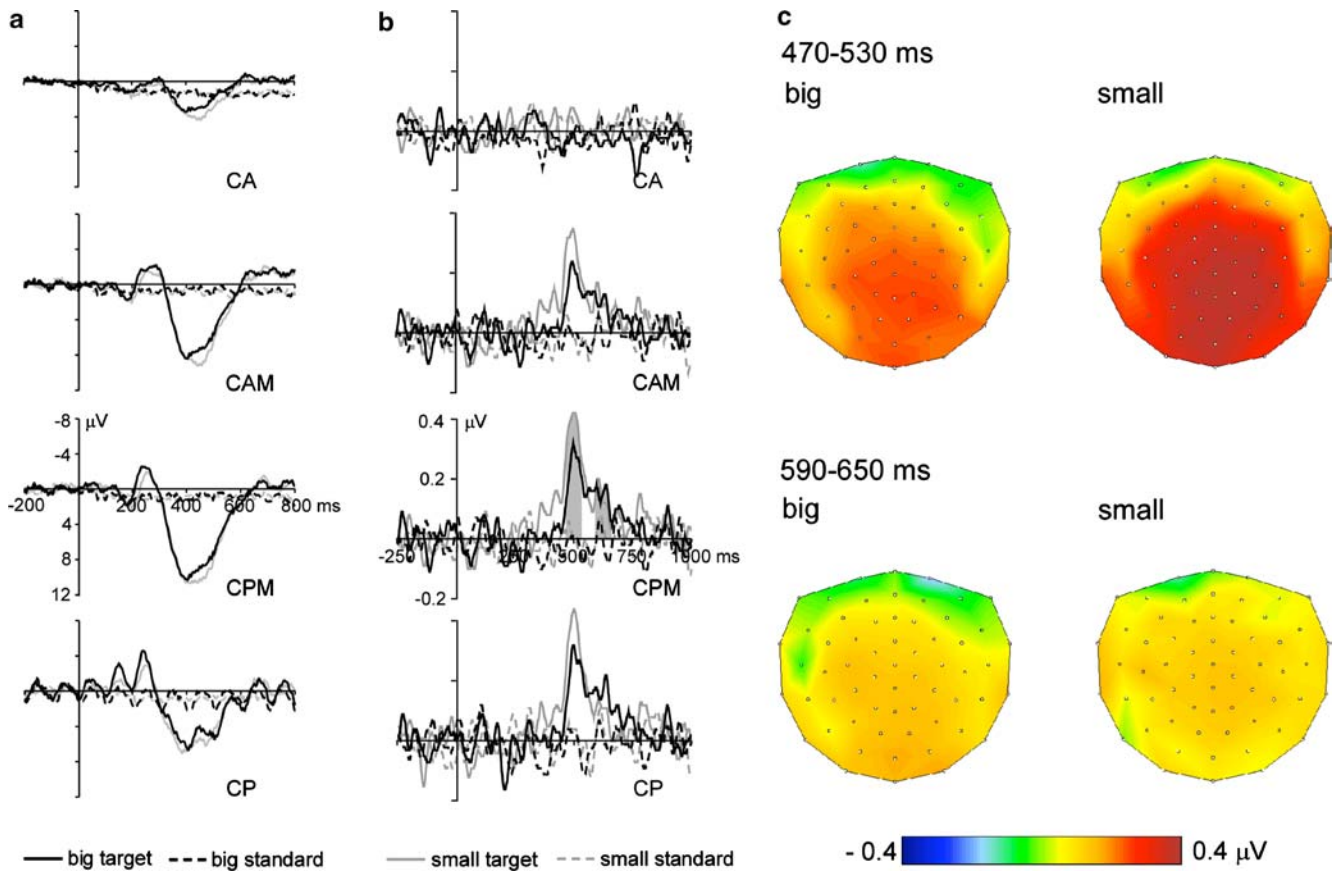
Fig. 3 Event-related potentials and induced gamma-band activity observed in Study 1. **a** Grand-mean ERPs at the four midline-ROIs. For ROI definition, see Methods section. **b** Grand-mean time courses of induced 70 Hz activity at the four midline-ROIs. Time windows as used for statistical analysis are *underlaid in grey* at ROI CPM. **c** Scalp maps of the 70 Hz induced gamma-band response to targets in the time windows 470–530 ms and 590–650 ms
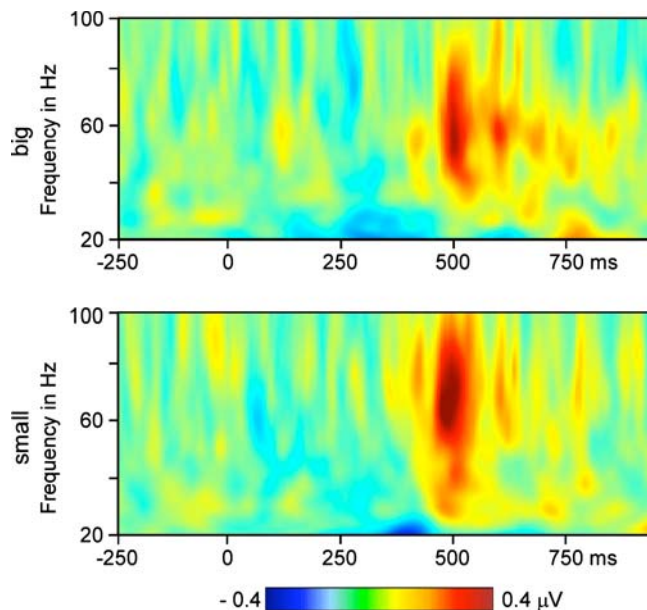

