EEG theta rhythm in infants and preschool children

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Abstract

Objective: To study behavioral correlates of theta oscillations in infants and preschool children.

Methods: EEG was recorded during baseline (visual attention) and two test conditions—exploration of toys and attention to 'social' stimulation. Age specific frequency boundaries of theta and mu rhythms were assessed using narrow bin analysis of EEG spectra.

Results: Theta spectral power increased whereas mu power decreased under test conditions in both age groups. In preschoolers theta rhythm increased predominantly over anterior regions during exploratory behavior and over posterior regions during attention to social stimulation. Theta frequency range changed with age from 3.6 to 5.6 Hz in infants to 4–8 Hz in children, and mu range from 6.4–8.4 Hz to 8.4–10.4 Hz.

Conclusions: In early life, theta oscillations are strongly related to behavioral states with substantial attentional and emotional load. The scalp distribution of theta spectral power depends on age and behavioral condition and may reflect engagement of different brain networks in control of behavior.

Significance: The findings contribute to the scanty knowledge about the developmental course of theta rhythm. Data on behavioral correlates of theta rhythm in early life may improve our understanding of cognitive and mental processes in healthy and neuropsychiatrically diseased children.

1. Introduction

It is now commonly acknowledged that in waking adults slow-wave EEG rhythms, in particular those in the theta range, are intimately related to cognitive and emotional processes (Aftanas et al., 2001, 2004; Inanaga, 1998; Kahana et al., 2001; Kirk and Mackay, 2003; Klimesch, 1999). Theta activity is abundant in the EEG of infants and young children and this feature is generally considered as a sign of immaturity (Clarke et al., 2001; Somsen et al., 1997). However, even in infancy spontaneous theta oscillations are closely related to behavior. The appearance of a peculiar 'hedonic' 4–6 Hz rhythm in infants and toddlers during positive affect, evoked by a new puppet or tactile stimulation, was described in 1971 (Kugler and Laub, 1971; Maulsby, 1971). Since then, a large number of

conditions provoking both positive and negative affective states in infants have been shown to be accompanied by high amplitude theta rhythm (Futagi, 1998 no. 121; Lehtonen et al., 2002; Nikitina et al., 1985; Paul et al., 1996; Posikera et al., 1986; Stroganova and Posikera, 1993). However, in spite of the effectiveness of emotional stimuli for provoking theta rhythm in infants, even in this early age the significance of theta oscillations probably extends far beyond their being the correlates of emotional arousal. The neurophysiological mechanism linking theta to behavior was proposed by Miller (1991) in his theory of Cortico-Hippocampal interplay. He argued that "… the periods of animal's activities when information important to that species requires to be gathered from the environment, are the times when theta synchronization is most likely to be generated in the hippocampus." He further argued that the phenomenon of the theta rhythm is common for mammalian species and reflects functional coupling of limbic and cortical neurons. Miller predicted that for primates,

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including man, "the most potent way of triggering theta rhythm… would be by the use of socially significant stimuli, or novel stimuli." Indeed, social stimulation and exploration of new objects very effectively elicit theta rhythm in infants (Nikitina et al., 1985; Posikera et al., 1986; Stroganova and Posikera, 1993). Experimental studies in humans and animals show that theta oscillations are important for neural plasticity and information coding (Kahana et al., 2001). Thus, the theta rhythm may be a unitary phenomenon in humans and animals. This line of reasoning leads us to suggest that the functional significance of theta rhythm in infants and children may be similar to that in adults. Indeed, in infants as well as in adults, theta rhythm is related to both emotional (Maulsby, 1971; Posikera et al., 1986) and cognitive (Orekhova et al., 1999; Stroganova et al., 1998) processes.

Taking into account the close relation of theta oscillations to cognition and emotions, the age-related changes of theta rhythm may provide valuable information for developmental neurophysiology. Surprisingly, theta oscillations and their relation to behavioral states have received little attention in developmental EEG research. Specifically, there is no information on scalp topography, behavioral correlates, and frequency range of the theta rhythm in young children, beyond the infancy period. In the present study, we focused on the properties of theta oscillations in preschool children in comparison with infant theta. We expected that the prominent state-related theta synchronization may not be exclusively the feature of infant EEG but can be evoked in older children during situations of species-specific and subjective importance, such as social interaction with an adult (e.g. child-addressed speech) and exploration of unfamiliar attractive toys.

The comparison of theta oscillations in infants and preschool children is complicated by the lack of consistent knowledge about frequency boundaries of functionally meaningful EEG bands in early life. The frequency characteristics of EEG rhythmical components change with development (Hudspeth and Pribram, 1992). Therefore, identification of alpha, theta and delta bands in EEG is important for correct interpretation of the results of any developmental EEG study. There is, however, a great discrepancy in opinions on the theta and alpha frequency ranges throughout ontogeny. In infant EEG research, for example, one recent study designated the frequency band 4–8 Hz as theta (Futagi et al., 1998), while another study described the same frequency band as alpha rhythm (Schmidt et al., 2003). Some authors use arbitrary frequency bands without denoting them as theta or alpha (Bell and Fox, 1997; Bell, 2002).

Such discrepancy inevitably leads to inconsistency in results and contradictions in their interpretation. To overcome this problem, we proposed to analyze narrow frequency bins of the spectrum using a 'functional topography' approach (Kuhlman, 1980; Stroganova et al., 1999). This strategy implies inspection of the 'behavior' of

the adjacent frequency bins (e.g. 0.4 Hz) under adequate functional load, provoking topographically specific amplitude changes in a given physiological rhythm. The similarity in reactive changes of adjacent frequency bins and correspondence of the direction of changes and the scalp topography with the well-known properties of the physiological rhythm of interest helps to identify the age-specific frequency boundaries. In our previous infant EEG studies using narrow-bin analysis, we have identified 4 co-existing rhythms that bear functional and topographic similarity with 4 EEG rhythms in adults: delta, theta, central alpha (mu) and occipital alpha (Orekhova et al., 1999; Stroganova, 1987; Stroganova et al., 1999). We found that the frequency band 6–9 Hz in infant EEG was similar to adult alpha (8–12 Hz) and, analogous to the alpha band in adults, comprised two rhythms of the 'alpha family'— occipital alpha and central mu rhythm. The frequency band 3.6–5.6 Hz was similar to adult theta (4–8 Hz) (Orekhova et al., 1999; Stroganova et al., 1999).

Less is known about the frequency boundaries of alpha, mu and theta rhythms in preschool children. Although recent EEG research on toddlers and preschool children applied 'infant' 4–6 theta and 6–9 Hz alpha frequency bands (Jones et al., 2000; Marshall and Fox, 2004; Wolfe and Bell, 2004) it is unclear whether this choice is adequate. The frequency of the theta rhythm, as well as the frequencies of alpha and mu rhythms, may increase with age and in older children the 6–9 Hz band may include an essential part of the functional theta range. A correct discrimination between functionally meaningful theta and alpha frequency bands is especially important, given the tendency of these rhythms to demonstrate opposite direction of state- and task-related changes (Klimesch, 1999).

In the present study, we used the narrow frequency bins analysis strategy to define a functionally meaningful theta band in preschool children and to compare it with that of infants. The EEG was registered in infants aged 7–12 months and in preschool children, under baseline and two experimental conditions. During baseline, the subject remained still and his/her attention was attracted by novel visual stimuli. We expected that this condition of behavioral stillness and sustained visual attention would be characterized by a relatively low level of theta activity and the expression of central sensorimotor (mu) rhythm (Mulholland, 1995; Stroganova et al., 1999). The other two experimental conditions represented natural behavioral situations involving a higher degree of emotional and cognitive load; exploration of unfamiliar attractive toys and attention to child-addressed speech during communication with an adult. Based on previous findings (Nikitina et al., 1985; Posikera et al., 1986; Stroganova and Posikera, 1993) we expected that both conditions would provoke a pronounced theta increase that would be widely distributed over the scalp with the most prominent theta response over associative (parietal, temporal, frontal) cortical areas. Concurrently, the reactive changes of spectral power in

mu frequency bins should be opposite to those of theta, at least under the condition of exploration of toys. An active manipulating with objects, accompanied by hand movements, should lead to reduced spectral power of frequency bins within the mu range compared to baseline. The topographical maximum of this state-related power decline should be over the central scalp regions. Thus, comparison of baseline and manipulation conditions allows separation of theta and mu frequency ranges based on two criteria: opposite direction of spectral power changes and differences in the distribution of maximal power changes across the scalp areas.

