# Developmental event-related gamma oscillations: effects of auditory attention

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## Abstract

This study describes maturational changes in topographical patterns, stability, and functional reactivity of auditory gamma band (31–63 Hz) responses (GBRs) as brain electrical correlates relevant for cognitive development during childhood. GBRs of 114 healthy children from 9 to 16 years were elicited in an auditory focused attention task requiring motor responding to targets, and analyzed by means of the wavelet transform (WT). The effects of age and task variables (attended side and stimulus type relevance) were examined for GBR power and phase-locking within 120 ms after stimulation. Similar to the spontaneous gamma band power, the power and phase-synchronization of GBRs did not depend on the age. However, the functional reactivity of GBRs at specific locations changed in the course of development. In 9–12-year-old children, GBRs at frontal locations were larger and better synchronized to target than to nontarget stimulus type, and were larger over the left hemisphere (contralateral to the responding hand), thus manifesting sensitivity to external stimulus features and motor task. In 13–16-year-old adolescents, GBRs at parietal sites were enhanced by active attending to the side of stimulation, thus being associated with a maintenance of attentional focus to stimulus location. The results indicate that (i) specific aspects of task-stimulus processing engage distinct spatially localized gamma networks at functionally relevant areas, and (ii) the neuronal substrates of gamma band networks and the ability to synchronize them in relation to task-specific processes are available in all age groups from 9 to 16 years. However, the mode and efficiency with which gamma networks can be entrained depends on the age. This age-dependent reactivity of GBRs to different task variables may reflect a transition in processing strategies emerging at approximately 12–13 years in relation to the maturation of cognitive and executive brain functions.

## Introduction

Recent findings from neuronal, electroencephalographic (EEG), and magnetoencephalographic (MEG) measurements indicate that fast oscillations in the gamma frequency range (30–70 Hz) are associated with basic aspects of brain functioning such as conscious perception, feature and temporal binding, attention, and memory (Steriade *et al.*, 1990; Pantev *et al.*, 1994; Basar-Eroglu *et al.*, 1996; Pulvermüller *et al.*, 1997; Singer, 1998; Tallon-Baudry & Bertrand, 1999; Traub *et al.*, 1999; Sannita, 2000). Neurocognitive development of children is accompanied by substantial alterations in neural substrates and higher brain functions (Piaget, 1970; Mussen *et al.*, 1984; Gazzaniga *et al.*, 1998) that have been correlated with gamma band activity in adults. Hence, age differences in event-related fast frequency oscillations can be expected to occur during cognitive task processing in children, but such effects have not been demonstrated so far. Because knowledge of whether and how functional gamma oscillations may vary from childhood to adulthood is highly relevant for both basic and applied neuroscience, the major objective of the present study was to analyze developmental changes in event-related gamma band EEG activity during cognitive task performance.

In humans, different types of gamma EEG activity have been identified to emerge after external stimulation. Event-related gamma oscillations may be strongly or loosely phase-locked to stimulus onset, may occur early or late after stimulus presentation, and may also vary in frequency as a function of specific processing conditions (Galambos, 1992; Basar, 1998; Tallon-Baudry & Bertrand, 1999). In the auditory modality, simple tone bursts elicit transient EEG and MEG gamma band responses (GBRs) around 40 Hz which are strongly phase-locked to the stimulus in the first 100–120 ms (Basar *et al.*, 1987; Pantev *et al.*, 1991, 1994; Makeig, 1993). This early phase-locked 40-Hz response has been demonstrated to originate in the auditory cortex (Pantev *et al.*, 1991; Bertrand & Pantev, 1994). Despite the modality-specific source of generation, auditory GBR power does not manifest a tonotopic organization as could be expected if it simply reflected sensory mechanisms (Pantev *et al.*, 1991, 1994). Instead, the GBR has been correlated with vigilance and arousal because it attenuates in the course of a long-term (5-h long) stimulation (May *et al.*, 1994) and disappears during deep sleep (Llinás & Ribary, 1993) and anaesthesia (Madler & Pöppel, 1987; Madler *et al.*, 1991). Further, actively processed auditory targets have been shown to enhance the early 40 Hz activity, thus pointing to the associations of the GBR with selective and focused attention (Tiitinen *et al.*, 1993; Makeig, 1993; Jokeit & Makeig, 1994; Yordanova *et al.*, 1997). These previous results strongly imply that, in humans, the early phase-locked GBR is related to attentive conscious behaviour in

TABLE 1. Group characteristics of children and adolescents included in the study

| Age group | 9-year-olds | 10-year-olds | 11-year-olds | 12-year-olds | 13-year-olds | 14-year-olds | 15-year-olds | 16-year-olds |
|---|---|---|---|---|---|---|---|---|
| (a) Group characteristics | | | | | | | | |
| Number of subjects | 15 | 12 | 17 | 13 | 15 | 14 | 15 | 13 |
| Mean age (years) | 9.51 | 10.51 | 11.38 | 12.46 | 13.45 | 14.52 | 15.46 | 16.37 |
| Mean age (months) | 114.07 | 126.17 | 136.59 | 149.54 | 161.40 | 174.21 | 185.47 | 196.46 |
| SD (months) | 0.71 | 1.41 | 4.95 | 2.83 | 4.95 | 4.95 | 0.71 | 4.24 |
| Sex (female/male) | 7/8 | 5/7 | 9/8 | 5/8 | 7/8 | 4/10 | 7/8 | 7/6 |
| Full-scale IQ (mean value) | 111 | 112 | 112 | 112 | 112 | 110 | 118 | 113 |
| Handedness* | 36 | 36 | 32 | 36 | 34 | 37 | 38 | 32 |
| (b) Psychopathology measures | | | | | | | | |
| Conners (mean values) | 3 | 3 | 3 | 4 | 3 | 4 | 3 | 4 |
| CBCL total T[†] | 47 | 45 | 48 | 53 | 51 | 51 | 51 | 51 |
| CBCL external T | 48 | 45 | 50 | 52 | 51 | 53 | 51 | 51 |
| CBCL internal T | 48 | 47 | 49 | 55 | 51 | 51 | 52 | 50 |
| MFFT (total time) | 174 | 207 | 196 | 188 | 206 | 175 | 226 | 171 |
| (c) Reaction times | | | | | | | | |
| Attend-right (Condition 1) | | | | | | | | |
| Hits | 43.73 | 43.92 | 45.59 | 46.46 | 46.47 | 44.21 | 47.40 | 47.38 |
| Mean RT (ms) | 515 | 537 | 508 | 470 | 457 | 435 | 391 | 392 |
| Attend-left (Condition 2) | | | | | | | | |
| Hits | 43.00 | 42.58 | 43.94 | 45.54 | 44.27 | 45.64 | 46.13 | 45.62 |
| Mean RT (ms) | 535 | 532 | 512 | 486 | 460 | 448 | 406 | 404 |
| Significance (P-values) | | | | | | | | |
| Hits attend-right vs. left | – | – | – | 0.001 | 0.001 | – | 0.001 | 0.05 |
| RT attend-right vs. left | – | – | – | – | – | – | – | – |

*Handedness: minimum = 8 (left hand dominance); maximum = 40 (right hand dominance). [†]T-scores, standardized scores on each dimension, with a score of 50 representing the mean and SD equal to 10.

the auditory environment (Sheer, 1989). Although the functional role of the GBR is not precisely known (Llinás & Ribary, 1992; Joliot et al., 1994; Basar, 1998; Tallon-Baudry & Bertrand, 1999), most recent findings from the visual modality further substantiate the notion that event-related gamma oscillations are associated with early attention processes (Gruber et al., 1999; Shibata et al., 1999; Sokolov et al., 1999; Mueller et al., 2000).