Fig. 4 Time-frequency plots of induced gamma-band activity measured in Study 1. The plots show the activity induced by big (*top*) and small (*bottom*) target stimuli at electrode Cz (ROI CPM), respectively

jitter in single subject peak data. This approach was used to obtain a single IGBR peak value for each subject. Within these time windows, sliding window averages were computed across three successive data points, that is, for 6 ms epochs. Peak amplitudes of P3 and IGBR were defined as the respective maximal value among these averages. Pearson correlations were computed for two electrodes, E34, which is equivalent to CZ (belonging to ROI CPM), and E59, a midline occipital channel (ROI CP). These electrodes were chosen because here amplitudes of P3 (E34) and/or IGBR (E34, E59) were particularly pronounced. To control for inflation of type I error probability due to multiple comparisons, the Bonferroni-Holm (Holm 1979) procedure was applied to *P*-values.

Results

Performance

For each subject, absolute values of the difference between actual number and counted number of targets were derived for each block and then averaged across

condition blocks to obtain a measure of performance. Group mean of this error value was 0.38% for big and 0.29% for small stimuli. That is, on an average, participants counted less than one target too many or too few.

Event-related potentials

Specifically at occipital electrode sites (ROIs LP, CP, RP) the ERP was dominated by the 10 Hz ssVEP (Fig. 3a). The ssVEP was slightly enhanced in amplitude for big as compared to small stimuli. Target stimuli evoked a prominent centro-parietal P3 ERP peaking around 400 ms.

Gamma-band responses

Wavelet analysis of the averaged signal did not reveal a distinct increase in evoked 40 Hz activity in response to target stimuli. Therefore no statistical analyses were performed on the EGBR.

Analysis of induced gamma activity revealed a late increase for target as compared to standard stimuli. As can be seen in the grand mean time–frequency plot, the frequency of the IGBR ranged between 30 and 90 Hz (Fig. 4). Figure 3b shows ROI time courses of induced 70 Hz activity. In central, posterior, and occipital ROIs, the IGBR showed two distinguishable peaks that were considerably enhanced for target as compared to standard stimuli. Figure 3c shows scalp maps of the 70 Hz IGBR in the two time windows, reflecting the occipito-parietal distribution of the IGBRs.