To summarize, as a first step we planned to corroborate our previous findings on theta and mu frequency boundaries in infants, and as a second step to justify the application of certain mu and theta frequency bands in the EEG of preschool children. As a final step, we compared the condition-related changes of the whole band theta spectral power in the two age groups. We expected that both the magnitude and scalp topography of the theta response would differ in infants and preschool children, reflecting developmental changes of theta-generating neural networks subserving behavior.

2. Method

2.1. Participants

2.1.1. Infants

Twenty eight healthy infant twins (19 male) were recruited in Moscow city. These subjects were included in a previous twin EEG study described elsewhere (Orekhova et al., 2003). In the present study, we considered the data obtained from only one member of a twin pair. The criterion of inclusion was at least 30 s of artifact-free EEG record sampled under each of the 3 experimental conditions described below. All infants were born between 32 and 40 weeks of gestation (mean 36.7, SD 2.0) and weighed between 1900 and 3500 (mean 2505, SD 364) grams at birth. Their chronological age ranged from 8.0 to 12.4 months (mean 10.0, SD 1.5) and the age corrected for the period of gestation ranged from 6.3 to 11.7 months (mean 9.2, SD 1.3). The psychomotor and mental developmental indexes, assessed by Bayley scales of infant development (Bayley, 1969) were within the normal range in all subjects.

2.1.2. Preschool children

Nineteen preschool children were recruited by advertisements in Gothenburg city and suburbs. The parents gave informed consent as approved by the Ethics Committee. According to parent reports, the children had no neurological or other known medical problems. Three children were excluded because of pathological paroxysmal activity in the EEG, excessive artifacts, or negative mood and the absence of eye contact with the experimenter under 'Speech'

condition. The 16 children included in the study (11 male) ranged from 3 years 8 months to 6 years 11 months in age (mean 5 years 5 months, SD 359 days). Fifteen subjects were right-handed and one was left-handed.

2.2. Experimental conditions

2.2.1. Infants

During the whole experiment, the infant was sitting on the mother's lap. EEG was registered under 3 experimental conditions, each of approx. 2 min duration. The infant behavior was video monitored throughout the session and synchronized with the EEG recording. During the first condition (baseline), the infant was looking at an adult blowing soap bubbles 1.5–2 m away. The situation was terminated if the subject demonstrated overt signs of emotional expression (smile, fussiness, vocalization, etc.). The periods when the subject remained still and attended to the soap bubbles were marked on-line at the EEG record and further analyzed. EEG corresponding to periods of overt affective reactions were also marked and not sampled. Thus, this baseline condition was characterized by absence of active movements and sustained visual attention. Under the second experimental condition (manipulation), the infant was presented with a box containing a number of relatively small unfamiliar toys. The EEG was sampled during periods of active exploration of toys (i.e. the infant grabs a toy, looks at it, keeps it in the hand or moves the toy from one hand to the other continuously tracking it visually, etc.). Periods when the infant was mouthing the toy or dropped it were excluded. During the third experimental situation (speech), the experimentor talked to the infant in the age-appropriate tone-modulated set (rhythmical speech, verse or song) in order to maximally attain her/his attention and interest. The distance between the infant and the adult was about 60 cm. The EEG was sampled during the periods of gazing at the face of the speaking adult. Throughout the study, these 3 experimental conditions will be addressed as 'Baseline', 'Manipulation' and 'Speech', respectively.

2.2.2. Preschool children

In children, EEG was recorded under 'Baseline', 'Manipulation' and 'Speech' experimental conditions similar to those for infants. The child's behavior was videotaped continuously throughout the session and synchronized with the EEG record. In the beginning of manipulation condition the experimentator presented the child with a box containing a number of small unfamiliar toys and suggested "look what we have here…" not giving other instructions. Periods when the child was actively manipulating the objects were chosen for EEG analysis. Under speech condition, the experimentor told a short fairy-tale story, sitting in front of the child at a distance of approx. 1 m. The fairy-tale was adapted from the Swedish collection of stories and fairy-tails for children (http://www.bums.nu/index.php, "Sagan om musen som hade gått vilse") and was

unfamiliar for participants. It was told with emotionally modulated tone. Periods when the child looked at the face of the speaking adult were selected for EEG analysis.

2.3. Recording and processing of EEG

2.3.1. Infants

The EEG recording was carried out in an electrically-shielded chamber. Ag/AgCl disc electrodes were placed at AF3, AF4, FC3, FC4, F7, F8, P7, P8, PO3, PO4, O1, and O2 positions according to the extended 10–20 positioning system (Pivik et al., 1993). The FC3 and FC4 electrode positions were used because they are more appropriate than C3 and C4 positions for registration of mu rhythm in infants, due to a more anterior location of the central sulcus in infants than in adults (Blume et al., 1974). Linked ears served as reference. The electrode impedance was kept below 10 kΩm. EEG was recorded on a Nihon Kohden 4217 G electroencephalograph using a time constant of 0.1 s and a high frequency cutoff of 30 Hz. The data were stored on magnitograph Teak XR-510 and digitized off-line at 256 Hz. The digitized EEG was visually checked for eye movements and motor artifacts. Periods of artifacts were eliminated from subsequent analyses. For each subject between 30 and 60 s of artifact-free record was obtained for each experimental condition. The EEG data were fast Fourier transformed using a 2.5 s window smoothed by Hanning weighting function and 50% overlap. Spectral power values were obtained for each of the 0.4-Hz bins within a 2.8–10 Hz range. The 10 Hz cut-off was applied because the small amplitude of the higher frequency EEG activity in infants did not allow distinction from myogenic artifacts. To normalize amplitude distributions, power values were log 10 transformed.

2.3.2. Preschool children

EEG was recorded using Quik-cap at 23 EEG electrode positions (Fp1, Fp2, AF3, AF4, F7, F8, F3, F4, T7, T8, C3, C4, P7, P8, P3, P4, PO3, PO4, O1, O2, Fz, Cz and Pz). EOG electrodes were placed above and below the left eyes as well as at the outer canti of both eyes. The ground electrode was positioned 3 cm anterior to Fz. Linked ears served as reference. The signal was amplified using a Schwarzer headbox with 0.4 s time constant and 70 Hz low-pass filter, and digitized on-line at 500 Hz. The electrophysiological data were saved on hard disk together with the video record. The EEG and EOG signals were post-hoc digitally filtered with 50 Hz notch and 0.5 Hz high pass filters. EEG was visually inspected and periods with movement artifacts, eye blinks or other vertical eye movements were rejected. Horizontal EOG artifacts were corrected separately for each condition, using ICA decomposition implemented in EEGlab software (Delorme and Makeig, 2004). The decomposition was based on all EEG and two symmetrical horizontal EOG channels. The ICA derived components were visually inspected and those reflecting horizontal eye movements were subtracted from the original signal. For each experimental condition, between 30 and 60 s of artifact-free EEG record was obtained for each subject. The EEG data were fast Fourier transformed using the same parameters as for infants. Log-transformed power was calculated for 0.4 bins within 2.8–11.6 Hz range.

2.4. Statistical analysis

This study was focused on comparison between baseline and each of the test conditions, separately within each age group. The data for infants and children were obtained in different laboratories using different recording parameters and artifact correction procedures. However, as the comparisons of spectral power values were performed separately within each age group, this fact was unlikely to influence the main results. In particular, the different time constants applied in infants and children are unlikely to influence the results systematically, because the linear filters used could only introduce a scaling coefficient that is eliminated when the difference between experimental conditions is analyzed.

Two types of repeated measures ANOVAs were performed, each one including baseline and one of the test conditions as the levels of condition repeated measures factor. The repeated measures factors were condition (manipulation vs. baseline or speech vs. baseline), electrode and hemisphere. The repeated measures ANOVAs were performed for each of the 0.4 Hz frequency bins within the 2.8–10.0 Hz (for infants) or 2.8–11.6 Hz (for children) ranges. The midline electrodes Fz, Cz and Pz were excluded from statistical analysis. In this study, only the effect of Condition and its interaction with the other repeated measures factors were analyzed. The application of ANOVA for a number of bins and electrode positions imposes a problem of correction for multiple comparisons (e.g. Bonferroni correction). However, due to the strong correlation of the power in adjacent frequency bins, application of such a correction would severely inflate the probability of false negative results (the type II error). Therefore, we choose to report uncorrected P values. We believe that this approach is appropriate for justification of the functionally meaningful EEG frequency bands. As soon as we had a clear prediction about condition-related behavior of theta and mu rhythms, the compliance of the direction of the spectral power changes in adjacent bins with such predictions constituted a strong argument in support of their inclusion in the same theta or mu range. This approach evidently requires cautiousness in interpretation of unpredicted results. We report such results, but did not derive the main conclusions of the study from them. Furthermore, narrow-bin analysis was just a preliminary step for the subsequent analysis of age and condition-related EEG changes within the whole theta and mu bands.