In an auditory selective attention condition, where target features are determined by both the side of stimulus presentation (attended channel) and physical stimulus characteristics, focusing attention to the side of stimulation enhances GBRs of adult subjects (Tiitinen et al., 1993). Notably, in a similar task, auditory GBRs of 9- to 12-year-old children have not manifested sensitivity to the attended channel processing (Yordanova et al., 2000). Instead, GBRs of children were larger to the target stimulus type appearing in either the attended or in the unattended channel (Yordanova et al., 2000, 2001). Several differences in the experimental designs including stimulus rate, probability, and discriminability, as well as motor vs. count task, can be accounted for a divergent task reactivity of auditory GBRs in children and adults. Apart from methodological sources of variation, however, it is possible that due to processes of brain maturation, the functional involvement of gamma oscillations differs in children and adults.

Indeed, the functional characteristics of EEG activity from slower frequency ranges have been indicated to mature as a function of development (Gasser et al., 1988; Yordanova & Kolev, 1997, 1998b; Krause et al., 2001). Event-related oscillations from alpha and theta bands have been shown to change with age such that their overall power decreases and stability of locking to the stimulus increases as children develop (Kolev et al., 1994; Yordanova & Kolev, 1996, 1998b). In addition, developmental changes in the power and phase-synchronization of theta and alpha responses depend differentially on the background EEG activity (Yordanova et al., 2000) which also

varies with age (Petersen & Eeg-Olofsson, 1971; Niedermeyer, 1997). These previous reports have concluded that both alpha and theta response systems are involved in stimulus information processing in children. However, for both frequency ranges, the level of functional maturity has not yet been reached at the age of 12 years, as revealed by prominent differences between children at that age and adults (Yordanova & Kolev, 1996, 1998b; Krause et al., 2001). It is therefore likely that cognitive maturation also affects event-related gamma oscillations and their functional reactivity.

Given this background, the aim of the present study was to analyze gamma band activity elicited in an auditory attention task from a large sample of children and adolescents whose age varied within a broad range between 9 and 16 years. One goal was to describe age-related variations in the spontaneous gamma EEG activity. In only one previous report, spontaneous gamma EEG has been analyzed in 3–12-year-old children at fronto-polar, central, and occipital locations (Takano & Ogawa, 1998). It was found that gamma band power increased significantly between 3 and 4 years at all leads, especially over the frontal region, and reached a maximum at 4–5 years of age. The spontaneous gamma EEG was analyzed in the present study to extend the range of evaluation up to 16 years, and also to control for possible effects of this activity on developmental variations in the poststimulus GBRs (Kolev et al., 1994; Yordanova & Kolev, 1996, 1997; Basar et al., 1997). Further, to assess developmental differences in the background level of gamma band power during the task, which might not be present during relaxation (as reflected by the spontaneous EEG), the prestimulus gamma activity was also analyzed. A second goal was to describe developmental changes in the stability and functional reactivity of auditory GBRs at specific scalp locations. GBRs were analyzed in the time-frequency plane by means of the wavelet transform (WT) (Ademoglu et al., 1997; Heinrich et al., 1993, 1999; Demiralp et al., 1999), with the stability of between-sweep synchronization (phase-locking) being further

evaluated independently of power measures (Kolev & Yordanova, 1997; Yordanova & Kolev, 1998a). Because the task reactivity of gamma oscillations is area-specific and spatially localized (Pantev *et al.*, 1991; Tiitinen *et al.*, 1993; Pfurtscheller *et al.*, 1994; Pulvermüller *et al.*, 1997; Tallon-Baudry & Bertrand, 1999), age-related differences in the functional involvement of GBRs were assessed at separate scalp locations. The effects of attended side and stimulus type relevance were examined for GBR power and phase-locking, and compared among age groups.

## Methods

### Subjects

Within the framework of a multilevel longitudinal study on central nervous regulatory mechanisms and child psychiatric disorders (Rothenberger & Schmidt, 2000), a total of 114 children and adolescents from 9 to 16 years of age were studied. They were divided into eight age groups of 9, 10, 11, 12, 13, 14, 15, and 16 years, each comprising from 12 to 17 subjects. Data of subjects' age, gender, handedness, and full-scale IQ are presented in Table 1a.

For all children, the Child Behaviour Checklist (CBCL, Achenbach & Edelbrock, 1983) was used as screening instrument for child psychiatric symptoms based on parents' reports. Level of hyper-activity was assessed by the 10-item Conners parent questionnaire (Goyette *et al.*, 1978). In addition, the Matching Familiar Figures Test (MFFT; Kagan & Kogan, 1970) was used to assess cognitive impulse control. As presented in Table 1b, all children and adolescents were healthy, and reported no history of neurologic, somatic, or psychiatric problems, nor did they have any learning, emotional or other problems. The study received prior approval by the local ethical review board. Informed consent was obtained from each child and from his/her parents.

### Task procedure

In each of the two recording conditions described below, a total of 240 auditory stimuli were used. Two stimulus types were presented randomly to the left and right ear via headphones. The stimuli were low nontarget (1000 Hz, $n = 144$, $P = 0.6$) and high target (1500 Hz, $n = 96$, $P = 0.4$) tones with a duration of 120 ms, r/f of 10 ms, and intensity of 85 dB SPL. Inter-stimulus intervals varied randomly from 1150 to 1550 ms. Equal numbers of each stimulus type were presented to the left and right. In the first condition, subjects were instructed to press a button in response to the high tones (targets) presented to the right, while in the second condition the attended targets were the high tones presented to the left. Thus, there were four stimulus types in each series: target-attended ($n = 48$), target-unattended ($n = 48$), nontarget-attended ($n = 72$), and nontarget-unattended ($n = 72$). During the entire recording session, subjects kept their eyes open and responded with the right hand.

### Data recording

EEG activity was recorded via Nihon Kohden Ag/AgCl cup electrodes (impedance kept below 3 kOhm) fixed to the scalp at F3, Fz, F4, C3, Cz, C4, P3, and P4 locations according to the International 10/20 system and referred to the two mastoid electrodes, which were connected via a 10-kOhm resistor (voltage divider, cf. Nunez, 1981). Spontaneous EEG was registered also at Oz. Vertical and horizontal electrooculograms (EOGs) were simultaneously recorded from electrodes above and below the right eye and at the outer canthi. Reaction time (RT) data were collected as behavioural measures. The EEG and EOG signals were amplified and filtered with cutoff frequencies of 0.03 and 120 Hz for EEG channels, and 0.03 and 70 Hz for EOG channels. Analysis epochs of 150 ms before and 1000 ms after stimulus onset were sampled with a sampling rate of 500 Hz.

