The present study assessed the effects of stimulus task-relevance and certainty on early and late 40 Hz (γ) band responses (GBRs) in humans. Auditory GBRs of nine young adults were recorded in passive listening, simple reaction task, and choice-reaction task (target probability = 0.5) conditions and evaluated in three consecutive post-stimulus periods (0–120, 120–250, 250–400 ms) corresponding to the serial occurrence of γ oscillation bursts. Amplitude and phase-locking of GBRs within these bursts were analysed separately at the level of single sweeps by applying a method that allows the independent quantification of between-sweep synchronization. Major results showed that the effects of stimulus certainty and task relevance on single response amplitude were specific and different from the effects on the phase-locking. The functional involvement of the early and late auditory γ responses was distinct: early auditory gamma band responses appear primarily associated with focused attention, while the late γ responses vary with motor-task relevance. It is concluded that along with power measures, the stability of phase-locking of γ band responses should be regarded as a functionally meaningful parameter that varies with processing demands and recording site.

Key words: Cognitive processes; EEG; Event-related brain potentials (ERPs); Gamma band response (GBR); Oscillatory brain potentials; Phase-locking

Introduction

Many findings from different levels of investigation, from neuronal measurements to global electroencephalographic (EEG) and magnetoencephalographic (MEG) recordings, strongly indicate that γ (or 40 Hz) oscillations are functionally relevant to information processing in the brain.1 EEG γ band activity has been associated with a variety of fundamental perceptual and cognitive brain processes, including feature binding,2 temporal processing3 and cognitive verbal processing;4 however, the functional role of γ activity is not fully understood. Recent findings show that functionally meaningful event-related γ oscillations may be strongly or loosely phase-locked to stimulus, may occur early or late after stimulus presentation, and may vary in frequency within the γ range (30–70 Hz).2,5 Hence, further analysis of these phenomena may contribute to elucidate the functional role of γ band activity.

In the auditory modality, simple tone bursts elicit transient EEG γ band responses (GBRs) that are strongly phase-locked to stimulus in the first 100–120 ms. Such GBRs can be recorded from various cortical and deep brain structures of animals6,7 and from the scalp in humans,8,9 which implies that auditory γ band oscillations may reflect sensory processing. However, no tonotopic presentation of the MEG γ band field in the auditory cortex has been found.10 It has also been demonstrated that the power of the early synchronized GBR is larger to attended than to unattended auditory stimuli and is thus associated with selective attention mechanisms in humans.11 The power of the early GBR also has been related with integrative sensory-motor mechanisms as it is enhanced in subjects who intensively focus their attention to motor response preparation.12 It is noteworthy that auditory GBRs later than 120 ms also correlate with attention to auditory targets13 and sensorimotor integration.12,14 It is not known, however, whether the involvement of early and late GBRs in the processing of attended motor-task stimuli is similar.

One major problem in approaching this question arises from the fact that the early GBRs are well synchronized with stimulus, whereas the late γ oscillations are weakly phase-coupled with stimulus and can not be detected in averaged potentials.2,10,12 Furthermore, in the averaged potential, amplitude and phase-locking effects are confounded and cannot
be evaluated separately. Usually, only power variations of single GBRs are analysed. However, the phase-locking of event-related oscillations from other frequency bands (α and θ) has been demonstrated to vary with processing conditions independently of amplitude/power alterations. Thus, apart from amplitude differences, changes in the stability of phase-locking of GBRs may be suggested to reveal specific functional aspects of the γ band activity during stimulus processing in task conditions.

The present study was designed to analyse in a systematic manner the effects of two independent task variables, stimulus certainty and motor-task relevance, on the early and late auditory responses in humans. Stimulus certainty was chosen as a variable that can modify expectancy or focused attention to stimulus. To study motor-task effects, high- and low-certainty stimuli differed in that they required or not motor responding. In addition, it was aimed to assess phase-locking independently of amplitude effects by quantifying the between-sweep synchronization of event-related γ oscillations at the level of single sweeps. Thus, the major questions addressed in the present work were: (1) Do stimulus certainty and motor-task relevance have independent effects on event-related γ activity? (2) Are these effects specific for γ response amplitude and phase-locking? and (3) Are these effects specific for early and late γ band responses?