Adjacent frequency bins demonstrating the predicted properties of the theta or mu rhythms were combined into the same age specific theta or mu band. To compare the whole band theta power changes in relation to baseline under the

two test conditions the changes scores were calculated according to the formula: (POWman − POWbas)/POWbas × 100 or (POWspe − POWbas)/POWbas × 100, where POWman, POWspe and POWbas were the mean spectral power values under speech, manipulation or baseline conditions for the whole age adjusted theta band. ANOVA with factors condition (manipulation, speech), electrode (6 levels) and hemisphere (left, right) was performed on change score values. For this type of analysis Bonferroni procedure with correction for the mean correlation between variables (Uitenbroek, 2004) was adopted for post-hoc multiple tests.

For all ANOVAs the within subject effects with two or more degrees of freedom were adjusted using the Greenhouse-Geisser correction. The original degrees of freedom and corrected *P*-values are reported. Planned comparisons were used as post-hoc tests.

3. Results

3.1. Theta frequency range

3.1.1. Infants

Both manipulation with objects and social interaction with an adult resulted in a sharp increase of EEG activity within the 3.6–5.6 Hz range, with a distinct peak at 4.4 Hz in the EEG spectra (Fig. 1). Samples of the original EEG records of an infant demonstrating pronounced EEG synchronization at 4–5 Hz frequency under these conditions are shown in Fig. 2 (upper part).

Fig. 3(I) represents the narrow bin ANOVA results and results of the planned comparisons between baseline and each of the test conditions performed for each electrode position. Highly significant main effects of condition or its interaction with Electrode were observed for spectral power within the 3.6–5.6 frequency range, and were due to power increase under each of the test conditions compared to baseline. During manipulation, the condition effect was also significant for the 2.8 and 3.2 Hz frequency bins. This increase of power in the lower frequencies could be a true EEG phenomenon related to increase of delta power caused by mental activity (Harmony et al., 1996) during exploratory behavior. Alternatively, it could represent an artifact, induced by minor head and body movements, which are unavoidable during manipulation with toys.

Thus, EEG activity within the 3.6–5.6 Hz range demonstrated a generalized increase of spectral power, as was expected for infant theta rhythm. A close inspection of condition × electrode interactions for 3.6–5.6 spectral power revealed a possible heterogeneity of this band in
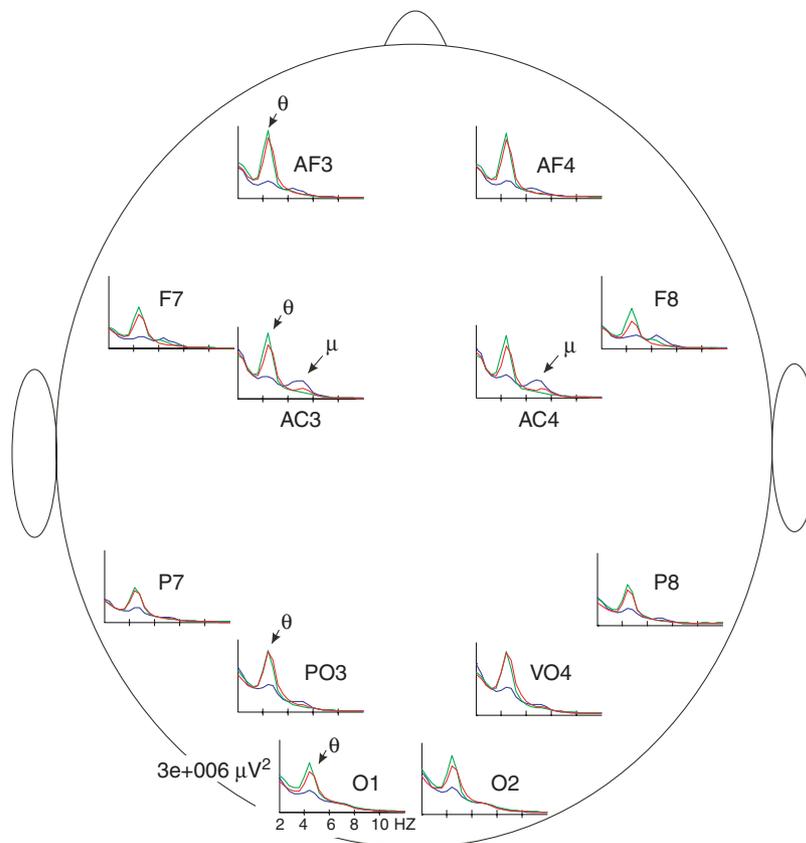

Fig. 1. Grand average power spectra in infants under three experimental conditions. Blue line—visual attention (baseline); green line—exploration of toys; red line—attention to social stimulation. The spectral peak of 6–8 Hz sensorimotor rhythm (μ) is evident over precentral regions under baseline condition. The prominent generalized theta peak (θ) with a maximum of 4.4 Hz is observed under both test conditions.
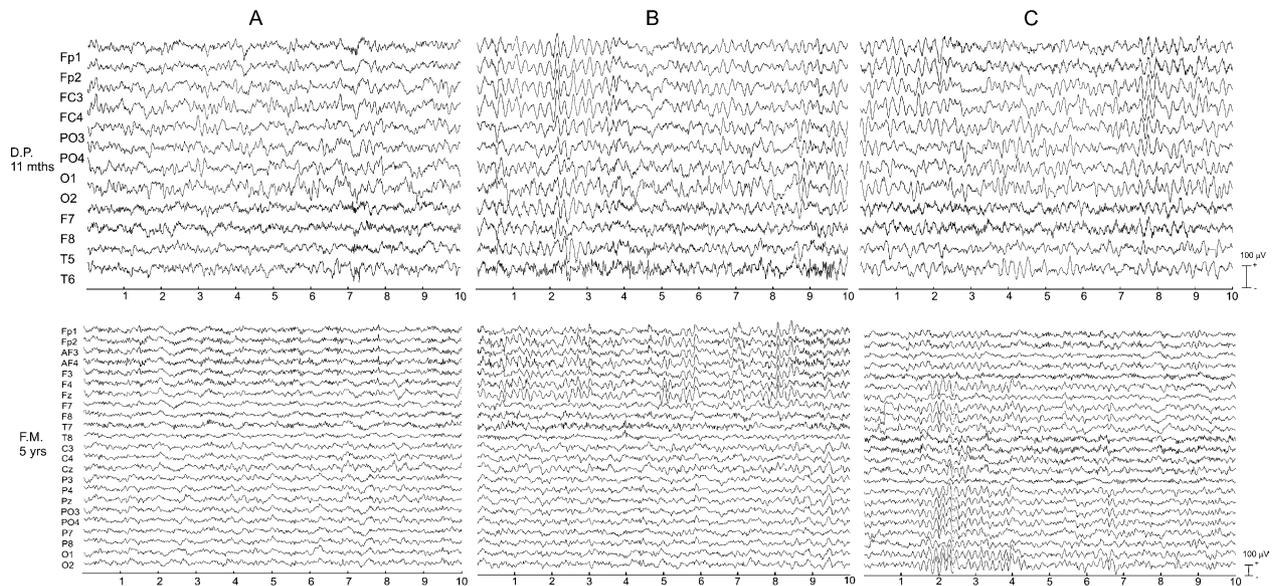
Fig. 2. Examples of 10 s EEG records in two boys (11 months and 5 years). (A) Visual attention (baseline); (B) exploration of toys; (C) attention to social stimulation. In the infant, prominent generalized 4–5 Hz theta rhythm is evident under conditions B and C. In the 5-year-old child, the 6 Hz theta rhythm is expressed over frontal regions during exploratory activity and predominantly over posterior regions during attention to speech.

infants. For the lower frequencies of this band (4.0 and 4.4 Hz), a predominantly frontal increase of power was observed under both experimental conditions. The planned comparisons of least square means showed that the power increase at 4.0 and 4.4 Hz during manipulation, relative to baseline, was significantly greater for the frontal electrodes that were pooled together (Fp1, Fp2, F7, F8) as compared to all other electrode sites combined (both $Fs_{(1,27)} > 8.3$, $P_s < 0.01$). This effect was even more prominent for the speech condition ($Fs_{(1,27)} > 6.0$; 4.0 Hz, $P < 0.05$; 4.4 Hz, $P < 0.001$, 4.8 Hz, $P < 0.0001$). In contrast, significant condition×electrode interactions at the high boundary of the range (5.6 Hz) was due to power increase over the posterior temporal scalp areas during manipulation and over temporo-parieto-occipital regions during speech (Fig. 3(I)A,B). Despite the differences in scalp topography between higher and lower frequencies within the 3.6–5.6 Hz range, in both cases the maximum power increase was over the associative cortical areas (frontal or TPO). This topographical distribution complies with that predicted for a theta rhythm.