### Data analysis

EEG epochs contaminated with ocular movements or muscle artifacts were rejected, with only traces lower than 200 µV peak-to-peak being accepted. To equalize the number of sweeps for each stimulus type and thus control for signal-to-noise ratio effects, for each subject, 35 sweeps were randomly selected from artifact-free trials of each stimulus type and used for further analysis. This number was limited by the minimal number of artifact-free target trials found at individual level.

#### Spontaneous gamma band EEG activity

The spontaneous gamma band activity was evaluated for artifact-free EEG epochs of 20 s recorded while the subjects were relaxing with closed eyes. The 20 s epoch was divided into 10 time segments of 2 s duration each. The EEG signal was filtered in the 31–63 Hz band, and the root-mean-square amplitude was measured for each 2 s epoch, then averaged for each subject and lead, and subjected to statistical evaluation.

#### Event-related gamma band activity – wavelet analysis

Unlike time-domain ERPs, or frequency-domain analyses (Fourier transform), the Wavelet Transform performs EEG signal analysis in both time and frequency domains. This means that wavelet representations provide precise measurements of when and how the frequency content of a neuroelectric waveform changes over time (Schiff *et al.*, 1994; Samar *et al.*, 1995, 1999). Hence, WT was employed in the present study to permit a better time localization of the event-related gamma responses. The WT uses a family of functions that are generated from a single function by operations of dilations and translations (Samar *et al.*, 1999; Heinrich *et al.*, 1999). Here, quadratic Beta-spline wavelet basis functions were used in the form of a multiresolution logarithmic scheme (Ademoglu *et al.*, 1997; Demiralp *et al.*, 1999). The application of a five-octave WT to the data yielded five sets of discrete coefficients representing the time evolution of different frequency components (Ademoglu *et al.*, 1997; Kolev *et al.*, 1997; Demiralp *et al.*, 1999). Figure 1a illustrates the gamma band (31.2–63.5 Hz) coefficients obtained by this procedure. The interpolation of the coefficients from the gamma range with quadratic spline function was performed to reconstruct the signal in the gamma frequency band and to represent its time course. In this way, the gamma band activity was reconstructed for each single sweep. To analyze phase-locked gamma band activity, the so obtained single gamma responses were averaged for each subject, stimulus type, series, and electrode. Then, as shown in the lower panel of Fig. 1a and b, the averaged gamma response was squared to obtain event-related gamma power. The GBR power was measured as the maximal value within 0–120 ms after stimulus onset, and a baseline level was measured as the mean value within 100–50 ms before stimulus onset. This baseline level was subtracted from the GBR measures before statistical assessment (Tiitinen *et al.*, 1993; Gruber *et al.*, 1999). The gamma band power of the baseline was also statistically analyzed. All power measures were log10-transformed to normalize values subjected to statistical analysis (Gasser *et al.*, 1982).

#### Event-related gamma band activity – phase-locking

Single sweeps subjected to WT analysis and reconstructed in the gamma frequency range were further analyzed to assess GBR
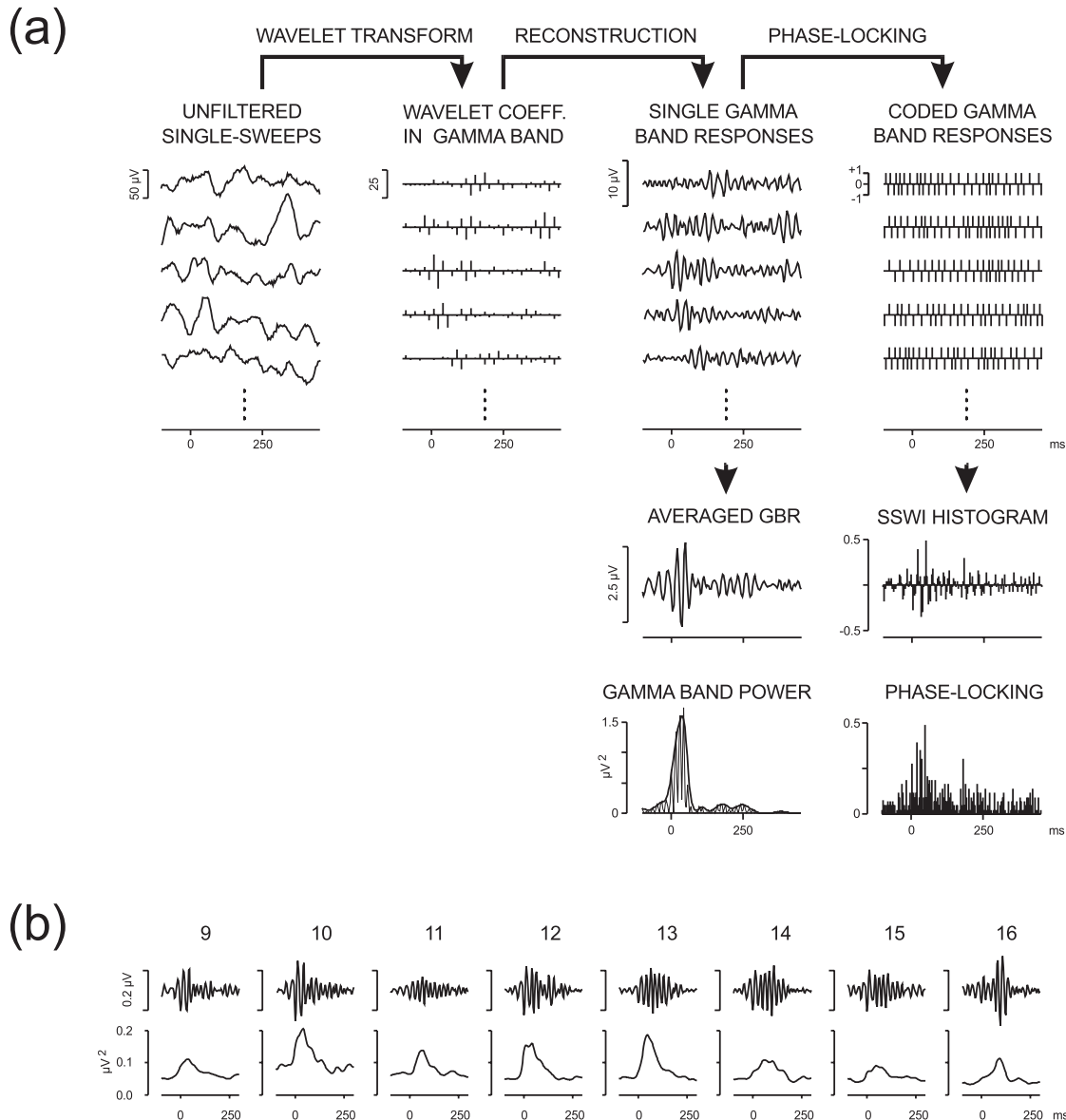
FIG. 1. Schematic illustration of analysis procedure. (a) EEG signal transforms are illustrated on single sweeps (upper panel). The average data shown in the lower panel are produced by a number of sweeps typically used for GBR measures. (b) Grand average gamma band responses for eight age groups at Cz. Upper raw shows grand averages of individual GBRs and contains information about intersubject GBR phase-synchronization. Lower raw shows grand averages of GBR power free of intersubject phase-stability effects. Time evolution of GBR power is presented at the bottom. SSWI, single-sweep wave identification.