Materials and Methods

EEG was recorded at Fz, Cz, and Pz sites with linked mastoids as reference in nine healthy volunteers (five female) aged 22–25 years. The stimuli were tones with intensity of 60 dB SPL and duration of 50 ms (r/f 10 ms). Inter-stimulus intervals varied randomly between 3.5 and 5.5 s. The recording conditions were: a passive listening condition (PLC), in which 50 identical 800 Hz tones were used (probability \( p = 1 \)), a simple reaction task (SRT), in which the same stimuli (\( p = 1 \)) required as fast as possible button pressing, a choice-reaction task (CRT), in which 800 Hz target (CRT-T) and 1200 Hz non-target (CRT-NT) tones (total = 100) were presented randomly with equal probabilities (\( p = 0.5 \)). The low tone required fast and accurate button pressing. Subjects kept their eyes closed and responded to the SRT and CRT targets with their right hand.

The cut-off frequencies of the EEG amplifiers were 0.1 and 120 Hz. Analysis epochs of 1024 ms before and 1024 ms after stimulus were sampled with a frequency of 250 Hz. Any EEG or EOG trial exceeding ± 50 μV was excluded from further analysis and 40–42 artifact-free sweeps of each stimulus type were used. Event-related power spectra were computed for the post-stimulus epochs by means of Fast Fourier Transform (FFT). Figure 1 shows that the spectral power in the higher frequency ranges (60–80 Hz) decreases for each stimulus type, which indicates that no muscle activity is present in the EEG data. Single EEG trials were digitally band-pass filtered with zero phase shift in the γ frequency range (band width 30–45 Hz, 12 dB/oct, roll-off negative).

To determine the post-stimulus time epochs in which both phase-locked and non-phase-locked γ responses developed, the envelopes of single EEG trials filtered in the 30–45 Hz range were extracted by means of the Hilbert transform and averaged for each subject, stimulus type, and electrode. As illustrated in Figs 2 and 3a, γ oscillation bursts occurred in consecutive time periods, with envelope peaks being mostly discernible at the frontal site. Latencies of three envelope peaks detected in the first 500 ms after stimulation were measured. Group means (± s.d.) were 53 ± 21.5 ms, 182 ± 29.3 ms and 312 ± 32.3 ms. The time windows used for further analysis

![FIG. 1. Power spectra of post-stimulus EEG in the passive listening condition (PLC), simple reaction task (SRT), and choice reaction task to targets (CRT-T) and non-targets (CRT-NT). Curves are shifted to show the monotone decrease in the power spectrum. Frequency range of analysis is marked.](image-url)
were determined by calculating the mean peak latency values of envelopes ±2 s.d., and were 0–120 ms (early), 120–250 ms (middle) and 250–400 ms (late), respectively. For each time window, amplitude and phase-locking of GBRs were analysed.

To assess the amplitude of phase-locked activity, the maximal peak-to-peak amplitude of the averaged GBR was measured. To evaluate the amplitude of both phase-locked and non-phase-locked oscillations, the maximal peak-to-peak amplitudes of single-sweep GBRs were measured and individual means were calculated for each stimulus type and electrode.

For a quantitative evaluation of the phase-locking, a modification of the single sweep wave identification (SSWI) method was applied. Briefly, extremes (minima and maxima) were identified in each filtered (30–45 Hz) single sweep. Maxima were replaced with (+1) and minima with (−1). The latency positions and coded amplitudes were stored. For each 12 ms time interval (nearly one half period of the 40 Hz rhythm), a summation of the coded extremes was performed across trials. The values obtained after summation were assigned to a histogram bar (SSWI histogram). Thereafter, the SSWI histogram was normalized by dividing the bar values by the number of single sweeps included in the analysis. Typical SSWI histograms reflecting the phase-locking of GBRs are illustrated at the bottom of Fig. 2. For statistical analysis, the absolute bar values of the normalized SSWI histogram were summed along the time axis for each time window separately. Thus, information is extracted about the strength of single GBR phase-locking in the successive post-stimulus periods corresponding to the serial γ bursts. The sums were determined for each subject, stimulus type, and electrode. Similar measurements were made for a reference period in the pre-stimulus epochs. Possible effects of frequency variations on the phase-locking parameter were controlled by measuring and analysing statistically the mean number of the identified extremes in each time window.

