

Probability interrelations between pre-/post-stimulus intervals and ERD/ERS during a memory task

Alexander A. Fingelkurts^{a,b,*}, Andrew A. Fingelkurts^{a,b}, Christina M. Krause^{a,c}, Mikko Sams^a

^aResearch Group of Cognitive Science and Technology, Laboratory of Computational Engineering, Helsinki University of Technology, 02015 HUT, Finland

^bHuman Brain Research Group, Human Physiology Department, Moscow State University, 119899 Moscow, Russia

^cCentre for Cognitive Neuroscience, University of Turku, 20014 Turku, Finland

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Abstract

Objectives: To investigate the functional relationship between oscillatory electroencephalographic (EEG) components (pre-/post-stimulus intervals) with audio-event-related desynchronization/synchronization (ERD/ERS).

Methods: In an experimental study (9 subjects), the probability-classification analysis of single-trial spectral EEG changes was utilized. Results were compared with auditory ERD/ERS.

Results: It was shown that (1) variability of EEG spectral patterns was considerable, (2) EEG activity was different at various task stages, (3) probability measures were different from the results of conventional frequency analysis, (4) probability of trials with alpha- and theta-patterns was characteristically different in various task stages, (5) the occurrence of alpha- and theta-trials were most probable, but not frequent enough to characterize all the trials. The results suggest that the ERD/ERS responses are influenced by EEG characteristics in the pre-stimulus interval, which also have a strong influence on the EEG in the post-stimulus interval.

Conclusions: Alpha- and theta-ERD/ERS responses during memory task performance are not typical for all trials. They reflect EEG changes only in ~39% for alpha-activity and ~43% for theta-oscillations of all trials, what reflects piecewise stationary EEG structure. © 2002 Published by Elsevier Science Ireland Ltd.

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1. Introduction

During either external or internal stimulation, the simultaneously recorded responses of different electroencephalographic (EEG) frequency bands differ from each other (Klimesch et al., 1997; Steriade et al., 1990; Karrasch et al., 1998; Krause et al., 1996, 1999). It has been proposed that the responses of the different frequencies within the EEG would reflect different parallel occurring mental processes or states (Boiten et al., 1992; Klimesch et al., 1994, 1998; Dumont et al., 1999). Regarding the functional significance of oscillatory activity, it is of interest to study how such brain oscillations get (de)synchronized by stimulation or during the performance of certain tasks.

Different approaches have been suggested to quantify how brain oscillations tuned in frequency by different processes. Here, the most popular are the study of event-related potentials (ERPs) and event-related desynchroniza-

tion/synchronization (ERD/ERS) (Pfurtscheller and Lopes da Silva, 1999).

Thus, utilizing the ERD/ERS approach, it has been demonstrated that working memory processes seem to be reflected as brain electric oscillations within the EEG theta frequency diapason (~4–7 Hz) (Klimesch, 1996a; Klimesch et al., 1997). The changes of the lower alpha activity at 8–10 Hz have been suggested to represent attentional and motivational processes (Klimesch et al., 1992) while the upper alpha frequencies (10–12 Hz) have been claimed to reflect stimulus-related aspects and/or semantic memory processes (Pfurtscheller and Klimesch, 1992; Klimesch, 1997; Klimesch et al., 1998).

The quantification of ERPs and ERD/ERS require averaging of the signal over several repetitions of a given stimulus. However, there are some aspects concerning the averaging of the EEG signal, which might not only mask the dynamics of possible EEG correlates of cognitive processes, but also give rise to ambiguous data interpretation (Effern et al., 2000; Laskaris and Ioannides, 2001).

* Corresponding author. Tel.: +358-40-8350345.

E-mail address: fintw@hotmail.com (A.A. Fingelkurts).