Repeated measures ANOVA of the 70 Hz IGBR with the factors TIME WINDOW, STIMULUS, SIZE, CAUDALITY, and LATERALITY revealed a main effect of the factor STIMULUS ($F(1,15) = 8.35$, $P \leq 0.01$), indicating that the IGBR was larger for target as compared to standard stimuli irrespective of time window and stimulus size. None of the main effects of the factors TIME WINDOW and SIZE reached significance, nor did any interaction that comprised a combination of the factors STIMULUS, SIZE, or TIME WINDOW. Additional analyses of the significant interaction of the factors STIMULUS, CAUDALITY, and LATERALITY ($F(6,90) = 3.27$, $P \leq 0.016$, $\varepsilon = 0.69$) indicated that the IGBR to target stimuli had an occipito-parietal distribution (CAUDALITY $F(3,45) = 11.75$, $P \leq 0.01$, $\varepsilon = 0.43$; LATERALITY $F(2,30) =$
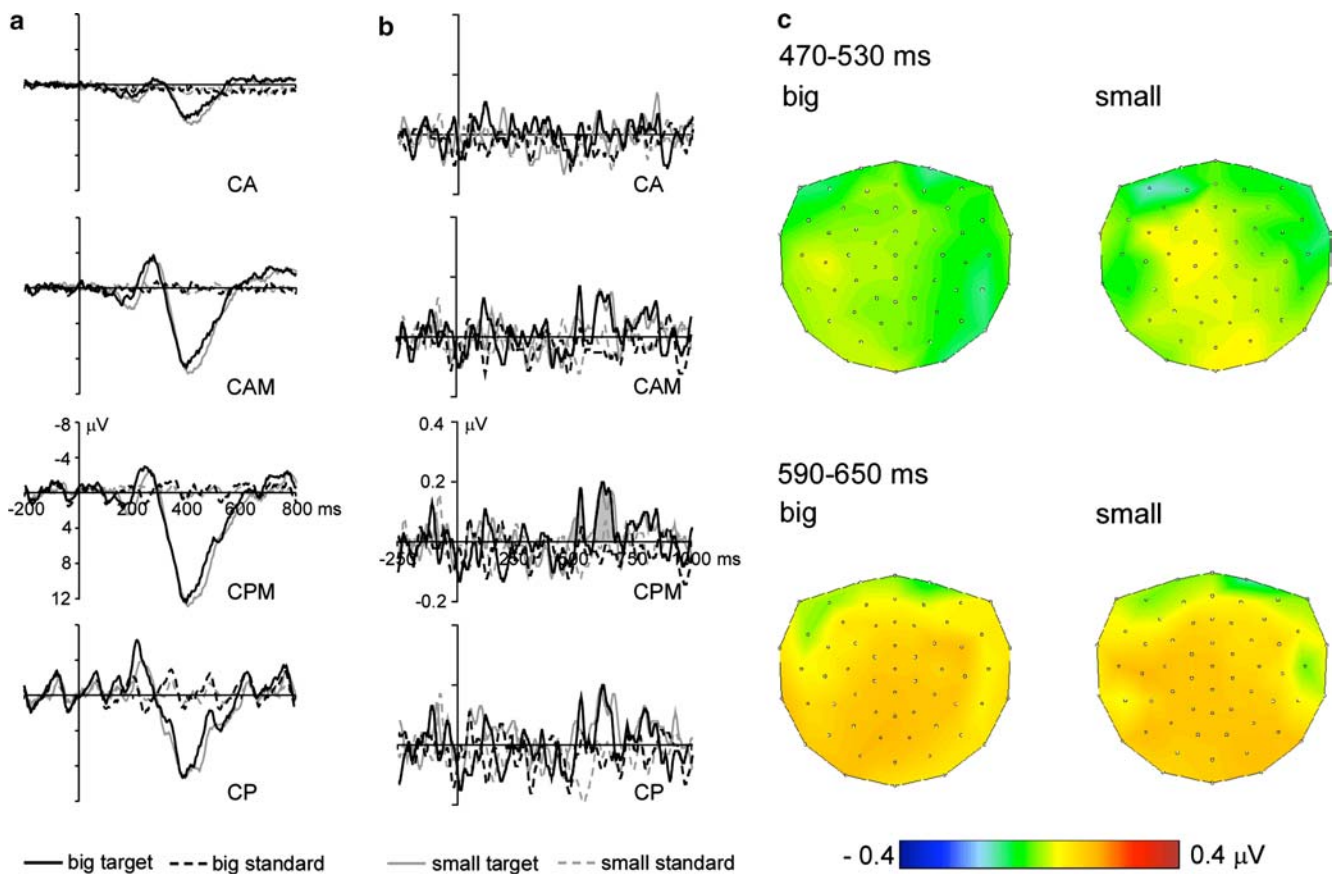