Figure 2 shows an example from the PLC and SRT conditions to demonstrate that the appearance of γ bursts may be accompanied by either strong or weak phase-locking of the γ waves within these bursts. In the early (0–120 ms) period, enhanced and phase-locked γ waves are observed for both stimulus types. Although envelope peaks are seen in the middle (120–250 ms) time windows of both envelope curves, the SSWI histogram of the GBR in PLC shows no phase-locking in this latency range, while a strong phase-locking is evident for the 120–250 ms epoch in SRT. For the 250–400 ms time window a synchronization of single γ oscillations is seen in both the PLC and SRT potentials.

Statistical analysis: Single-sweep measures of amplitude and phase-locking from each time window were subjected to MANOVAs with three within-subjects factors: task [targets (SRT and CRT-T) vs non-targets (PLC and CRT-NT)], certainty [high (PLC and SRT) vs low (CRT-NT and CRT-T)], and electrode (Fz, Cz and Pz). Maximal peak-to-peak amplitude of averaged GBRs was also subjected to the same analysis. For all MANOVAs the degrees of freedom were corrected by using the Greenhouse-Geisser procedure. The original df and corrected probability values are presented in the results. The phase-locking of GBRs in each time window was compared with the level of the pre-stimulus γ activity phase-locking by means of non-parametric Wilcoxon-Wilcoxon test.
Results

Figure 3a illustrates grand average upper envelopes of event-related γ activity. Although a decrease in envelope amplitude is seen after 100–120 ms, the presence of envelope peaks indicates that repeatable γ bursts occurred in the later post-stimulus epochs.

0–120 ms: At each lead and for each stimulus, the phase-locking of the GBR within 0–120 ms was significantly stronger than the pre-stimulus level \((p < 0.001)\). The phase-locking of early GBRs did not vary with stimulus certainty and task relevance. Single GBR amplitudes tended to be larger to targets than to non-targets (task: \(F(1,8) = 4.36, p = 0.07\)). As shown in Fig. 3b, the effect of task relevance reached significance only for the highly predictable targets in the SRT (certainty \(\times\) task: \(F(1,8) = 5.42, p < 0.05\)). Averaged GBR amplitude did not depend on task variables and was maximal at Cz and Fz (electrode: \(F(2,16) = 11.02, p < 0.01\)).

120–125 ms: The phase-locking did not differ from the pre-stimulus level. Single-response amplitude within 120–250 ms did not depend on the examined factors. In contrast, as illustrated in Fig. 4a, the phase-locking was significantly stronger for targets than for non-targets (task: \(F(1,8) = 11.94, p < 0.01\)). Accordingly, amplitude of averaged GBR was larger to targets (task: \(F(1,8) = 21.08, p < 0.01\)).

250–400 ms: In the late period, no significant main effects of the examined variables were revealed for the amplitude of averaged and single-sweep GBRs. As illustrated in Fig. 4b, over the parietal area, targets produced a significantly stronger phase-locking than non-targets (task \(\times\) electrode: \(F(2,16) = 5.27, p < 0.05\)). The number of extrema identified for each time window did not vary with task, stimulus certainty, and electrode, which excludes that the effects on phase-locking are due to variations in GBR frequency.

Discussion

Analysis of single-sweep envelopes showed that during auditory stimulus processing event-related γ oscillations occurred in serial bursts peaking within 0–120, 120–250 and 250–400 ms. Serial modulations of γ power with similar latencies have been described in previous studies. \(^{12,13}\) In the present report, the effects of two independent task variables (stimulus certainty and task-relevance) on single-γ responses within these bursts were assessed. The separate analysis of amplitude and phase-locking helped to obtain the following new results: first, the amplitude and phase-locking of γ oscillations manifest independent functional responsiveness; second, the functional involvement of the early and late auditory γ responses is specific: the early γ oscillations depended on the integrative effect of stimulus certainty and motor task-relevance, whereas the late γ oscillations varied with motor-task relevance.