First, there exists a so-called induced modulation of ongoing EEG. ERD/ERS is defined as the relative difference in EEG power between two conditions (pre-stimulus or reference period and immediate post-stimulus period) as a function of time (Pfurtscheller et al., 1988), therefore, such event-related phenomena in the EEG depend on the amount and the type of rhythmic activity in the reference interval (Romani et al., 1988; Brandt et al., 1991; Arieli et al., 1996; Basar et al., 1998; Doppelmayr et al., 1998). At the same time, the stimulus may influence the EEG in the post-stimulus interval (Laskaris and Ioannides, 2001), especially if the stimulus has semantic content (for example can be verbalized). In this case, the presentation of each new stimulus lays on new functional substratum (Fingelkurts et al., 1998). It has been shown that ERD/ERS responses vary in magnitude and latency as a function of stimulus type (novelty effect) and previous stimulus type (Karrasch et al., 1998). The same has been shown for the ERPs: ERPs to novel stimuli decline with repetition (Knight, 1984; Friedman et al., 1998) and are neither stable nor wholly independent of the background EEG (Basar, 1980). Additionally, it has been reported that the so-called priming effect might be seen in the EEG responses longer than hitherto recognized (Deacon et al., 1999; Krause et al., 2001). Such observations have, however, been neglected in basic cognitive EEG research.

Second, the ongoing EEG is also characterized by natural dynamics and piecewise stationary structure (Lehman, 1980; Lehman et al., 1995; Kaplan et al., 1997; Kaplan and Shishkin, 2000). Piecewise stationary structure of EEG means that a recorded signal may be presented as a result of ‘gluing’ of stationary casual processes with different probability characteristics (see reviews Kaplan and Shishkin, 2000; Fingelkurts and Fingelkurts, 2001). Usually experiments in cognitive brain research are lengthy, and might last for hours in order to accumulate enough repetitions for the generation of reliable ERPs or ERD/ERS responses. However, brain systems involved in information processing do not necessarily remain constant through many hours or many repetitions of a cognitive task. During this time the functional state (and brain state) of the subject is altered several times (Kaplan et al., 1999b). This leads to a paradox: it is necessary to use the averaging procedure in order to obtain statistically stable ERP or ERD/ERS responses but the averaging techniques inevitably cannot take into account the non-stationary nature of EEG. Thus, regardless of how powerful or statistically significant the different estimations of averaged event-related EEG phenomena may be, there might be difficulties in the meaningful interpretation of these if they are not matched to the EEG piecewise stationary structure (Effern et al., 2000; Laskaris and Ioannides, 2001). When ERPs and/or ERD/ERS responses are calculated without regard to the piecewise stationary EEG segmentation parameters, these techniques lose a substantial part of their power for studying discrete functional states of the brain. Moreover, it will

not be obvious how typical the obtained ERP and/or ERD/ERS responses are for each trial.

A new promising area of the study of EEG transformations during cognitive processing, is based on the reduction of the signal to the elementary SP sequences (Fingelkurts, 1998; Kaplan et al., 1999a,b). In this analysis, the dependence of the probability of the occurrence of SPs of particular type and repetitive ‘external’ events, such as presentation of a stimulus to a subject is estimated. It has been suggested that the operational elements of behavioral and mental activity originate in the periods of short-term meta-stable states of the whole brain and its individual subsystems (see reviews Kaplan, 1998; Fingelkurts and Fingelkurts, 2001). Several reports indicate (review Kaplan, 1999; Kaplan and Shishkin, 2000) the indubitable functional significance of the segmental EEG architectonics (Fingelkurts et al., 1998). Some researchers have showed that the EEG signal consists of a limited number of typical segments, which are stationary and usually do not exceed 1–10 s. (McEwen and Anderson, 1975; Barlow and Creutzfeldt, 1981; Creutzfeldt et al., 1985; Inouye et al., 1995). These results suggest that the quasi-stationary segments reflect the operational acts of nervous activity which continue to occur even without external stimulation (Kaplan and Shishkin, 2000; Kaplan et al., 2001). From this viewpoint, it is justified to use the calculation of single spectral estimations of the elementary EEG segments for their subsequent adaptive classification (Kaplan et al., 1999a). In such a way, the dynamics of brain activity can be considered as a sequence of relatively stable and fixed EEG SPs (Fingelkurts, 1998). It has been shown that the parameters of relative representations of elementary EEG segments of every class, and regularities of its alteration in analyzed EEG are adequate characteristics of brain operational activity (Bodenstein and Praetorius, 1977; Kaplan et al., 1997, 1999a,b; Fingelkurts, 1998).