Fig. 5 Event-related potentials and induced gamma-band activity observed in Study 2. **a** Grand-mean ERPs at the four midline-ROIs. For ROI definition, see Methods section. **b** Grand-mean time courses of induced 70 Hz activity at the four midline-ROIs. Time windows as used for statistical analysis are underlaid in grey at ROI CPM. **c** Scalp maps of the 70 Hz induced gamma-band response to targets in the time windows 470–530 ms and 590–650 ms

5.19, $P \leq 0.02$, $\varepsilon = 0.98$; CAUDALITY x LATERLITY $F(6,90) = 3.02$, $P \leq 0.05$, $\varepsilon = 0.50$).

Pearson correlations for P3 and IGBR peak amplitudes were calculated for big and small stimuli. Because ANOVA did not reveal an effect of the factor TIME WINDOW on the IGBR, peak amplitude was determined for both time windows together. Neither at the central channel (E34, corresponding to Cz) nor at the occipital channel (E59) were correlations significant at the Bonferroni-Holm corrected P-values.

Study 2

As described above, our first study did not provide any evidence for an EGBR with target or standard stimuli. A possible explanation for this null-finding might be that with a stimulus presentation rate of 10 Hz and the resulting stimulus onset asynchrony (SOA) of 100 ms, the standard stimulus following the target coincided with the time point at which the EGBR response would have been expected (i.e., 100 ms post stimulus). Under this condition the EGBR usually measured in the scalp EEG might have been disrupted or masked by the signal generated by the standard stimulus. To investigate this hypothesis and to test whether the finding of a late target-related IGBR could be replicated, a follow-up study was conducted in which the stimulus presentation rate was reduced to 7.1 Hz. By this, the RSVP characteristic of the task was maintained, yet stimulus onset asynchrony was increased to 140 ms.

Methods

For Study 2, 29 new participants were recruited from the population described above. Participants were included in data analysis if they had at least 50 artifact-free trials in each condition. Sixteen subjects (nine female) met this criterion, and the mean age of these subjects was 22.8 years (SD = 3.8). The experimental setup was identical to Study 1 with the exception that in Study 2, letter stimuli were presented at a frequency of 7.1 Hz. Each stimulus was presented for 80 ms, and between two successive stimuli, the screen remained blank. Experimental blocks lasted between 113 and 140 s, and there was a short break of about 30 s between two blocks. All procedures for electrophysiological recording, data preprocessing and data analysis were identical to the ones used in Study 1.

Results

Performance

Group mean of the error value (see Study 1 for details) was 0.24% for big and 0.56% for small stimuli. That is,

on an average and similar to Study 1, participants counted less than one target too many or too few.

Event-related potentials

Specifically at occipital electrode sites (ROIs LP, CP, RP) the ERP was dominated by the 7.1 Hz ssVEP (Fig. 5a). The ssVEP was slightly enhanced in amplitude for big as compared to small stimuli. Target stimuli evoked a prominent centro-parietal P3 ERP peaking around 400 ms.

Gamma-band responses

Again, wavelet analysis of the averaged signal did not reveal a distinct increase in evoked 40 Hz activity in response to target stimuli. Therefore no statistical analyses were performed on the EGBR.

Repeated measures ANOVA of the 70 Hz IGBR with the factors TIME WINDOW, STIMULUS, SIZE, CAUDALITY, and LATERALITY revealed main effects of the factors STIMULUS ($F(1,15) = 7.92$, $P \leq 0.013$) and TIME WINDOW ($F(1,15) = 8.01$, $P \leq 0.013$), and a significant STIMULUS x TIME WINDOW interaction ($F(1,15) = 12.14$, $P \leq 0.0003$). As indicated by subsequent pair-wise T-tests amplitude of the IGBR was only significantly larger for target as compared to standard stimuli during the second time window ($t(15) = 4.01$, P(one-tailed) ≤ 0.0006, not during time window 1 ($t(15) = 1.31$, P(one-tailed) ≤ 0.105. Neither the main effect of the factor SIZE nor any interaction comprising this factor reached significance. Significant interactions of the factors STIMULUS and CAUDALITY ($F(3,45) = 7.1$, $P \leq 0.001$, $\varepsilon = 0.86$), and STIMULUS and LATERALITY ($F(2,30) = 7.19$, $P \leq 0.004$, $\varepsilon = 0.86$) indicated that the IGBR to target stimuli had its maximal values over parietal and occipital scalp sites and along the midline ROIs. Figure 5b shows ROI time courses of induced 70 Hz activity, scalp maps of the 70 Hz IGBR in the two time windows analyzed are depicted in Fig. 5c.