To compare the whole-band theta power changes under the two test conditions in relation to baseline, the ANOVA was performed for the change score values calculated for the mean spectral power across the whole theta band (3.6–5.6 Hz). There was a highly significant main effect of electrode ($F_{(5,135)} = 8.3509$, $P < 0.0003$) due to the distinct predominance of theta increase over anterior frontal electrode positions under the both test conditions (Fig. 4).

3.1.2. Preschool children

In children, both manipulation of objects and attention to social stimulation resulted in a prominent increase of 4.0–7.6 Hz spectral power, as compared to baseline. The EEG power spectra of both test conditions were characterized by distinct peaks, with a peak frequency of about 6 Hz (Fig. 5). The main effect of condition was significant for both manipulation and speech ANOVAs for all frequency bins within the 4.0–7.6 Hz range (Fig. 3(II)).

There was a striking topographical difference in the state-related change of 4–7.6 Hz power under the two test conditions. This was evident from the grand average power spectra (Fig. 5), and clearly observable also in some individual EEG records (Fig. 2, lower part). During manipulation with toys 4–7.6 Hz power increased predominantly over the frontal and temporal scalp areas, whereas during attention to speech in the situation of interaction with an adult it increased mainly over posterior scalp regions. The condition×electrode interaction was significant in the case of both manipulation and speech ANOVAs (Fig. 3(II)A,B). Planned comparisons of the pooled frontal and temporal (Fp1, Fp2, AF3, AF4, F7, F8, F3, F4, T7, T8) electrode sites against pooled central and posterior (P7, P8, P3, P4, PO3, PO4, O1, O2) electrode sites revealed significant fronto-temporal predominance of the power increase during manipulation ($F_{(1,15)} > 8.85$, $P < 0.05$ for all bins within 4.4–7.6 Hz range) and a more posterior predominance during speech ($F_{(1,15)} > 7.6$, $P < 0.05$ for all bins within 4–7.6 Hz range) as compared to baseline.

For the 8.0 Hz bin, the main effect of Condition was not significant. However, as evident from significant condition×electrode interactions (Fig. 3(II)A,B), the pattern of state-related power changes at this frequency resembled that of the 4–7.6 Hz range.

Thus, in children spectral power in frequency bins within the 4–7.6 Hz range increased under the test condition, when a theta increase would be expected. Moreover, all frequency
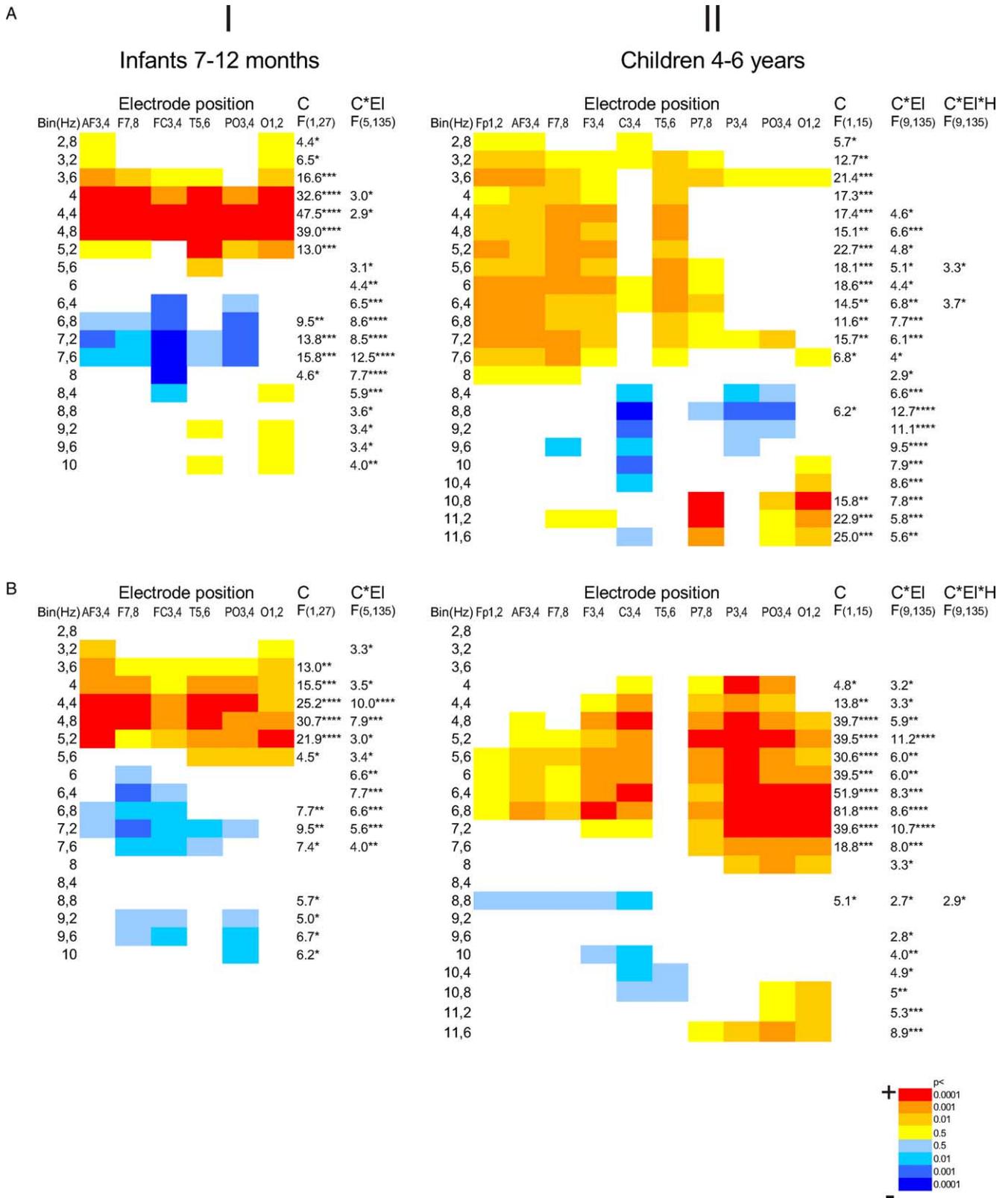
Fig. 3. ANOVA results and frequency-by-location probability plot. ANOVAs were performed separately for each age group (I—infants, II—children) and frequency bin. The color plots show the spatial distribution of P values for planned comparisons of spectral power between baseline (visual attention) condition and one of the test conditions: manipulation with toys (A) or attention to social stimulation (B). The planned comparisons were performed for pairs of symmetrical electrode locations pooled together. Yellow to red colors denote an increase, and light-blue to blue a decrease, of spectral power under the test condition relative to baseline. Color maps are shown only for frequency bins demonstrating significant main effect of condition (C) or its interaction with electrode position (C×El) or electrode and hemisphere (C×El×H). The F- and Pvalues for significant ANOVA effects are shown on the right side of the corresponding bin color plot: *P<0.05, **P<0.01, ***P<0.001, ****P<0.0001.
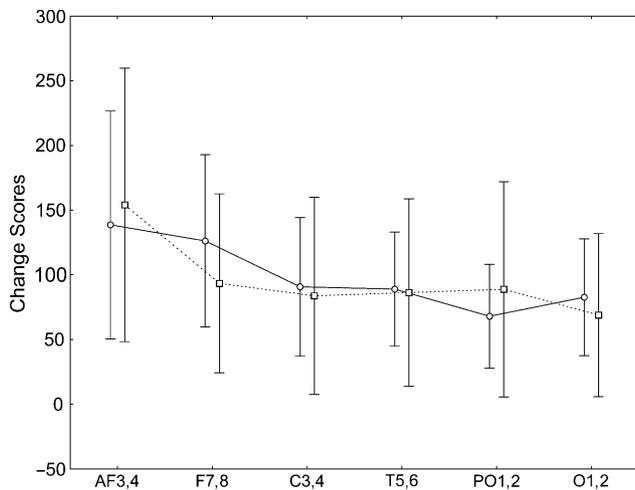
Fig. 4. The change scores of the wide-band (3.6–5.6 Hz) theta spectral power in infants. Solid line represents manipulation with toys; dashed line represents attention to social stimulation. Change scores were calculated according to the formula: (testcondition − baseline)/baseline × 100. Under both conditions theta increases predominantly over frontal regions as documented by the main effect of electrode: $F_{(5,135)} = 8.35$, $P < 0.0003$ and absence of significant electrode × condition interaction. Here and further on, vertical bars denote 0.95% confidence intervals.

bins within the 4–8 Hz range demonstrated similar task-related scalp topography. These facts strongly support assigning all discrete frequency bins of the 4–7.6(8) Hz range to the functional theta band in 4–6-year-old children.