In connection with this, it seems reasonable to examine the pre- and post-stimulus EEG intervals (free from the direct ERP and/or ERD/ERS influences) in addition to ERP and/or ERD/ERS measurements. By means of the single-trial classification technique, based on the quantification of brain oscillatory activity, it might be possible to detect ‘internal’ events (brain activity transformations following after a certain time delay), and ‘external’ events and to separate these from each other. Pre-/post-stimulus intervals are usually short enough (1–2 s) to be relatively stationary and at the same time to reflect the brain elementary operational act. Thus, by using the adaptive classification procedure, it could be possible to characterize each pre-/post-stimulus interval on the basis of short-term spectral descriptions. In that case, each interstimulus interval (ISI) would be characterized by specific SPs. One might assume that steady EEG patterns may exist for certain pre- and/or post-stimulus intervals. On the other hand, by monitoring changes in brain functional microstates (in terms of EEG microstructure), it could be possible to average

ERD/ERS data at the frame of each homogeneous functional state. In other words, classification profiles of the trials, each of which are characterized by particular types of SPs, would present the variety of brain states during the particular interval of the EEG recording.

The purpose of the present paper was to investigate pre- and post-stimulus EEG intervals in the auditory stimulus modality by using the original approach of adaptive classification of single EEG spectra (Kaplan et al., 1999a), during a modified version of Sternberg's memory task (Sternberg, 1966). The choice of this experimental paradigm allowed the control of the subjects' attentiveness to the auditory stimuli, as well as to study changes in the electrical activity of the brain, associated with memory encoding and retrieval.

2. Materials and methods

2.1. Subjects

Nine healthy, right-handed adult volunteers participated in the experiment. Four of the subjects were males and five were females in the age range from 20 to 29 years (mean = 24 years, SD = 2.9). The handedness of the subjects was verified with an unpublished Finnish version of the 'Boston V.A. Handedness Questionnaire' comprising 12 questions about the hand and foot used in different tasks such as handwriting, kicking a ball and lighting a match.

Subjects were only considered as right-handed if they used the right limb in 10 or more situations. None of the subjects reported any hearing deficits, neurological disorders, or were on medication. In addition, none of them had professional musical education and all were native Finnish speakers.

2.2. Stimulus materials

The stimuli consisted of 24 auditory Finnish verbs (spoken with a female voice). The mean length of the stimuli was 6.72 letters (SD = 0.93). Mean stimulus duration was 764 ms (SD = 82).

The auditory stimuli were recorded to the hard disk of a Macintosh IIFX computer, using the 'Digidesign' sound tools software package. Thereafter the digitized stimuli were stored in the 'Neuroscan Stim' file format (within and at the beginning of a time window of 1000 ms). However, the length of each auditory stimulus window was 1000 ms, with the auditory stimuli always appearing in the very beginning of this time window. The 'Neuroscan Stim' system was used to control the presentation of the auditory stimuli. The stimuli were presented through E-A-RTONE ABR insert earphones (10 Ω) at a comfortable sound pressure level (\sim 70 dB). The stimulus intensity was assessed by means of a Bryel and Kjaer (Denmark) type 4152 artificial ear and type 2235 decibel meter.

The experimental design was a modified version of Sternberg's memory search paradigm (Sternberg, 1966; Krause et

al., 1996). The memory set (*encoding*) consisted of 4 auditorily presented stimuli. The frame set (*retrieval*) size was kept constant and consisted of one stimulus. The maximum set size was reduced to 4 items because supraspan lists (>5) may also engage long-term memory encoding processes (Durgerian et al., 2001). A total of 192 4-verb memory sets were constructed such that each of the verbs had to occur with equal frequency and only once in the same memory set. In 50% of the cases, the frame set verb was among the previously presented 4-stimulus block. In total, there were 192 trials, which were presented to the subjects in a pseudorandomized order.

2.3. Procedure

Following electrode placement and instrument calibration, a subject was seated in a comfortable chair in a dimmed registration room and the experimental procedure was explained. To reduce muscle artifacts in the EEG signal, a subject was instructed to assume a comfortable position and to avoid movement. A subject was instructed to look at a TV screen placed in front of him/her (1.5 m) and to avoid unnecessary eye movements. The behaviour of the subject was observed on a TV monitor throughout the experiment.