Similar to Study 1 a single peak amplitude was determined for the IGBR. Pearson correlations of peak amplitudes of P3 and IGBR were calculated for big and small stimuli. Again, neither at the central channel (E34, corresponding to Cz) nor at the occipital channel (E59) were correlations significant at the Bonferroni-Holm corrected P-values.

Discussion

The aim of our studies was to investigate gamma-band activity under RSVP conditions. No increase in phase-locked gamma activity following target presentation was observed. However, target stimuli were clearly followed by a late induced response in the gamma-band. In a first

time window (470–530 ms), this increase was only significant for a stimulus presentation rate of 10 Hz (Study 1). In the second analyzed time window (590–650 ms) the induced response was significant for presentation frequencies of 10 Hz (Study 1) as well as 7.1 Hz (Study 2). The IGBR had a midline, parieto-occipital maximum. Peak amplitudes of the IGBR and of the P3 ERP which was also evoked by target stimuli were not correlated.

Evoked gamma-band responses

Typically, in the visual domain the EGBR occurs around 100 ms post target onset and centers at a frequency of about 40 Hz (Tallon-Baudry and Bertrand 1999). No such EGBR was observed in the present studies. The lack of this early EGBR to target stimuli is in partial conflict with previous research: While some visual oddball studies also did not observe an increased EGBR to target as compared to non-target stimuli (Sannita et al. 2001; Watanabe et al. 2002), other studies in the visual domain did (e.g., Tallon-Baudry et al. 1996; Herrmann et al. 1999). At present, it is unclear whether the EGBR reflects primarily stimulus-related or task-related aspects. Several studies have provided clear evidence for the latter. Debener et al. (2003) report that in an auditory novelty-oddball experiment, the EGBR was increased for target as compared to non-target frequent and task-irrelevant novel stimuli. This finding is in accordance with earlier findings like those of Herrmann et al. (1999, 2001), who also demonstrated that the EGBR to visual stimuli is sensitive to attention.

Considering these studies, it may seem surprising that our data do not show evidence for an EGBR to targets. Several factors might contribute to this. Typically, experiments investigating evoked gamma-band activity in the visual domain use stimulus presentation frequencies of 1 Hz and below. By contrast, in the present study, stimulus presentation rates were 10 and 7.1 Hz, and thus, at least with respect to Study 1, the stimulus following the target coincided with the time point at which the EGBR response would be expected. The possibility that by this temporal coincidence, the EGBR had been disrupted or masked was tested by presenting stimuli with an SOA of 140 ms (Study 2). Yet, after this reduction of speed of presentation also no EGBR was observed.

On the other hand, it cannot be ruled out that there was intracranial gamma activity which could not be recorded with the EEG due to prominent activity in the respective frequency of stimulus presentation. Both, the occipital ssVEP and the EGBR have been suggested to be generated in primary visual areas (Hillyard et al. 1997; Rager and Singer 1998; Bertrand and Tallon-Baudry 2000; Herrmann 2001; Krolak-Salmon et al. 2003; Pastor et al. 2003; Busch et al. 2004). Hence, generators of the high-amplitude ssVEP and the low-amplitude EGBR might substantially overlap and, as a consequence, the currents contributing to the ssVEP measured at the scalp may mask the currents associated with the EGBR. Additional experiments will be needed to explore whether EGBRs emerge at still lower stimulus presentation frequencies, but with otherwise unchanged experimental properties. Thereby, conclusions about an upper limit for stimulus presentation rates in studies investigating EGBRs might be drawn.