During manipulation, the power growth was significant also at the lower frequencies (2.8, 3.2, 3.6 Hz). However, there was no significant condition × electrode interaction in this case, suggesting a more wide-spread scalp distribution of the spectral power. The increase of slow wave power in children, like in infants, could be either a true EEG phenomenon (Harmony et al., 1996) or stem from the artifacts of mild head and body movements.

For manipulation, narrow bin ANOVAs revealed a significant condition × electrode × hemisphere effect for the 5.6 and 6.4 Hz frequency bins. Planned comparisons suggested that this effect was due to the right-side predominance of state-related power increase over pre-frontal (Fp1 < Fp2), anterior frontal (AF3 < AF4), and frontal regions (F3 < F4) and its left-side predominance over middle and posterior lateral sites (T7 > T8, P7 > P8).

To compare the whole band theta power changes under the two test conditions in relation to baseline, the ANOVA
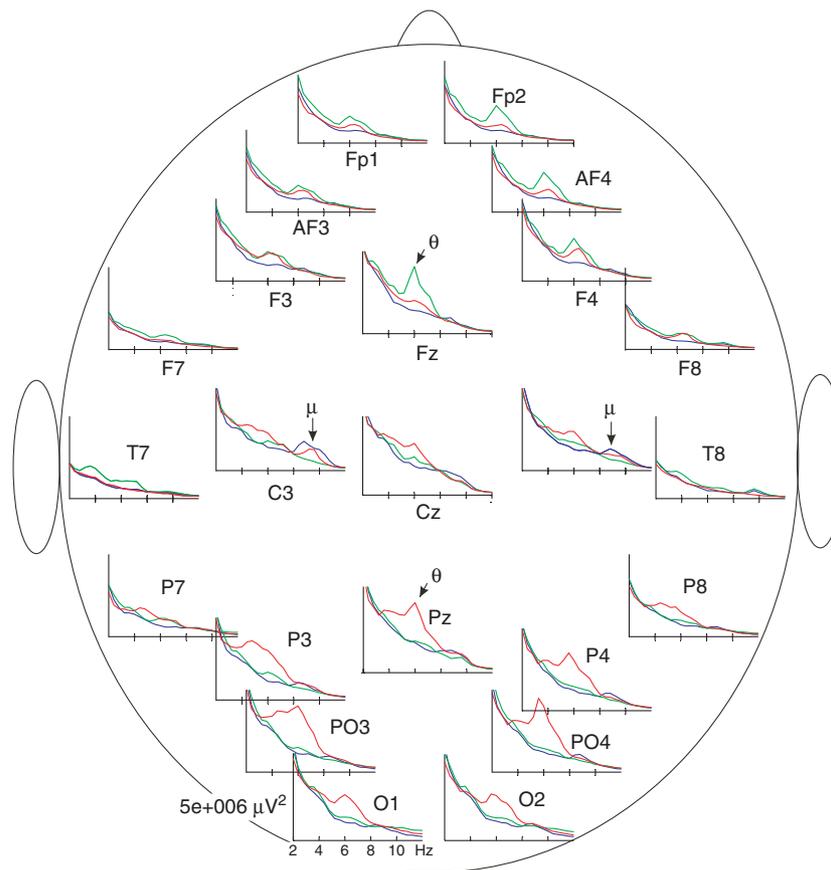

Fig. 5. Grand average power spectra in preschool children under 3 experimental conditions. Blue line—visual attention (baseline); green line—exploration of toys; red line— attention to social stimulation. The spectral peak of 8–10 Hz sensorimotor rhythm (μ) is evident over central regions under baseline condition. The prominent peaks of theta rhythm (θ) with maximum of about 6.0 Hz are observed over anterior regions during manipulation with toys and predominantly over posterior regions during attention to social stimulation. Note, that the absolute power values on Figs. 1 and 5 are not directly comparable due to different sampling frequencies and high-pass filters applied.
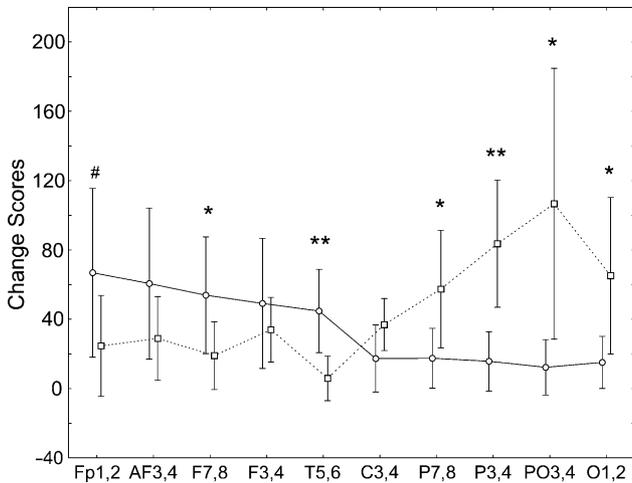
Fig. 6. Change scores of the wide-band (4.0–7.6 Hz) theta spectral power in children. The designations are the same as in Fig. 4. Theta power increases predominantly over frontal electrode locations during manipulation with toys and over parietal locations during social stimulation. The electrode × condition interaction effect is highly significant: $F_{(9,135)} = 17.515$, $P < 0.00002$. The Bonferroni adjusted probabilities of difference between manipulation and speech change scores at the separate electrode locations: #$P < 0.1$, *$P < 0.05$, **$P < 0.01$.

was performed on the change score calculated for the whole 4–7.6 Hz range. There was highly significant condition × electrode interaction ($F_{(9,135)} = 17.5$, $P < 0.00002$), due to a predominance of theta increase over prefrontal and anterior frontal areas during manipulation and over parietal and posterior parietal regions during speech (Fig. 6).

3.2. Mu frequency range

3.2.1. Infants

Compared to baseline, both experimental conditions were accompanied by a significant reduction of spectral power for the majority of frequency bins lying within previously defined (Stroganova et al., 1999) infant alpha range (6–9 Hz) (Fig. 3(I)A,B). In addition, during manipulation the power increased at the 8.4 Hz and higher frequency bins over occipital and temporal regions. The probable explanation for this increase is that myogenic artifacts, originating from the neck muscles involved in the head movements during manipulation, contaminated the EEG at these electrode locations.

As implied by significant electrode by condition interactions, the alpha power reduction depended on the electrode location under both test conditions. In the manipulation/baseline comparison, the condition × electrode interactions for alpha frequency bins (6.4–8.4 Hz) were due to the predominant suppression of the power over the precentral scalp regions, where the spectral peak of the mu rhythm was observed (Fig. 1). This result corresponds well with our previous results on the frequency range of the

mu rhythm (6.0–8.8 Hz) in infants in the second half of the first year of life.

In the speech/baseline comparison the same phenomenon—predominant suppression of alpha frequency bins power over the anterior scalp regions—was seemingly less prominent (Fig. 3(I)B). As planned comparisons revealed, reduction of alpha power within the 6.4–7.6 Hz frequency range during speech was greater over pooled precentral and lateral frontal electrodes as compared to all other electrodes pooled together ($F_{(1,27)} > 12.3$, $P < 0.05$ for all bins within this range).

To compare the dynamics of the central mu rhythm under the 3 experimental conditions, a separate ANOVA with repeated measures factors condition (baseline, manipulation, speech) and hemisphere was performed for the mean 6.4–8.4 Hz power over precentral electrode positions (FC3, FC4). The main effect of condition was highly significant ($F_{(2,54)} = 27.1$, $P < 0.000001$). The planned comparisons showed that the spectral power of the central mu rhythm decreased from attention to speech ($F_{(1,27)} = 13.0$, $P < 0.002$) and further decreased from speech to manipulation condition ($F_{(1,27)} = 13.5$, $P < 0.002$). Thus, in accordance with the well-known properties of mu rhythm (Pfurtscheller and Neuper, 1994) the experimental condition that was associated with active hand movements provoked the greatest reduction of mu spectral power over the precentral scalp areas. There was also a significant effect of hemisphere ($F_{(1,27)} = 13.4$, $P < 0.002$) due to the left-side predominance of the central rhythm.