Each trial began with a 3500 ms intra-experimental reference condition. A reference mark indicated the beginning of 1500 ms resting period (R). After this, a visual warning signal (a red spot), appeared for 100 ms on the TV screen, marking a waiting period (W). After 1500 ms, the 7000 ms 4-verb memory set was presented (auditory encoding: 4 1000 ms auditory stimuli with an ISI of 1000 ms). These three ISI formed encoding period (E). Following an interval of 2000 ms after the presentation of the 4-verb memory set (this being keeping-in-mind period (K)), the frame set (auditory retrieval: one 1000 ms auditory stimulus) was presented. A subject then had to decide whether the fifth verb had appeared in the memory set or not. In order to avoid muscle and motor artifacts, a subject was asked to wait with his/her response until a visual warning signal (a green spot), appeared on the TV screen. After 1500 ms after the presentation of the probe verb (identification period (I)), the green spot appeared on the TV screen, marking the end of the identification period and reminding a subject to respond by pressing either the 'yes' or 'no' button on a response pad (see Fig. 1A). The following trial started when a subject had given his/her answer on the response pad. The length of a single trial was 16.7 s (+response time) and there were 192 trials in all. The total registration time was about 60 min.

2.4. Recording

Twenty Ag/AgCl electrodes (Siemens-Elema) were placed bilaterally on the subject's scalp using electrode cream (Berner) and the 10/20 system of electrode placement at FP1, FP2, F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3,