phase-locking independently of power. For a quantitative evaluation of the phase-locking, a modification of the single-sweep wave identification method was applied, with methodological details on the procedure presented elsewhere (Kolev & Yordanova, 1997; Yordanova et al., 1997; Yordanova & Kolev, 1998a). In sum, the method identifies extrema (minima and maxima) in each single sweep and replaces them by codes of −1 or +1, respectively, placed on the corresponding latency positions (illustrated as coded GBR in Fig. 1a). Then, a summation of the modified sweeps is performed across trials, with the sum value at each time point assigned to a histogram bar. The histogram is thereafter normalized by dividing the bar values by the number of sweeps included in the analysis. For statistical assessment of phase-locking, the maximal absolute bar values of the normalized rectified histogram were measured for the period 0–120 ms after stimulus presentation (Fig. 1a, bottom). This procedure is employed to evaluate any level of between-sweep synchronization, but not to extract and compare only significant (above background) levels of phase-locked components.

*Statistical analysis*

Developmental effects of two major task-related variables (attended channel and stimulus task relevance) were primarily focused on under the assumption that these effects should be area-specific and spatially localized. ANOVA designs with repeated measures were applied to each of the GBR parameters (maximal GBR power within 0–120 ms after stimulus onset and maximal GBR phase-locking for the same time window).

As a first step, GBR parameters were subjected to an ANOVA with one between-subjects variable Age group (eight levels corresponding to 9-, 10-, 11-, 12-, 13-, 14-, 15-, and 16-year-old children), and within-subjects variables Laterality (left-hemisphere electrodes/F3,

TABLE 2. Statistical results (*F*-values and corresponding significance) of Age × Laterality × Region ANOVAS

| Source (degrees of freedom) | Spontaneous gamma band activity | Pre-stimulus gamma band activity | GBR | GBR phase-locking |
|---|---|---|---|---|
| Age (7,106) | – | 2.70** | – | – |
| Laterality (1,106) | – | – | – | 4.11* |
| Age × Laterality (7,106) | – | – | – | 2.13* |
| Region (2,212) | 50.79*** | 60.55*** | 49.06*** | 11.32*** |
| Age × Region (14,212) | – | 1.84* | – | – |
| Laterality × Region (2,212) | – | 7.03*** | – | – |
| Age × Laterality × Region (14,212) | – | – | – | – |

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; –, not significant.

C3, P3/vs. right-hemisphere electrodes/F4, C4, P4/) and Region (frontal/F3, F4/vs. central/C3, C4/vs. parietal/P3, P4/). The aim was to describe the overall scalp distribution of the GBR as a function of age. Spontaneous and prestimulus gamma band measures were subjected to the same analysis.

As a second step, the effects of series sequence and side of stimulation were tested to control for a possible influence of each of these experimental task-irrelevant factors on GBRs. To control further for spatial effects of these variables, the Laterality and Region factors (as described above) were included. The analysis design was Age × Series sequence (first vs. second) and Side of stimulation (left-side vs. right-side stimuli) × Laterality × Region. No main effects or interactions with age or electrode variables were detected for Series sequence. In contrast, significant effects (described in the Results) were obtained for Side of stimulation. Therefore, only Side of stimulation was included as a factor in subsequent analyses (see below). For all ANOVAS applied in step one and two, the degrees of freedom were controlled by using the Greenhouse-Geisser correction. The original d.f. and corrected probability values are reported in the Results.

As a third step, effects of task-relevant variables on developmental GBRs were analyzed. Because the functional reactivity of the GBR is expected to be spatially localized, this was carried out at each electrode separately by performing regional ANOVAS. The between-subject variable was Age, and the within-subjects variables were Attended channel (attended vs. unattended), Stimulus type relevance (target vs. nontarget), and Side of stimulation (right-side vs. left-side stimuli). For regional ANOVAS, the probability alpha level was controlled by using the Bonferroni procedure (see below). The approach to perform regional ANOVAS was verified in a preliminary analysis, in which the between-subjects variable was Age, and the within-subjects variables were Attended channel, Stimulus type relevance, Side of stimulation, Laterality, and Region (or Electrode/Fz, Cz/in a second analysis). These analyses indicated that the Attended channel significantly interacted with Age and Region variables ($F_{14,212} = 2.34$, $P < 0.05$), and the effect of Stimulus type relevance was modulated by the age at anterior locations (Age × Stimulus type relevance for the Fz/Cz analysis, $F_{7,102} = 3.46$, $P < 0.05$), which confirmed the relevance of the statistical procedure used.

In this way, the hypothesis that task-related effects on developmental GBR should occur at specific scalp locations was tested by assessing two parameters, GBR power and GBR phase-locking, at eight different electrodes. Within this hypothesis, a correction for multiple tests (a Bonferroni correction) is required for the two parameters used (Bland & Altman, 1995; Sankoh *et al.*, 1997; see also Simple Interactive Statistical Analysis – SISA on http://home.clara.net/sisa/). However, Bonferroni alpha adjustment is largely unrecommended for the eight-electrode multiple tests because such a correction may produce erroneous results as being based on a wrong physiological hypothesis accepting an overall (area-unspecific) task effects on the developmental GBRs (Perneger, 1998). This means that in this study, the alpha level *P* should be reduced for two tests with a full Bonferroni adjustment from $P = 0.05$ to $P = 0.025$, but only if the two variables (GBR power and GBR phase-locking) were fully uncorrelated ($r = 0$). A mean correlation of $r = 1$ would require no adjustment at all, and for other values of the correlation, a corrected alpha should be between the two extremes depending on the correlation (Sankoh *et al.*, 1997; Perneger, 1998). After correlating GBR power and phase-locking at specific locations for each stimulus type, mean values of *r* were found to be between 0.47 and 0.52. Thus, the alpha level was adjusted to $P = 0.036$, and effects were accepted as significant only if $P \leqslant 0.036$.

## Results

### Behavioural data

All subjects performed the task accurately, with the percentage of omission and commission errors being less than 3%. Number of correct responses and mean reaction times are presented in Table 1c. It is shown that, in general, the number of correct responses increased and response speed decreased as a function of age from 9 to 16 years. In adolescents, the number of correct hits showed an overall decrease in the second relative to the first experimental condition, whereas RTs of subjects from all age groups did not differ between the two conditions (Table 1c).

### Spontaneous and prestimulus gamma band activity

Statistical results of developmental scalp distribution of spontaneous, prestimulus, and poststimulus gamma band EEG activity are presented in Table 2. Figure 2a illustrates developmental gamma band power in the spontaneous EEG. No significant main effect of the Age factor was obtained (Table 2). For each group, the spontaneous gamma activity was larger at frontal sites and decreased from anterior to posterior locations, as indexed by the main Region effect ($P < 0.001$), and lack of interactions of the Region and Laterality factors with the Age variable.