Early γ band activity: In addition to the evidence from averaged GBRs, \(^{8-10,12,13,20}\) the separate analysis of phase-locking proved that the early GBR was strongly synchronized with stimulus. Nevertheless, early GBR phase-locking did not differ between the processing conditions related to stimulus certainty and task relevance. By contrast, γ response amplitude was significantly larger for highly expected (predictable and relevant) motor-task stimuli, which was not evident from average data analysis. Hence, an amplitude increase of the early GBR appears specifically related with high expectancy and focused attention to response preparation. This finding is consistent with previously reported associations of γ band EEG power with states of high arousal, alertness, and focused attention. \(^{12,14,21}\) Increased γ band power has also been observed over localized sites of the primary motor cortex ~200 ms before finger movement, \(^{15,22}\) which makes it possible that activity related to motor preparation may have contributed to the present results from the SRT condition (mean RT 240 ms). However, low-certainty targets (mean RT 390 ms) also produced larger amplitudes than did non-targets (Fig. 3a,b). Hence, motor-task stimuli expected with either high or low certainty can enhance the amplitude of the early GBR. This indicates that a focused attention mechanism of...
controlled processing rather than motor-related activity is likely to have increased the amplitude of the early (phase-locked and non-phase-locked) GBRs. Given the role of cortico-thalamo-cortical systems in the activation of task-specific cortical areas, the enhancement of both phase-locked and non-phase-locked early GBRs may be regarded in the context of increased recurrent thalamo-cortical activation involved in the generation of neocortical \( \gamma \) band activity in man. The strong and task-independent phase-locking of the early GBR at the three midline electrodes implies that irrespective of \( \gamma \) power variations substantiating functionally relevant processes, sets of stable and well defined constraints are tuned to oscillate synchronously in the \( \gamma \) range at distant cortical locations, which may subserve the dynamic linkage among distant cortical areas in order to integrate auditory percepts.

**Late \( \gamma \) band activity:** In line with previous reports on averaged data, the present results show that the late \( \gamma \) band activity can be characterized as weakly phase-locked to stimulus. In spite of this, it is noteworthy that the phase-locking of the late \( \gamma \) activity was associated with motor task-relevance. This finding is of interest, because only amplitude (power) effects have been previously described for the late \( \gamma \) band activity in task conditions. The separate quantification of phase-locking performed here showed that within 120–400 ms after stimulation with both predictable and unpredictable targets produced more strongly phase-locked late GBRs relative to non-targets. It is not likely that motor programming and execution are responsible for this effect. First, motor response preparation and execution affect the power of \( \gamma \) band activity. In the present study, no amplitude differences related to the motor task were found for the late GBRs. Second, motor-related activity should have produced significant task \( \times \) certainty interactions in each of the 120–250 and 250–400 ms windows because of the significant difference in reaction times in the SRT (mean 240 ms) and CRT (mean 390 ms), but no such interactions were found. Third, the task effect on \( \gamma \) phase-locking did not differ between the recording sites for the 120–250 ms period and was focused to the parietal brain area for the 250–400 ms period. The parieto-temporal brain areas have been found to be predominantly engaged when high demands to sensory-cognitive processing are imposed. The possible contribution of muscle activity to the observed effects can also be ruled out because a decrease of spectral power was observed for the 60–80 Hz range. In addition, no significant effect was found for late \( \gamma \) response amplitudes that should be most sensitive to possible muscle activity contribution. In contrast, a significant effect was obtained for the phase-locking that is insensitive to random or non-locked signals like the EMG. There was also no significant task \( \times \) certainty interactions for the amplitude, which was to be expected if muscle activity has contributed to the recorded \( \gamma \) activity, due to the significantly different reaction times. The shifts in topography effects can not be explained with contamination from EMG. Therefore, the observed differences in the between-sweep synchronization of \( \gamma \) responses may be primarily attributed to the processing demands of the motor task-relevance. The stronger and site-specific phase-locking of the late \( \gamma \) response to targets may therefore reflect a more general cognitive process related to an endogenous resetting of selected and defined networks during motor-task performance. It will be an object of a future study to explore whether it is the motor response integration, the task-relevance per se, or both, that cause a stronger phase-locking of late \( \gamma \) responses to targets relative to non-targets.

**Conclusion**

The present results indicate that early auditory \( \gamma \) band responses appear primarily associated with focused attention, while the late \( \gamma \) responses vary with motor-task relevance. The specific functional involvement of early and late event-related \( \gamma \) activity was revealed after single response amplitude and phase-locking were analysed separately, which may not be detected in average data. Thus, along with power measures, the stability of phase-locking of \( \gamma \) band responses should be regarded as a functionally meaningful parameter varying with processing demands and recording site.

**References**


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