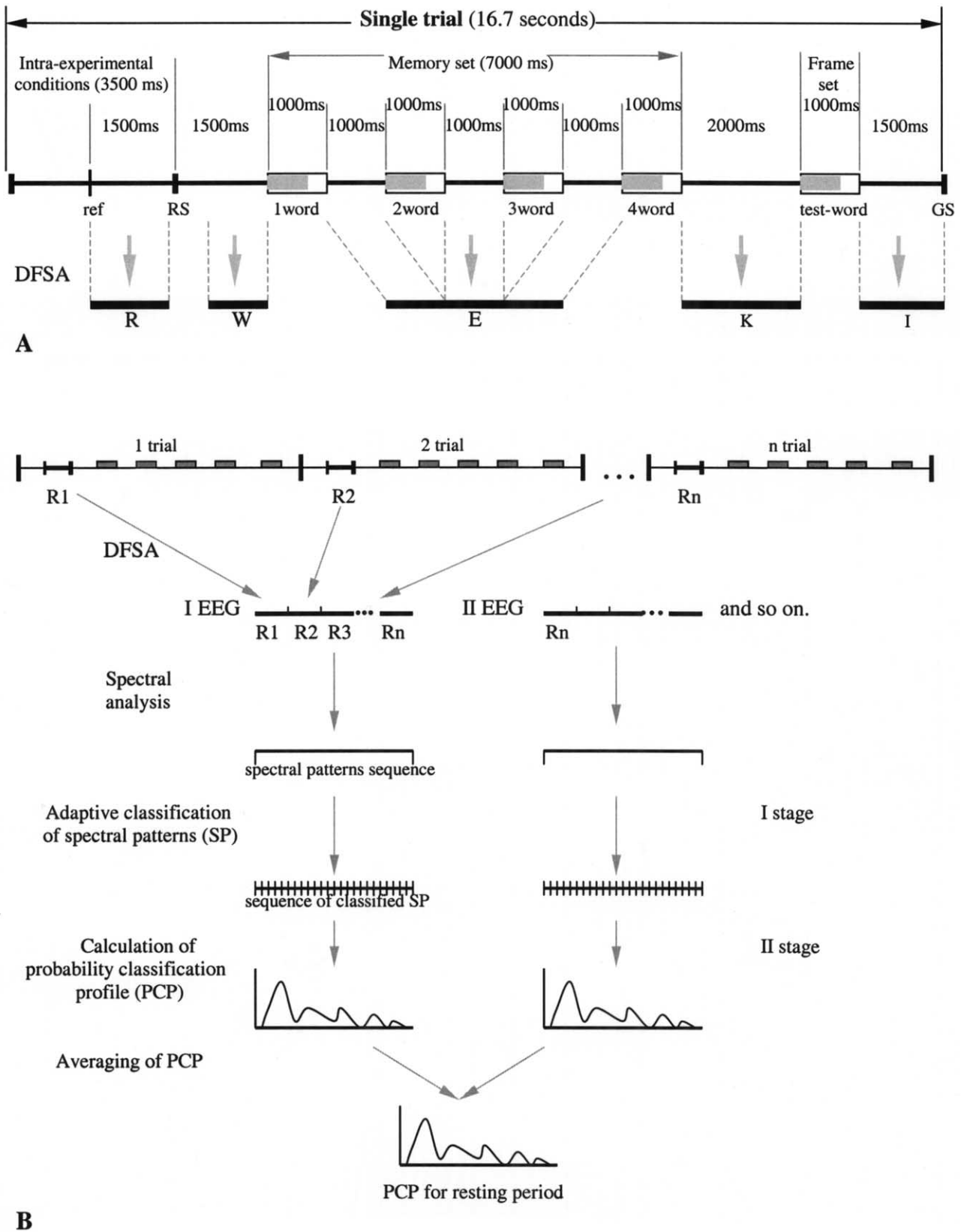


Fig. 1. The scheme of the experimental paradigm (A) and data processing (B) (example for resting period is presented). Ref, reference moment. RS, red spot; GS, green spot. DFSA, adapted model of the 'deterministic finite state automaton'. R, resting period, W, waiting period, E, encoding period, K, keeping-in-mind period, I, identification period. The gray area in the squares for each stimulus indicates that the length of every word was less than the stimulus window (mean stimulus duration was 764 ms (SD = 82)). This means that there were no direct influences of ERD/ERS on interstimulus intervals.

Pz, P4, T6, O1, Oz and O2. Additionally, two electrooculogram (EOG) electrodes were placed on the outer side of the eyes. All electrodes were referred to linked ears, which also served as the ground electrodes. The data was recorded using a sampling rate of 200 Hz.

Raw EEG signals were recorded using the Neuroscan 386 Scan3.0 data acquisition system, with a Braintronics CNV/ISO-1032 amplifier with a frequency band of 0.3–70 Hz. The impedance of recording electrodes was monitored for each subject with a Braintronics electrode impedance meter prior to data collection; this was always below 5 k Ω . The presence of an adequate EEG signal was determined by visual inspection of the raw signal on the computer screen.

2.5. Data processing

A full EEG stream contained 192 experimental trials. For each raw EEG stream, there was a reference file with a chronological sequence of the events during the experiment for all the trials.

An adaptation of the model of a ‘deterministic finite state automaton’ (DFSFA) (Hopcroft and Ullman, 2000) was used (Fig. 1) to extract data with specific common characteristics (belonging to R, or W, or E, or K, or I). Thus, depending on the sequence of input events the state-machine either accepts/stores or rejects the incoming data. The full data-stream was given simultaneously to 5 different virtual state-machine extraction units.

Each state-machine selects the inter-stimulus data, which is not influenced by any artifact of the stimulus-events themselves (Fig. 1A). When necessary, and after the acknowledgement of the correct event, the state-machine enters into a data skipping state for a given period of time and only after this period it starts accepting the data.

In order to eliminate any possible short-term non-stationarities in the neighborhood of the gluing point, the data of these areas were smoothed. According to preliminary calculations a number of ± 3 data points around the gluing point ($\Delta t = 25$ ms) were chosen to symmetrically average the data in these areas.

Thus, the full EEG streams were split into 5 distinct segments: R for resting period, W for waiting period, E for encoding period, K for keeping-in-mind period and I for identification period (Fig. 1).

Due to the technical requirements of the tools to be used later for data processing, only 16 EEG channels (F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, T6, P3, P4, O1, O2) were taken into use, with a converted sampling rate of 128 Hz. This conversion was done taking the in-between values of only two points, i.e. getting the correct projected mean-point in the y-scale from the required point in the slope defined by the existing intermediate points and their respective time-stamps. This method was considered sufficient since the sampling-rate of the source signal was significantly higher than that of the one required.

Thereafter, the individual spectra were calculated in the

range of 3–15 Hz with 0.5 Hz discretization, using fast Fourier transform (FFT) in 2 s analysis epochs with a shifting window of 50 points (0.39 s) (Fig. 1B). This frequency diapason was chosen in order to compare results of this study with ERD/ERS measurements made for 4–6, 6–8, 8–10 and 10–12 Hz on the same material earlier (Krause et al., in preparation).