Figure 2b and Table 2 demonstrate that the prestimulus gamma band activity decreased with age from 9 to 11–16 years (Age, $P < 0.01$). Pre-stimulus gamma power was largest at frontal sites and decreased in posterior direction (Region, $P < 0.001$). The anterior vs. posterior difference decreased with age (Age × Region, $P < 0.05$). Notably, for each group, the prestimulus gamma power was significantly larger at the left than at the right frontal sites, with no laterality effects detected at central and parietal locations (Laterality × Region, $P < 0.001$, Fig. 2b).
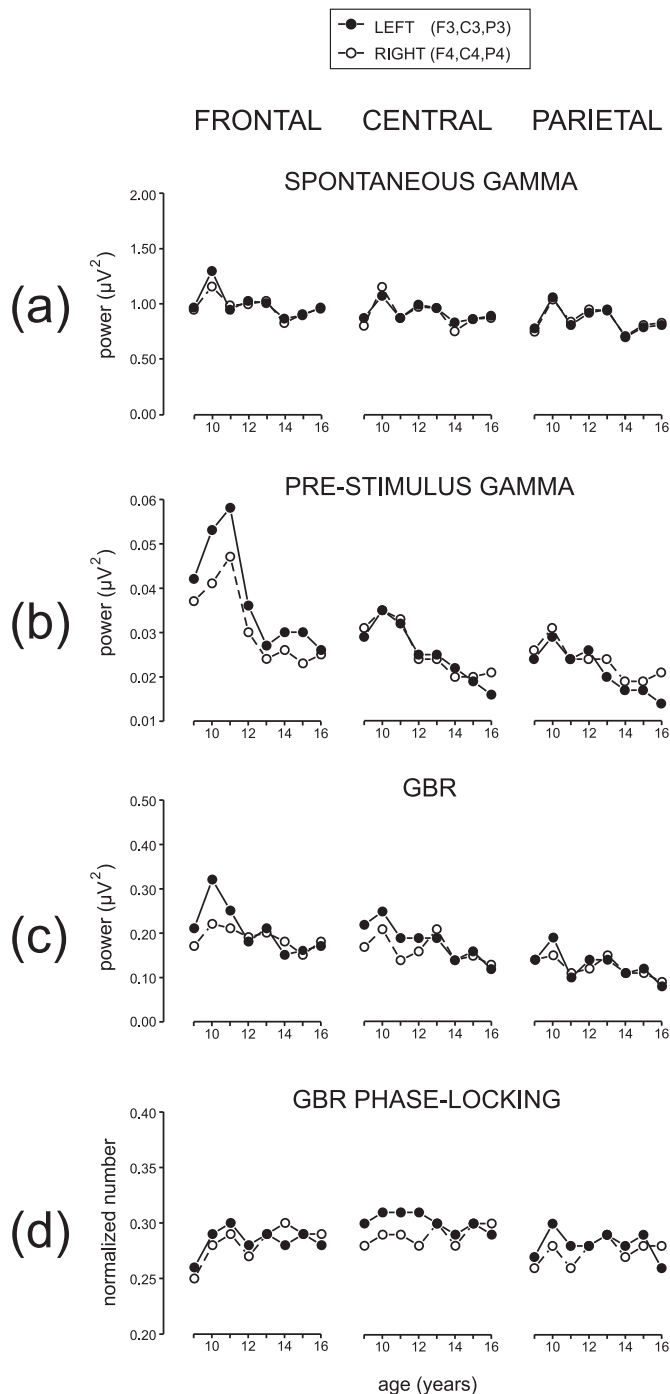
FIG. 2. Group means of different age groups for (a) power of the spontaneous gamma band EEG activity (b) power of the prestimulus gamma band activity (c) power of maximal phase-locked GBR (0–120 ms), and (d) phase-locking of GBR as measured by normalized between-sweep synchronization. Frontal, central and parietal electrodes are pooled together and presented in the left, middle and right columns, respectively. Root-mean-square values of the spontaneous gamma band EEG activity were measured and analyzed, but in a, power values are shown for the sake of consistency with (b) and (c).

### Gamma band response

#### Age effects

Figure 2c and d demonstrates that GBR power and phase-locking did not vary significantly as a function of age from 9 to 16 years (Age,

$F_{7,106} = 0.62$; 0.44, $P > 0.7$). Across age groups, GBR power was overall larger at anterior (central-frontal) than at parietal locations (Region, $P < 0.001$, Table 2), with no significant Age–Region interaction observed. For all age groups, the GBR was better phase-locked at central sites (Region, $P < 0.001$, Table 2).

As seen in Fig. 2c, there was a nonsignificant trend for only the 9–12-year-old children to produce larger GBRs over left-hemisphere locations (Age × Laterality, $F_{7,106} = 2.62$, $P < 0.1$). Figure 2d illustrates that the Laterality effect reached a level of significance for the GBR phase-locking that was overall stronger at left vs. right-hemisphere sites (Laterality, $P < 0.05$), but this effect stemmed from GBRs of 9–12-year-old children who, in contrast to 13–16-year-old adolescents, manifested better synchronized GBRs over left-hemisphere locations, especially at the central sites (Age × Laterality, $P < 0.05$, Table 2; Laterality effect in 9–12-year-olds, $F_{1,53} = 10.12$, $P < 0.005$, with no significant interaction with Age from 9 to 12 years, $F_{3,53} = 0.99$, $P > 0.3$; Laterality effect in 13–16-year-olds, $F_{1,53} = 0.49$, $P > 0.4$, with no significant interaction with Age from 13 to 16 years, $F_{3,53} = 0.92$, $P > 0.4$).

#### Series sequence and Side of stimulation effects

As mentioned previously, the main effect of Series sequence on GBR power and phase-locking was not significant, nor were there significant interactions of the Series sequence factor with other variables. In contrast, GBR power was significantly larger for left- vs. right-side stimuli (Side of stimulation, $F_{1,106} = 6.15$, $P < 0.05$), with this effect being most prominent for the 9–12-year-old children (Age × Side of stimulation, $F_{7,106} = 2.42$, $P < 0.05$; Side of stimulation, $F_{1,53} = 8.04$, $P < 0.01$ for 9–12-year-olds and nonsignificant for 13–16-year-olds), and over right central-parietal locations C4 and P4 (Side of stimulation × Laterality × Region, $F_{2,212} = 4.63$, $P < 0.01$; simple effects of Side of stimulation at C4 and P4, $F_{1,106} > 6.03$, $P < 0.05$). This is reflected also by results of regional ANOVAs in Table 3a (Age × Side of stimulation interaction was significant at specific locations – C4, $P < 0.036$, and P4, $P = 0.04$ (marginal)).

As found for GBR power, the Side of stimulation affected GBR phase locking ($F_{1,106} = 5.97$, $P < 0.05$): Fig. 3 demonstrates that GBRs to the left-side stimuli were overall better phase-locked than those to the right side stimuli. This Side of stimulation effect did not depend on the Age, as also shown by nonsignificant Age × Side of stimulation interactions (Table 3b). The difference between left- and right-side stimuli was reliably pronounced at P4 and Cz, and marginally at C4 (Table 3b).