3.2.2. Preschool children

The ANOVA results and inspection of the respective means showed that at 8.4 Hz and higher frequency bins, in sharp contrast to the lower frequencies, EEG power predominantly decreased during the test conditions as compared to baseline (Fig. 3(II)A,B). In addition, there was significant increase of the power at 10.0 Hz and higher frequencies over the occipital and posterior temporal scalp regions. This appeared more pronounced during manipulation, and may reflect a myogenic artifact from the neck muscles.

Under baseline (visual attention) condition there were distinct peaks of spectral power between 8 and 11 Hz at the central regions. Similar spectral peaks, although of smaller magnitude, were evident during speech but were not observed during manipulation (Fig. 5). In the manipulation/baseline comparison, ANOVAs revealed significant electrode × condition interactions for all the bins within the 8.4–10.4 Hz range. The planned comparisons confirmed that all the bins of this range showed decreased power over the central regions during manipulation, as compared to baseline (for planned comparisons all $P_s < 0.01$). Hence, by its topography and functional reactivity this 8.4–10.4 Hz rhythmic component represents the mu rhythm of child EEG.
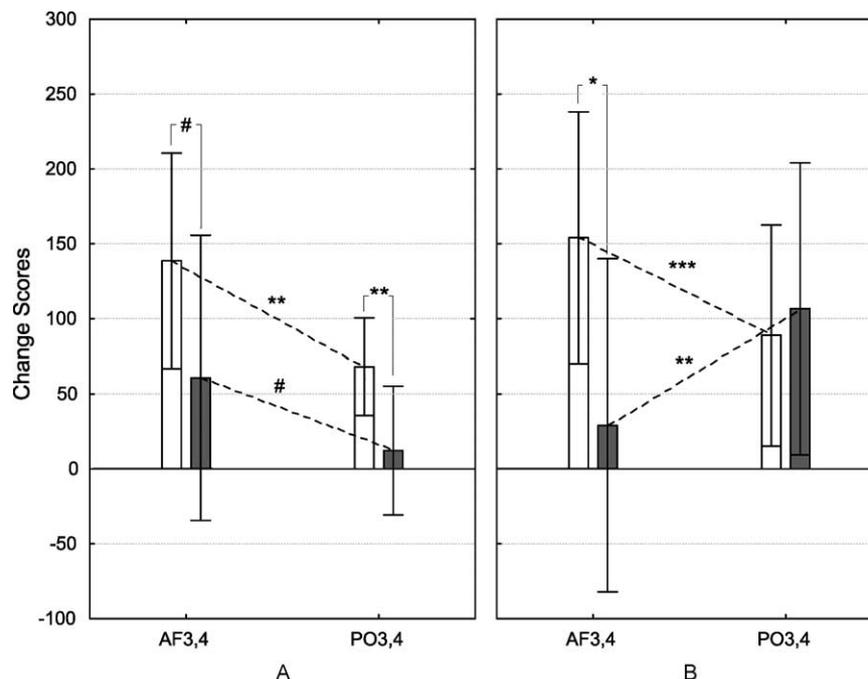
To compare the dynamics of the central mu rhythm under the 3 experimental conditions, a separate ANOVA with repeated measures factors condition (baseline, manipulation, speech) and hemisphere (left, right) was performed for the mean 8.4–10.4 Hz power over central electrode positions (C3, C4). The main effect of condition was highly significant $(F_{(2,30)} = 16.428, P < 0.00002)$. The planned comparisons showed that, similar to infants, the amount of central mu rhythm in children decreased from attention to speech $(F_{(1,15)} = 5.5, P < 0.05)$ and decreased further from speech to manipulation $(F_{(1,15)} = 10.6, P < 0.006)$. Furthermore, there was a significant condition × hemisphere effect $(F_{(2,30)} = 4.1969, P < 0.03)$ due to the left-side predominance of the central mu power during baseline (attention) condition $(F_{(1,15)} = 5.2, P < 0.05)$.

The decrease of 8.4–10.4 Hz power under the test conditions was not exclusively due to suppression of the central mu rhythm. The spectral power of some frequency bins within this range decreased symmetrically over parietal and parieto-occipital regions during manipulation and over frontal regions during speech as compared to baseline (Fig. 3(II)A,B).

3.3. Comparison of condition-related theta power changes in preschool children and infants

Verification of the age-specific frequency boundaries of the theta band in infants and preschool children allows tracking of the developmental changes in scalp topography and functional reactivity of the theta rhythm from infancy to childhood. The difference in recording parameters and artifact rejection techniques used in the two laboratories prevents direct statistical comparison of EEG power values between the two age groups. Nevertheless, the condition-related power changes relative to the baseline level (change scores) were unlikely to depend on these methodological differences. As the age-related differences in topographical distribution of the theta power seemed to be most prominent in anterior–posterior direction, we compared change scores in infants and children for the electrode positions AF3, AF4, PO3 and PO4 that were the same for the two age groups. Change scores were calculated for the mean spectral power of the whole theta bands (3.6–5.6 Hz in infants and 4.0–7.6 Hz in children). ANOVA was performed with factors group, condition (manipulation vs. speech), electrode and hemisphere. There was a significant group effect due to a greater state-related increase of theta power in infants than in children $(F_{(1,42)} = 4.1, P = 0.05)$. There was also a significant group × condition × electrode interaction effect $(F(1, 42) = 10.8, P < 0.002)$ that is illustrated in Fig. 7. During manipulation theta power increased predominantly over anterior scalp areas in both groups, whereas during speech it increased predominantly over anterior scalp areas in infants and over posterior scalp areas in children.

Fig. 7. The comparison of whole-band theta power change scores in infants (open bars) and preschool children (closed bars). (A) manipulation with toys; (B) social stimulation. Differences between groups or electrode locations: $^{#}P < 0.1$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. During manipulation, a frontal maximum of the theta increase is observed in both groups, whereas during attention to social stimulation the topography of the theta response is different in infants and preschool children.

4. Discussion

4.1. Identification of theta and mu frequency bands in infants and preschool children

According to the narrow-bin functional topography approach described in the introduction, the EEG theta frequency band in infants and children can be defined as the cluster of adjacent narrow frequency bins whose properties comply with the previously described properties of the theta rhythm. The theta rhythm is known to synchronize under conditions of emotional (Aftanas et al., 2001, 2004; Kugler and Laub, 1971; Maulsby, 1971; Nikitina et al., 1985; Orekhova et al., 1999; Posikera et al., 1986; Walter and Walter, 1949) and/or cognitive (Inanaga, 1998; Kahana et al., 2001; Kirk and Mackay, 2003; Orekhova et al., 1999) load. Its other defining feature is a predominance of these task-related changes over associative (parietal, temporal, or frontal) cortical areas (Demiralp and Basar, 1992; Maulsby, 1971; Nikitina et al., 1985; Orekhova et al., 1999). A frequency component with these properties did exist in both age groups. The spectral power increased under theta-provoking test conditions (attention to an adult's speech and exploration of toys) over the associative cortical areas in both infants and children, but within different frequency ranges. Infant's theta band included frequency bins from 3.6 to 5.6 Hz, whereas in preschool children it ranged from 4.0 up to 7.6 (8) Hz.

In infants the scalp distribution of the higher theta frequency bin (5.6 Hz) power was different from that of the bins near the theta peak frequency (4–4.8 Hz). The 5.6 Hz theta power increased predominantly over posterior temporal (during manipulation) or occipito-parieto-temporal (during speech) scalp regions. In an earlier study in infants of the same age range, we also observed predominantly posterior temporal increase of the high frequency (5.2–6.0 Hz) theta during anticipatory attention, whereas theta rhythm of the lower range (3.6–4.8 Hz) increased predominantly over the frontal regions. Only low-frequency theta rhythm correlate with anticipatory behavior. The different scalp topography and functional correlates of low- and high-frequency theta activities may point to their different origin in infants.

The central mu rhythm was expected to behave in a different way than theta. Specifically, a mu rhythm in the EEG of the central scalp areas should be maximal during 'behavioral stillness' and sustained visual attention (Mulholland, 1995; Neuper and Pfurtscheller, 2001; Rougeul-Buser et al., 1975; Rougeul et al., 1979) and decrease during both test conditions associated with greater motility. The strongest attenuation of mu rhythm would be expected during exploratory behavior accompanied by voluntary hand movements. According to the narrow bin analysis, the cluster of frequency bins demonstrating the properties of mu rhythm fell within 6.4–8.4 Hz frequency boundaries in infants and within 8.4–10.4 Hz boundaries in children.