Parameters of EEG spectral patterns (SPs) variability, for each period of memory task (R, W, E, K, I) were estimated with the help of *probability-classification analysis of EEG SP*. This procedure, named SCAN-M, was developed and approbated at Moscow State University. Analysis was performed at two stages. At the first stage, the *adaptive classification* of sequential single EEG spectra was performed in each EEG channel in reference to a versatile set of 22 standard SPs (Fig. 1B). Details of this procedure can be found in one of our previous reports (Kaplan et al., 1999a). In the present paper, it was observed that this SP classification method made it possible to identify up to 97% of individual single spectra in the initial EEG realizations. Thus, each multichannel EEG was reduced to the sequences of individual SPs (Fig. 1B). At the second stage, the probability classification profiles (PCPs) of SPs for EEG recordings from one subject were calculated. This was also done for the group of subjects as a whole (Fig. 1B). This index was calculated as the relative number of cases of SP type occurrence in percentage of the total amount of all SPs.

First, PCPs were averaged for each task period separately for each subject. After this, the data for each period were averaged over those subjects, who had similar PCPs. It was proposed that these PCPs would make it possible to portray different periods of the EEG during a memory task.

2.6. Statistical analyses

In order to reveal statistically significant transformations of PCP, we used the Student *t* test. Only statistically significant *P*-values are displayed.

3. Results

3.1. Subject performance

All the subjects performed well in the retrieval task. The mean percentage of incorrect answers was 4.4 (SD = 1.97). In the EEG analysis, only such trials, which corresponded to right performance were included.

3.2. General characteristic of the PCPs of the SPs

Analysis of the individual PCPs of the SPs showed that each subject had his/her own dominant peak in the PCP. This verified that the subjects’ EEGs differed from each other according to the dominant frequent activity. Mean spectral power analyses, calculated for the resting period (Table 1), confirmed this (subgroup II is absent from this

Table 1

Mean spectral power (\pm mean error) for 4 frequency bands (alpha diapason) calculated for 3 subgroups' EEG, which were characterized by alpha activity (subgroup II was characterized by dominant theta activity, so data for this subgroup not presented)^a

EEG channels	7.5–8.5 Hz	9–10 Hz	10.5–11.5 Hz	12–13.5 Hz
I subgroup				
O1	10.0 + 0.9	13.2 + 2.8	<i>14.3 + 1.2</i>	14.2 + 2.9
O2	9.4 + 0.5	12.9 + 3	<i>14.9 + 2.2</i>	14.3 + 3.2
P3	9.6 + 1.2	12.9 + 3.2	<i>14.4 + 1.9</i>	13.9 + 4
P4	9.3 + 1.3	13.1 + 4.1	<i>15.4 + 2.8</i>	13.7 + 3.3
T5	10.2 + 1.4	13.3 + 2.6	13.9 + 1.5	<i>14.1 + 3.8</i>
T6	9.5 + 1.3	13.4 + 3.8	<i>15.6 + 2.1</i>	14.8 + 4
C3	10.4 + 1	11.8 + 2.3	<i>12.1 + 1.5</i>	10.6 + 1.9
C4	7.0 + 1.3	<i>12.8 + 3.2</i>	12.6 + 1.7	10.8 + 1.7
III subgroup				
O1	6.8 + 1	14.2 + 2.4	<i>14.8 + 2</i>	13.5 + 2.3
O2	9.6 + 1.3	15 + 2.6	<i>15.5 + 2.1</i>	13.6 + 3.7
P3	10.7 + 1.1	<i>14.5 + 1.6</i>	13.9 + 2.4	11.8 + 2.2
P4	10.3 + 1.2	<i>15.3 + 2.3</i>	13.7 + 2.8	11.9 + 2.6
T5	10.7 + 1	<i>13.3 + 1.4</i>	13.3 + 1.8	12.2 + 1.9
T6	10 + 1.1	<i>14.3 + 1.5</i>	14 + 2.7	13.1 + 3.5
C3	11.1 + 1	<i>13.1 + 2.4</i>	11.2 + 2.2	11 + 2
C4	10.8 + 1	<i>13.1 + 1.7</i>	11.1 + 2.1	10.7 + 1.8
IV subgroup				
O1	<i>15.3 + 2.2</i>	13.8 + 1.1	10.4 + 1	11.3 + 1.5
O2	<i>15.3 + 2.4</i>	14.2 + 0.9	10.4 + 0.6	10.7 + 1
P3	<i>15.9 + 1.9</i>	14.1 + 7.6	9.3 + 0.5	9.2 + 1.1
P4	<i>15.4 + 2.2</i>	13.8 + 1	9.1 + 0.6	8.7 + 9.3
T5	<i>15.7 + 2.1</i>	14.6 + 1.2	10.4 + 0.6	10.3 + 1.4
T6	<i>15.4 + 2.2</i>	14.4 + 0.9	10.2 + 0.6	9.7 + 0.9
C3	<i>13.9 + 0.8</i>	13.6 + 0.9	8.7 + 0.6	8.6 + 0.6
C4	<i>13.1 + 1.1</i>	12.1 + 1	8 + 0.7	8.3 + 0.5

^a The values in italics indicates the maximum values for four frequency bands.

analysis because the PCPs did not exhibit dominant peaks at SPs which describe alpha diapason).