#### Task-related effects

The effects of the Attended channel and Stimulus type relevance on GBR power and phase-locking tested at separate locations by means of regional ANOVAs are presented in Tables 3a and 3b.

A main effect of the Attended channel on GBR power was yielded at the right frontal location F4, where GBRs of unattended stimuli were larger than those of attended ones (Table 3a). As presented in Table 3b and illustrated in Fig. 4a, only at the left parietal location P3, was there a significant interaction of the Attended channel factor with the Age variable. The figure shows that GBRs of children (9–13-years-old) were better phase-locked to unattended relative to attended stimuli, whereas in adolescents (14–16-year-olds), attended stimuli produced better synchronized gamma responses than did the unattended ones.

An overall Stimulus type relevance effect on GBR phase-locking was detected at F3 (Table 3b), arising from significantly better

TABLE 3. Regional ANOVAs, Age × Attended Channel × Stimulus Type Relevance × Side of Stimulation

| Source (degrees of freedom) | (a) GBR | | | (b) GBR phase-locking | | |
|---|---|---|---|---|---|---|
| | Lead | *F*-value | *P*-value | Lead | *F*-value | *P*-value |
| Age (7,106) | – | – | – | – | – | – |
| Attended Channel (1,106) | F4 | 6.32 | 0.01 | – | – | – |
| Age × Attended Channel (7,106) | – | – | – | P3 | 3.15 | 0.034 |
| Stimulus Type Relevance (1,106) | – | – | – | F3 | 6.52 | 0.012 |
| Age × Stimulus Type Relevance (7,106) | Fz | 2.28 | 0.034 | – | – | – |
| | F4 | 2.75 | 0.012 | | | |
| | Cz | 2.20 | 0.04, marginal | | | |
| Side of Stimulation (1,106) | Cz | 4.90 | 0.029 | Cz | 5.79 | 0.018 |
| | C4 | 18.2 | 0.0001 | C4 | 4.27 | 0.04, marginal |
| | P4 | 6.03 | 0.016 | P4 | 6.58 | 0.01 |
| Age × Side of Stimulation (7,106) | C4 | 2.52 | 0.02 | – | – | – |
| | P4 | 2.16 | 0.04, marginal | | | |
| Attended Channel × Stimulus Type Relevance (1,106) | Fz | 7.16 | 0.009 | – | – | – |
| | Cz | 6.12 | 0.015 | | | |

Only significant effects according to Bonferroni adjustment ($P \leqslant 0.036$) are shown: Lead (*F*, significance of *P*).
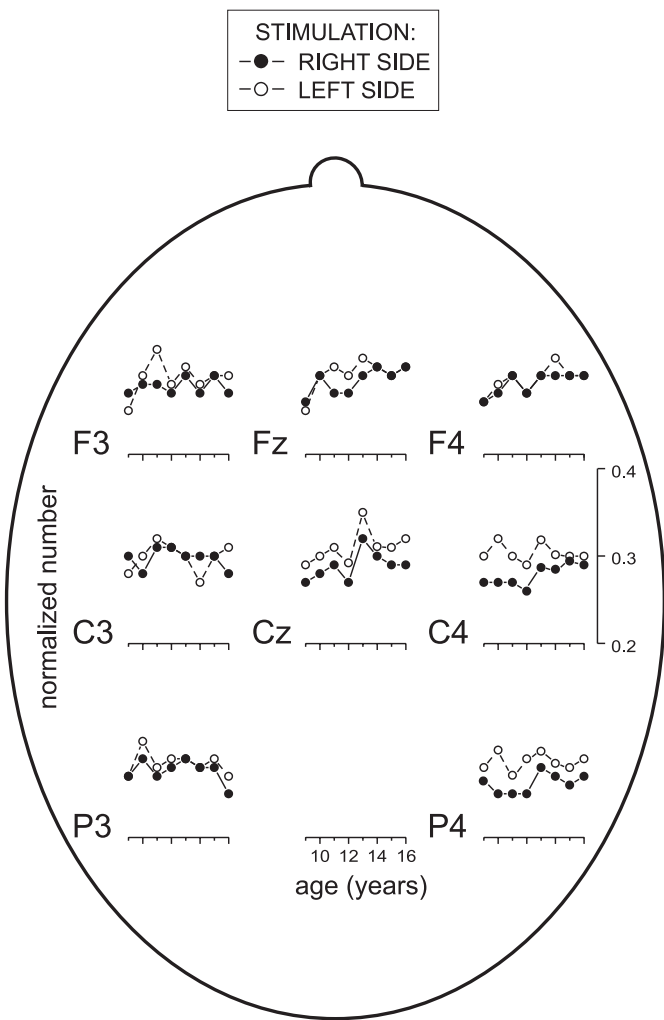


FIG. 3. Group mean of phase-locking of children from different age groups to right-side and left-side auditory stimuli. The increase of GBR phase-locking to left-side stimuli is clearly observed in all age groups at Cz, C4, and P4.

phase-locked GBRs to targets relative to nontargets. Figure 4b additionally illustrates that only in 9–12-year-old children, did the targets elicit larger frontal GBRs relative to the nontargets (significant interaction Age × Stimulus type relevance), which was observed at frontal locations (Fz, F4). At midline anterior sites Fz and Cz, a significant Attended channel × Stimulus type relevance interaction was found, arising from a lack of difference between GBRs to attended and unattended targets, whereas GBRs to unattended nontargets were larger than GBRs to attended nontargets.

## Discussion

The present study was designed to assess developmental changes in gamma band EEG activity of 9–16-year-old children during auditory attention task. Spontaneous gamma band power was also analyzed to describe the neurobiological development of fast-frequency EEG rhythms. Pre-stimulus activity was evaluated to reveal developmental variations in the involvement of background gamma oscillations in task processing conditions. Finally, gamma band responses to auditory task stimuli were compared among age groups at specific locations to test if differences in the power, stability and functional reactivity of fast-frequency EEG responses accompany developmental ageing.