There was a left-side predominance of the central (mu) rhythm in infants under all experimental conditions and in children under the condition of its maximal expression (stillness and visual attention). According to experimental studies in animals and human research, mu rhythm synchronization during sustained visual attention reflects an active inhibition of the sensorimotor areas whose activation may interfere with processing of visual stimuli (Rougeul-Buser et al., 1975; Rougeul et al., 1979; Suffczynski et al., 2001). Therefore, the left-side predominance of mu rhythm observed in the present study may be linked to relatively greater inhibition of motor areas involved in the control of the dominant right hand.

In both age groups the decrease of activity within alpha range under the test conditions was not confined to the central areas, but occurred over frontal and parietal scalp regions as well (Fig. 3(II)A,B). This finding implies that emotional and cognitive loads in children are accompanied by a concurrent increase of EEG theta power and a decrease of alpha power, that is not restricted to changes of sensorimotor mu rhythm. Interestingly, the suppression of alpha-range activities and parallel increase of the power in the theta range under conditions of cognitive and emotional loads has been consistently reported in adults (Klimesch, 1999).

Despite the differences between infants and children in the precise frequency boundaries of mu and theta bands, the interrelation between theta and mu frequency ranges was the same in the two age groups. Theta and mu rhythms belong to adjacent frequency bands and the theta frequency range (3,6–5.6 Hz in infants and 4.0–7.6 (8) Hz in children) is lower than the mu range (6.4–8.4 Hz and 8.4–10.4 in infants and children, respectively). There was opposite dynamics of theta and mu range rhythms under the test conditions, compared to baseline, in both age groups. Thus, despite the difference in frequency ranges of theta and mu, their principal features remain the same for infants and children. This similarity justifies application of age-adjusted frequency bands in developmental EEG research.

The peak frequency of theta rhythm increases with age from 4.4 Hz in infants to about 6 Hz in preschool children (Figs. 1 and 5). This developmental increase of theta frequency resembles that of alpha frequency (Hudspeth and Pribram, 1992). However, the increase in theta frequency was mainly due to expansion toward higher frequencies and not due to an upward shift of the whole theta band—the theta range in preschool children is broader than in infants and is close to the conventional adult theta band (4–8 Hz).

Although theta in 4–6-year-old children is clearly distinctive from alpha activity, the upper boundary of the theta frequency band is very close to the reported occipital alpha peak frequency for this age (Fisch, 1999). Apparently, theta and alpha bands may overlap, due to age-related and inter-individual variability. Furthermore, one cannot exclude that theta and alpha frequency bands partly overlap in the same subject. Hence, it is not surprising that

borderline frequencies (7.6 and 8.0 Hz) may demonstrate properties of alpha or theta rhythms, depending on predominance of particular oscillations (alpha or theta) in the ongoing EEG. In our study, the increase of theta power, observed in 4–6-year-old children during exploration of objects and social interaction, was so strong that it was significant even on the upper boundary of the wide theta range (8.0 Hz). On the other hand, it is probable that 8.0 Hz and even lower frequency bins will demonstrate properties of the alpha rhythm in the same group of children, under conditions favoring the expression of alpha (e.g. eyes closed). These considerations underline the necessity of analyzing the whole EEG spectrum rather than concentrating on only one predefined EEG band, when one describes EEG changes under a particular functional load. For example, in a recent study of anticipatory postural adjustment in normal and autistic children aged 6–10 years, Martineau et al. (2004) interpreted rhythmic activity in the 6–8 Hz range as mu rhythm. The present study shows that even in younger preschool children, the 6–8 Hz frequency range covers the high-frequency part of the functional theta band but does not even overlap with the mu rhythm.

It is possible that the effects of inter-individual and age-related variability could be reduced by application of EEG bands that are individually adjusted (Klimesch, 1999). However, more studies are needed to apply such an approach to the EEG of infants and young children, because the rules for extraction of individually adjusted EEG bands may differ at different ages.

To summarize, the narrow-bin approach appears to be helpful for the analysis of independent frequency components of EEG power spectra in infants and children. It disclosed age-specific boundaries of functionally meaningful EEG theta and mu rhythms that would otherwise be obscured by application of conventional or arbitrary frequency bands. Considering the lack of consistent knowledge about frequency of theta and mu rhythms in early life, the results of the current study provide a necessary basis for future developmental EEG research.

4.2. Topography of theta response

The scalp topography of the theta response depended on both age and experimental condition (Figs. 4, 6 and 7). Infants in general demonstrated more widespread theta increase over the scalp surface than preschool children. During both test conditions (attention to social stimuli and exploration of toys) theta change scores, reflecting increase of theta power compared to baseline, were generally higher in infants than in children (Fig. 7). This finding suggests more generalized involvement of the cerebral cortex in regulation of behavior in early age. Such an interpretation is consistent with the results of developmental fMRI and ERP studies reporting reduction and narrowing of task-related

cortical activation over the course of brain maturation (Brown et al., 2005; Casey et al., 2005; Mills et al., 1997).

During exploration of unfamiliar attractive toys, both infants and children demonstrated a predominantly frontal increase of theta power (Fig. 7). Manipulation with toys apparently represents a different behavioral condition in infants vs. children. Infants mainly explore sensory-perceptual characteristics of the toys, while the older children take a more imaginative role in governing their own behavior (McCall, 1974). However, irrespective of age, exploratory behavior requires performance of self-generated goal-directed intentional actions. The expression of theta rhythm over the frontal cortex may reflect involvement of frontal cortical areas in the control of such actions (Jahanshahi and Frith, 1998). Task-related frontal theta activity in infants and children could be, at least partly, homologous to the frontal midline theta rhythm of adults. This rhythm is provoked by mental arithmetic and other working memory tasks (Inanaga, 1998) and is generated in anterior cingulum and prefrontal cortices (Asada et al., 1999; Gevins et al., 1997; Ishii et al., 1999). The appearance of a frontal maximum of theta increase during manipulation with toys, already at the second half-year of life, corresponds well with earlier evidence on the important role of the frontal lobes for behavioral regulation already in this age (Diamond, 1990; Orekhova et al., 1999).

During attention to social stimulation, the topography of the theta response was strikingly different in the two age groups. Theta activity increased predominantly over the frontal scalp areas in infants and over parieto-occipital scalp areas in children (Fig. 7). One cannot exclude that this difference may be caused by differences between experimental manipulations, undertaken to provoke 'social' attention, in infants and children (rhythmical and intonated infant-directed speech in the former and story telling in the latter case). However, there are strong arguments against a specific relation of theta synchronization to the processing of perceptual or semantic features of speech per se. First, the social interaction with an adult provokes an increase of EEG theta activity in infants even in the absence of verbal communication (Bazhenova, in press). Second, temporo-occipito-parietal theta synchronization in toddlers and children has been observed not only during adult speech, but also in response to a new attractive puppet (Kugler and Laub, 1971) or during drawing (Denisova, 1978). Third, listening to an emotionally neutral tape-recorded speech in children did not result in any increase of theta power as compared to baseline (Galin et al., 1992). Thus, the theta response is certainly unspecific with respect to perceptual or semantic quality of stimulation, and is rather related to the emotional and attentional processes associated with its perception.

The age-related topographical differences in the theta response observed in the current study may reflect the maturation of neuronal mechanisms regulating attention during processing of 'social' stimuli. Increase of theta

power at frontal scalp areas occurs when the behavioral and/or cognitive task engages a large amount of attentional recourses (Gevins and Smith, 2000; Jausovec and Jausovec, 2004). As soon as learning (Gevins et al., 1997; Lang et al., 1987) or maturation (Orekhova et al., 1999) takes place, the task-related frontal theta synchronization decreases. So far, the age-related decrease of frontal theta synchronization during social interaction may reflect less involvement of frontal cortical areas as the neural circuits subserving attention to adult's speech become more fine-tuned and the behavior becomes more automatic. From this point of view, a greater frontal theta response to speech communication in infants than in children may reflect that a greater amount of neural recourses are allocated to cope with 'social' task demands during infancy.

Another, not necessarily alternative, explanation for the predominantly frontal theta increase during attention to speech in infants stems from the unique value of speech stimulation for human infants. Infant-addressed speech provokes in young infants a specific behavioral response integrating motor, emotional and vocalization components (Shelovanov, 1955). In our study infants, in sharp contrast to the 4–6-year-old children, often demonstrated vocalizations, imitative responses and attempts to reach for the adult during attention to speech. These intentional behaviors might be accompanied by activity of frontal cortical areas (Jahanshahi and Frith, 1998) that may contribute to the frontal theta increase under this condition.