Alternatively, the oddball task applied here might not have been complex enough to evoke an EGBR sufficiently large to be detected in the EEG. In their 'match-and-utilization-model' Herrmann et al. (2004) suggest that the EGBR reflects the rapid matching of bottom-up signals with memory contents. In the present oddball design, this match might not have been sufficiently resource demanding. That is, the target-defining stimulus attribute was always evident from the prevailing context. Moreover, for people with unimpaired color vision, the differentiation between 'green' and 'black' obviously is very easy, as shown by the low error rates in our subjects. Thus, in the present studies, an elaborate memory matching process may have been superfluous, and accordingly the EGBR may have remained undetectable for the EEG.

Induced gamma-band responses

Strong target effects were observed for the IGBR. The increase in induced gamma activity occurred later than the target P3, i.e., at a time when the P3 was already descending (time window 1, 470–530 ms) or had almost reached baseline levels (time window 2, 590–650 ms). At least for the IGBR in the first time window, it might be argued that the increase in high-frequency activity could be a by-product of the steeply trailing edge of the P3. Then, however, one would expect a similar increase in high-frequency activity for the rising edge of the P3, which was not the case. In addition, a correlation between the P3 amplitude and the magnitude of the IGBR would be expected, which we also did not observe. Nonetheless, it seems remarkable that the IGBR coincides with P3 decay, specifically as it has been suggested that gamma-band activity might be suppressed by the P3 (Fell et al. 2002). Indeed, for the auditory modality, it has been reported that gamma activity occurs after but not during the P3 (Marshall et al. 1996; Fell et al. 1997). On the other hand, studies in the visual as well as auditory domains found the opposite pattern (Basar-Eroglu and Basar 1991; Sannita et al. 2001; Watanabe et al. 2002).

The IGBR was observed to be stronger for a presentation rate of 10 as compared to 7.1 Hz. Because subjects in Study 1 and Study 2 were drawn from the same population and groups were comparable with regard to age, gender, and education, it seems unlikely that this difference reflects preexisting inter-individual differences, even though this cannot fully be ruled out. Rather, differences are more likely to reflect differences

across studies resulting from experimental variables, i.e., presentation frequency. It seems conceivable that detection of targets during the higher presentation frequency required more mental effort than during the lower frequency, which in turn might be reflected by differences in the IGBR. Due to ceiling effects in task performance, this assumption cannot be tested for the present data, yet indirect support is provided by a study investigating size of the attentional blink effect with different stimulus presentation frequencies of 6.67, 7.41, 8.33 and 9.52 items per second, respectively (Arnell and Jolicoeur 1999). The magnitude of the attentional blink increased linearly with increasing presentation rate from about 25% to about 60% missed targets. Thus, processing demands were apparently lower or interference between target and distracter stimuli was weaker when presentation rate was slower.

As the IGBR observed in the present studies was unique for target stimuli, it most probably reflects aspects of attentive target processing. The difference in latencies of IGBR and P3, their difference in topography, and also the lack of correlation between their peak amplitudes suggest that the IGBR reflects aspects of target processing beyond those associated with the P3. With regard to the P3, Donchin and Coles (1988) have suggested that the P3 is a correlate of the updating of a model of the environment held in working memory, while Verleger (1988) proposed that the P3 might reflect context closure or the termination of a perceptual epoch. With respect to the late IGBR, the 'match-and-utilization-model' of gamma activity (Herrmann et al. 2004) suggests an interpretation that may well fit our observations. As part of this model, it has been proposed that the IGBR might be a signature of the utilization of information for coordinating behavioral performance, redirecting attention, or storage in memory. In the present case, utilization might be recall of the current count of targets held in working memory and the integration of the just detected target for later report. This interpretation would also account for the observation that the IGBR followed the P3 and that it was found to be smaller in Study 2, where presentation frequency and thus presumably task difficulty as well were reduced. In support of this interpretation, IGBRs occurring as late as in the present study or even later have been associated with explicit recall or rehearsal processes (Tallon-Baudry et al. 1998; Gruber et al. 2001). At this point, however, this interpretation remains speculative.

Conclusion

The present findings demonstrate that in a visual oddball and RSVP context, the processing of target stimuli is accompanied by a significant modulation of induced responses in the gamma-band. The results fit well with the 'match-and-utilization-model' model proposed by Herrmann et al. (2004), suggesting that the late gamma-band response observed here may constitute a temporal signature of the neural interactions leading to updating of working memory.

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