Major results demonstrated that (i) the spontaneous gamma band power did not undergo substantial developmental changes, whereas the gamma activity generated during an auditory attention task decreased with age from 9–11 to 16 years. (ii) Although the power and stability of stimulus-locked gamma responses did not depend on the age, the functional reactivity of auditory GBRs at specific locations changed in the course of development. In children (9–12-year-olds), GBRs were sensitive to target stimulus features because GBRs at frontal locations were larger to target than to nontarget stimulus type. Also, only in 9–12-year-old children were the auditory GBRs larger and better phase-synchronized over the left hemisphere locations. In contrast, in adolescents (14–16-year-olds), GBRs were associated with internal focusing of attention because the phase-locked GBRs at parietal sites were synchronized by processing in the attended vs. unattended channel. (iii) Independently of the age, enhanced phase-locked GBRs were produced at right central-parietal scalp locations by left-side stimuli.
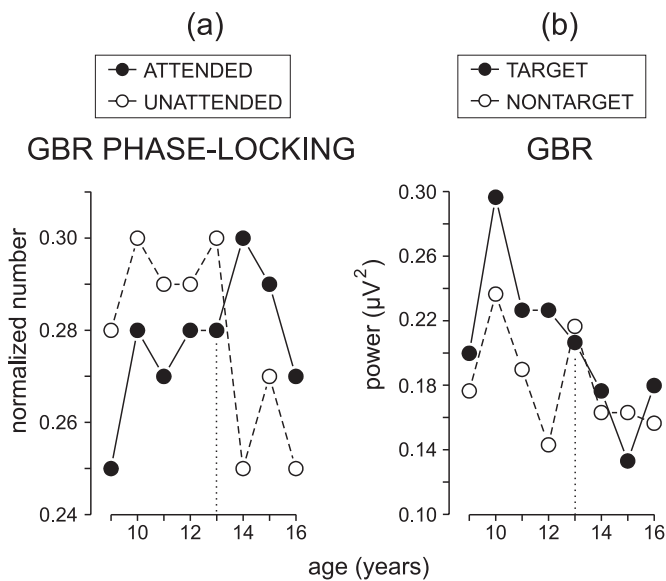
FIG. 4. Effects of (a) attended channel on GBR phase-locking at P3 and (b) stimulus type on GBR power at frontal sites in different age groups.

Taken together, these results indicate that (i) specific aspects of task-stimulus processing engage distinct spatially localized gamma networks in functionally relevant areas, and (ii) the neuronal substrates of gamma networks and the ability to synchronize them in relation to task-specific processes are available in both children and adolescents from 9 to 16 years of age. However, the mode and efficiency with which a particular task component can entrain functional gamma oscillations depends on the age. This differential task-specific reactivity of GBRs in children and adolescents may therefore reflect developmental differences in task processing strategies, each engaging specific spatial patterns of gamma networks.

### Methodological considerations

It is well recognized that gamma band EEG activity is prone to contamination from extra-cerebral high-frequency signals (Sheer, 1989; Pulvermüller et al., 1997). In the present study, electromyographic (EMG) activity from face, neck, and forearm muscles has not been analyzed in parallel with the EEG/ERPs. Despite the lack of precise EMG control, electromyographic activity seems unlikely to have produced the observed task and age effects on the GBR because phase-locked gamma oscillations as assessed here might not result from random EMG activity (Kolev & Yordanova, 1997; Yordanova et al., 1997, 2000, 2001; Yordanova & Kolev, 1998a). In addition, task and age effects on GBRs were verified by means of phase-locking parametrization, which detects the between-sweep synchronization independently of power. Whereas total GBR power measures may be sensitive to EMG contamination (Pulvermüller et al., 1997), the phase-locking is not. Also, mean reaction times of children were around 400–500 ms. Hence, random or nonrandom EMG and EEG activity stemming from motor response production (Brown et al., 1998) cannot be expected to grossly interfere with EEG gamma responses generated within 100–120 ms after stimulus onset. Finally, spontaneous, prestimulus and poststimulus measures showed differential age effects. This indicates that differences in the motor activity of younger and older children may not have produced developmental and task variations in GBRs, because motor activity contribution would have affected each of the gamma band measures in a similar way. Thus, it may be concluded that the gamma-band activity

analyzed here reflects brain electrical involvement in auditory attention task in children and adolescents.

In the present study, scalp topography effects were analyzed only to describe developmental variations in the scalp distribution of gamma band activity. Differences in scalp distribution are recognized to reflect spatially distinct activations. Particularly, the gamma responses recorded at distant individual scalp sites are most likely to reflect underlying cortical activations, because the spatial propagation of gamma oscillations is largely limited and they vanish quickly over distance (Bullock, 1997). Yet, no definite conclusions about sources of gamma band activity generation can be made on the base of EEG records (Picton et al., 2000).

Several other methodological considerations appear relevant to the present study. (i) Fluctuations stemming from a common reference electrode that could compromise laterality differences refer to amplitude measures, whereas the laterality effects described here were extracted also by measuring the between-sweep synchronization, independently of amplitude. In addition, amplitude fluctuations were minimized by connecting the two reference electrodes via a resistor (voltage divider, cf. Nunez, 1981). (ii) In the present study, the number of sweeps used to obtain average responses was restricted to 35 due to the smaller number of artifact-free target stimulus types in children. For analysis of low amplitude signals like the gamma band ones, a larger number of sweeps is typically employed to produce averages (Tiitinen et al., 1993; Tallon et al., 1995; Pulvermüller et al., 1997). Although other studies have employed numbers of sweeps similar to that used here for analysis of GBRs (e.g. Karakas & Basar, 1998; Sakowitz et al., 2001), a note of precaution should be introduced because it has not been precisely established how the sweep number affects average responses within the relatively broad gamma frequency band. It is therefore worthwhile to explore the effects of gamma frequency stability/variability on results obtained with different numbers of sweeps.

### Spontaneous gamma band activity

According to the present results, the power of the spontaneous gamma band EEG activity did not undergo substantial changes from 9 to 16 years of age. A previous study on 3–12-year-old children has demonstrated an increase of gamma band EEG power after the age of 3 years that reached a maximum at 4–5 years (Takano & Ogawa, 1998). Extending the age range of observations shows that in the course of development from 9 to 16 years, the spontaneous gamma activity did not change significantly. Yet, it is noteworthy that similar to findings in 3–12-year-old children, the spontaneous gamma EEG activity was maximal at frontal locations and decreased in the posterior direction, with this distribution pattern observed as late as 16 years of age. It has been proposed that the frontal maximum of gamma band power and its robust increase at 4–5 years may reflect a functional maturation of fast-frequency EEG accompanying changes in cognitive abilities of children (Takano & Ogawa, 1998). Within this line of argumentation, the lack of significant age variations in the spontaneous gamma band power implies that cognition-related processes presumably associated with the spontaneous gamma band power reach a level of maturation at early stages of development.

### Ongoing gamma band activity during task processing

In contrast, the power of background (or prestimulus) gamma activity recorded during an auditory attention task decreased significantly with age. The differential developmental variations of spontaneous and prestimulus gamma powers generally indicate that (i) an active task condition specifically modifies ongoing gamma EEG activity, and (ii) the extent or mode of modification depends on the age. In

addition, a left frontal predominance emerged only for the prestimulus gamma oscillations. This laterality effect was observed consistently across age groups, further implying a correlation with the auditory attention task used here.

Earlier results from adults support this notion. Jokeit & Makeig (1994) have demonstrated that subjects who intensively focus their motor rather than sensory attention to forthcoming stimuli (fast responders) manifest an increase in the prestimulus gamma band power. In contrast, subjects employing a different behavioural strategy characterized by stimulus-orientated rather than response-orientated bias (slow responders) did not produce a substantial increase in the prestimulus gamma band activity. Hence, an intensive preparatory process engaging motor preprogramming seems to correlate with augmentation of the prestimulus gamma power. Thus, the observation of left-over-right frontal predominance of the prestimulus gamma band power may correspond to a preactivation of right-hand motor programs at contra-lateral (left) premotor frontal areas, which was observed at each age from 9 to 16 years. Analysis of averaged potentials as performed in the present study additionally implies a contribution from a stronger synchronization of gamma band activity during active expectation of motor-task-relevant stimulus.