Despite a decreased frontal theta response during social interaction over the course of development, preschool children still demonstrated very prominent theta synchronization over the parietal scalp regions during listening to an adult's speech (Fig. 3(II)B, 5, 7). Similar but short periods of parietal rhythmic 6–8 Hz theta activity have been observed in adults during emotional experiences, such as revulsion, exasperation or pleasurable sensations (Walter and Walter, 1949). Recent quantitative EEG studies have demonstrated a predominantly posterior theta increase during perception of positive and negative emotionally salient pictures, as compared to neutral ones (Aftanas et al., 2004). Infants, like adults, also demonstrate a posterior theta increase in response to emotionally salient stimuli of different sensory modalities (e.g. pleasant tactile stimulation, puppet presentation, rattle sound) (Maulsby, 1971; Nikitina et al., 1985; Posikera et al., 1986; Stroganova and Posikera, 1993). Therefore, we interpret the parietal theta increase in preschool children during attention to speech in the present study as predominantly related to emotional salience of the stimulation.

Our data show that the posterior theta rhythm in children is a very robust phenomenon. For example, the increase of 4–7.6 Hz power over the Pz location during speech condition relative to baseline was observed in all 16 preschool children. Although the source of this scalp-recorded posterior theta rhythm is unknown, its comparison with the frontal midline theta rhythm (Inanaga, 1998) may

provide some cues. The posterior cingulate cortex, in particular the retrosplenial cortex (Brodman areas 29 and 30), has dense reciprocal connections with limbic structures and posterior cortical areas, in particular the temporo/parieto/occipital associative cortex (Morris et al., 1999), just as the anterior cingulum is reciprocally connected with limbic structures and the dorsolateral prefrontal cortex (Asada et al., 1999; Duvernoy, 1998). Hence, the retrosplenial cortical region may be involved in the generation of a scalp posterior theta rhythm, in the same way as the anterior part of cingulum engages in the generation of frontal midline theta. Recent functional neuroimaging studies show that the retrosplenial cortex is consistently and robustly activated by emotionally salient stimuli and plays an important role in the processing of emotionally salient information and in the interaction between emotion and episodic memory (Maddock, 1999). Specifically, activation of retrosplenial cortex has been reported in association with emotionally meaningful spoken words as compared with neutral ones (Maddock and Buonocore, 1997). It would be interesting to investigate whether the source of posterior theta in preschool children is also localized in posterior cingulate cortex. It is noteworthy that both anterior and posterior cingulate areas are the targets of hippocampal projections to the cortex through the anterior thalamic nuclei and in turn constitute one of the largest sources of input to the hippocampus through the entorhinal cortex (Duvernoy, 1998). The appearance of the theta rhythm over the associative parietal and frontal midline scalp regions in infants and children could reflect a cortico-limbic interplay (Miller, 1991).

Vogt et al. (1992) characterized functions of the posterior cingulate cortex as 'evaluative' in contrast to the 'executive' functions of the anterior cingulate cortex. This hypothetical structural–functional subdivision of the cingulate cortex agrees well with our data showing a prevalence of frontal theta during exploratory behavior accompanied by intentional actions, and posterior theta synchronization during 'evaluative' listening to a story in children.

4.3. Functional meaning of the EEG theta rhythm in infants and children

The main finding of the current study is the strong relation of theta rhythm synchronization to infant and child behavior. As Miller (1991) predicted, a prominent theta synchronization in the EEG of infants and children was observed during important species-specific behaviors, such as social interaction and exploratory activity.

Theta synchronization ('slowing') in the EEG is common during drowsiness (Fisch, 1999) Therefore, a high amount of theta in baseline EEG of waking subjects is often interpreted as indicating a low level of arousal. For instance, excess of theta activity in ADHD patients is commonly interpreted as an index of chronic hypo-arousal (Clarke et al., 2002; Lazzaro et al., 1999). Even in young children

and infants, who have generally higher amounts of theta activity than adults, a decrease of theta synchronization or a low level of theta in the background EEG, is often interpreted as indicative of cortical activation (e.g. Clarke et al., 2002; Cochin et al., 2001). However, the present study as well as previous findings of a prominent theta increase during brain states characterized by a high level of cognitive and emotional load argue against such a simple interpretation and calls for a reevaluation of the functional correlates of theta rhythms in the EEG of infants and children. Recently, Barry et al. (2004) reported that in normal waking 8–12-year-old children autonomic arousal, measured by skin conductance level, tended to correlate positively with baseline theta EEG power over posterior regions. This finding underlines the notion that a high amount of theta rhythms in the baseline EEG of waking subjects cannot be regarded as an unambiguous sign of low autonomic arousal. Mizuhara et al. (2004), using parallel EEG and fMRI registration, observed that during mental arithmetic the blood perfusion of some brain regions correlated positively with the appearance of frontal midline theta, while other regions displayed a negative correlation. Pizzagalli et al. (2003) registered EEG and PET concurrently at rest and found a positive correlation between theta current density and glucose metabolism in anterior cingulum and some other frontal and temporal cortical regions. These data show that the relation between cortical activation and theta is not a simple one and that presence of theta rhythm in the scalp EEG of waking subjects cannot be ultimately explained by low (or high) cortical arousal.

The task correlates of human scalp-recorded theta resembles in many aspects those of mammalian theta generated in limbic structures (Kahana et al., 2001). Neurophysiological studies in animals have shown that the overall effect of 'theta states' is a change in the information processing, which extends beyond the simple activation or inhibition of brain structures. Theta synchronization in the hippocampus and cortical structures takes place when attention is highly focused on a specific stimulation. Other stimuli, appearing against the background of ongoing theta, do not evoke responses of hippocampal neurons. It has been suggested that the theta rhythm plays a role as an attentional double-gating mechanism, which provides the necessary conditions for 'filtering-in' and effective registration and encoding of selected information, simultaneously supporting the 'filtering-out' of interfering inputs (Vinogradova, 1995).

Scalp recorded theta rhythm in infants and children may reflect such highly focused attention driven by internal significance of the particular stimulation or its representation in memory. This interpretation explains the appearance of a scalp theta rhythm during a variety of cognitive as well as affective states. We hypothesize that regardless of the differences in topographical distribution of maximal theta power, the expression of theta signifies the engagement of neural networks in a highly focused mode of processing ('theta state'). The predominantly frontal theta during exploratory behavior, and posterior theta during attention to social stimulation, that we observed in children may indicate the predominant engagement of either 'executive' or 'evaluative' cortical networks into this double-gating mode of processing.

The suggested interpretation may explain previously reported correlations between excessive theta oscillation in the baseline scalp EEG and a variety of neurological and educational problems (Clarke et al., 2002; Fernandez et al., 2002; Gasser et al., 2003; Marshall and Fox, 2004; Matsuura et al., 1993), as well as a negative correlation of baseline theta with task performance (Klimesch, 1999). Against a background of spontaneous theta, the responsiveness of cortical and hippocampal neurons to newly incoming sensory stimulation is strongly reduced. This means that ongoing theta oscillations, triggered by previous events or related to pathological processes, may prevent ('filter-out') the admission of new signals (Vinogradova, 1995). Consistent with this assumption, standard visual stimuli presented against the background of high amplitude cortical theta evoke brain responses of significantly lower amplitude (Basar et al., 1998). Hence, a low baseline or prestimulus theta power may reflect a readiness of the brain for effective encoding and registration of sensory events, whereas a high prestimulus theta indicates the presence of some competing or pathological process that may interfere with processing of sensory input.

Why are theta oscillations so prominent in infants and young children but rarely observed in healthy adults? First, infants and children, as compared to adults, usually experience more intense affective states in the laboratory setting and their attention is to a higher degree driven by internal significance of the particular stimulation. Second, they have a lower degree of behavioral automatization and engage more brain resources to regulate behavior than adults (Casey et al., 2005). A high amplitude generalized theta rhythm in infants and young children may reflect wide-spread engagement of the cortex in behavioral regulation and/or task performance (Gevins et al., 1997; Jausovec and Jausovec, 2004). Third, theta oscillations are important for establishment of new synaptic connections and strengthening of existing synapses in the animal brain (Diamond and Rose, 1994) and memory and learning in humans (Klimesch, 1999). Therefore, the great amount of task-related theta oscillations in early life may play a significant role in the high plasticity of the young brain.

Acknowledgements

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