### Developmental gamma band responses

As opposed to the overall age-related decrease in prestimulus gamma band activity, the power of phase-locked GBRs to auditory stimulation did not vary as a function of age from 9 to 16 years, nor were there any developmental changes in the stability (phase-locking) of stimulus-related gamma oscillations. Generally, these dissimilar developmental time courses point to a differential functional involvement of background and event-related gamma oscillations for attention task performance, as previously found for developmental alpha and theta oscillatory responses (Yordanova & Kolev, 1996, 1998b). Thus, the ability to synchronize evoked fast-frequency responses reflects processing abilities in children that are not identical to those indexed by power values of the ongoing EEG activity.

### Side of stimulation effects

The side of stimulation effectively modulated GBRs in children from all age groups because left-side stimuli produced better synchronized gamma oscillations mainly over the right centro-parietal locations, i.e. over the hemisphere contralateral to the sensory input.

Traditionally, a right-ear advantage has been found for processing of verbal information (e.g. Ahonniska *et al.*, 1993; Gootjes *et al.*, 1999). Neuroanatomical investigations have correlated this effect with specific intrinsic circuitry in the left temporal cortex of humans in relation with language-relevant mechanisms (Salmelin *et al.*, 1999; Galuske *et al.*, 2000). In contrast, in a dichotic complex tone test, a left-ear advantage was evident in 70% of the subjects, with right-hemisphere brain potentials at parietal sites manifesting greater amplitudes than the left-hemisphere ones (Tenke *et al.*, 1993). Also in contrast to verbal discrimination, during a pitch discrimination task, a left-ear advantage has been observed, with lateralization effects expressed for the latencies of early ERP components (Wioland *et al.*, 1999). By studying patients with focal temporal lobe damage, it has been shown that structures in the right temporal gyrus are specialized for the retention of pitch in auditory short-term memory (Zatorre & Samson, 1991). Moreover, a previous MEG study has found that both the spectral gamma band amplitude and coherence manifest right-hemisphere increases to left-lateralized auditory deviants, whereas right-lateralized deviants have produced equally strong effects over both hemispheres (Kaiser *et al.*, 2000). In the context of these previous findings, the present results of larger GBR power and phase-locking at right central-parietal locations to left-side stimuli in the auditory focused attention task may be suggested to reflect a spatially localized gamma-band network specifically involved in auditory short-term memory and, accordingly, in tone discrimination or spatial orientation (Kaiser *et al.*, 2000). Currently established absence of significant age effects implies that no variations in this type of functional involvement seem to accompany development.

### Task-related effects on developmental GBR

Importantly, age-related changes were found for the functional reactivity of phase-locked gamma responses. In 9–12-year-old children, GBRs depended primarily on stimulus type relevance (target or nontarget type), whereas in 13–16-year-old adolescents, GBRs depended on the attended channel. It appears therefore that the mode of task-stimulus evaluation in early processing stages is reflected by activated processing networks in the gamma range.

As previously stated (Yordanova *et al.*, 2000, 2001), frontal GBR increase to target stimulus type in the groups of 9–12-year-olds is likely to reflect the fact that, in these children, target selection is guided by external stimulus features. In contrast, after the age of 12 years, focusing to the attended channel became effective in guiding relevant stimulus selection, as established for adults (Tiitinen *et al.*, 1993). These age effects may be suggested to reflect a developmental increase in the ability to form and actively maintain an attentional focus. In addition, the interstimulus intervals used in this study (1150–1550 ms) were longer than those capable of imposing an effective selective-attention focus in adults (Tiitinen *et al.*, 1993). Thus, the enhancement of frontal gamma responses to target features in younger children may also be associated with increased attentional orientation to external stimuli due to a greater distractability as promoted by the long interstimulus intervals in these children (Coull, 1998).

In addition, a prominent increase in GBR power and phase-locking over the hemisphere contra-lateral to the responding hand was found only for younger age groups, which may be associated with motor response programming (Jokeit & Makeig, 1994). Preparatory motor preprogramming is further implied by the present observation of left over right frontal dominance in the prestimulus gamma band activity, which was detected for all age groups. Hence, a modulatory effect of preactivated motor programs on poststimulus GBR is conceivable only for young children (Murthy & Fetz, 1992; Jokeit & Makeig, 1994; Murthy & Fetz, 1996; Roelfsema *et al.*, 1997). Altogether, the functional reactivity of the GBR in the age of 9–12 years may reflect a less developed capability of younger children to efficiently disentangle sensory and motor preparatory sets associated with motor target selection (Rothenberger, 1990). In adolescents, a developmental increase in the capacity to maintain attentional focus and tune motor vs. sensory expectations leads to an age-specific mode of task stimulus processing, which is subserved by different gamma band networks.

### Theoretical implications

The present findings on age-, task-, and topography-specific reactivity of GBRs imply that phase-locked gamma oscillations are associated with early attention processes, perhaps by modifying the strength of neural representation of sensory input at the entry level of cortical representation systems (Nagarajan *et al.*, 1999). Also, it appears that scalp-recorded GBR may reveal the maturation of task processing modes or strategies, possibly induced by differential functional engagement of brain attentional networks controlling behaviour (Posner & Dehaene, 1994; Posner, 1994). Among them, an executive-control network including the frontal areas has been related to the

control of goal-directed actions, target detection, error and conflict resolution. Another, a so called orienting network covering the parietal cortex is thought to be responsible for covert orienting to the spatial location of sensory signals (Berger & Posner, 2000). The present developmental findings from the GBR may reflect a differential involvement of the anterior and posterior attentional networks in children and adolescents. The transition of GBR functional reactivity took place at 12–13 years. Given that the age of 12 years marks a step-wise shift in cognitive development (Piaget, 1970; Mussen *et al*., 1984; Stauder, 1992), this age-related transition in GBR reactivity may be linked to the employment of different attentional networks subserving new processing strategies emerging in the course of development.

## Conclusions

Phase-locked gamma oscillations generated within 120 ms after an auditory task stimulus are associated with early attention processes. The activation of functionally relevant gamma networks can be identified at spatially localized scalp areas as enhancement of power and synchronization of phase-locked gamma oscillations.

Both the neuronal substrates of gamma networks and the ability to synchronize these networks in relation to task-specific processes are available in children and adolescents from 9 to 16 years of age. Developmental changes in the task reactivity of synchronized gamma oscillations may provide evidence for a transition in cognitive processing strategies emerging at the age of 12–13 years.

## Acknowledgements

## Abbreviations

CBCL, Child Behaviour Checklist; d.f., degree of freedom; EEG, electroencephalogram; EMG, electromyogram; EOG, electrooculogram; ERP, event-related brain potential; GBR, gamma band response; MEG, magnetoencephalogram; MFFT, Matching Familiar Figures Test; RT, reaction time; SPL, sound pressure level; WT, wavelet transform.

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