Following this, the subjects were assigned to 4 analysis subgroups according to their individual PCPs (Fig. 2.): I subgroup (two subjects) – dominant peak at SP No. 3 (peak at 11.5 Hz), II subgroup (3 subjects) – no dominant peak at SPs from alpha diapason, III subgroup (three subjects) – dominant peaks at SP No. 2 (peak at 10 Hz) and SP No. 7 (peaks at 9.5–10.5 Hz), and IV subgroup (one subject) – dominant peaks at SP No. 1 (peak at 8.5 Hz) and SP No. 6 (peaks at 8–9 Hz). All the peaks in SPs, which described alpha diapason, were typical for the O1, P3, T5, O2, P4, and T6 EEG channels. At the same time, all subjects exhibited dominant peaks at SPs, which were characterized by theta diapason: SP No. 14 (peak at 4 Hz) and SP No. 18 (peak at 3.5–5.5 Hz). These were typical for the F7, F3, Fz, F4, and F8 EEG channels.

Analysis of the PCPs calculated separately for each task period showed that all EEG channels were characterized by a dominant peak in the PCP (Fig. 3A–D). Some EEG channels had two, but rarely 3 dominant peaks. If there was more

than one dominant peak, then one was always most pronounced. The existence of the dominant peak(s) in the PCP reflects the fact that there was one more frequent (probable) EEG spectral pattern, which corresponded to the particular memory task period (pre-/post-stimulus interval). The total combination of the most probable SPs for all EEG channels was considered as the most probable brain state for a particular memory task period.

The magnitude of the dominant peaks changed from the occipital to the frontal electrodes. This was such that alpha activity, which was observed most prominently in the occipital electrodes, decreasing in magnitude towards the frontal electrodes. The sagittal gradient of a peak's pronouncement was opposite to the occurrence of alpha- and theta-SPs. The PCPs (Fig. 3A–D) for the EEG channels T3, C3, Cz, C4 and T4 showed less pronounced dominant peaks.

3.3. The peculiarities of PCP for different periods of memory task

The comparative analysis of PCPs for different periods of the memory task showed that there were no particular types of EEG SPs associated with certain memory task stages (Fig. 3A–D). At the same time, different periods of memory task differed from each other according to the probability estimation of the occurrence of particular EEG SPs (Figs. 3 and 4). Since each of the different trials was characterized by its own SP, the occurrence of a particular type of trial is directly reflected in the probability of occurrence of its SP type.

As can be seen in Fig. 4, in all subgroups, there were no statistically significant differences in PCP between the resting and waiting periods during the memory task in any EEG channels. In contrast, all other memory task stages showed considerable transformations in the PCPs. The common effect was the following. The probability of the occurrence of the trials, which were described by alpha SPs, significantly increased from resting and waiting periods to encoding stage ($P < 0.05$ – 0.001). This continued to increase in probability until the keeping-in-mind period ($P < 0.05$ – 0.001) (see Fig. 4). Then, during the identification stage the probability of the occurrence of the trials with alpha SPs significantly decreased ($P < 0.05$ – 0.001) (Fig. 4). The trials, which were described by theta SPs revealed opposite behavior. Here, the probability of the occurrence of the trials with theta SPs decreased ($P < 0.05$ – 0.01 ; in subgroups II, III and IV – not significant) during encoding period as compared to the resting and waiting stages, and continued to decrease ($P < 0.05$ – 0.01 ; in subgroups II, III – did not change) until the keeping-in-mind period (Fig. 4). During the identification stage, the probability of the occurrence of trials with theta SP strongly increased ($P < 0.05$ – 0.001 ; for subgroups III, IV – not significant). The details of PCP transformations are presented in Fig. 4.

Conventional 'energetic' estimation (mean spectral power) of the task-related EEG spectral changes for the

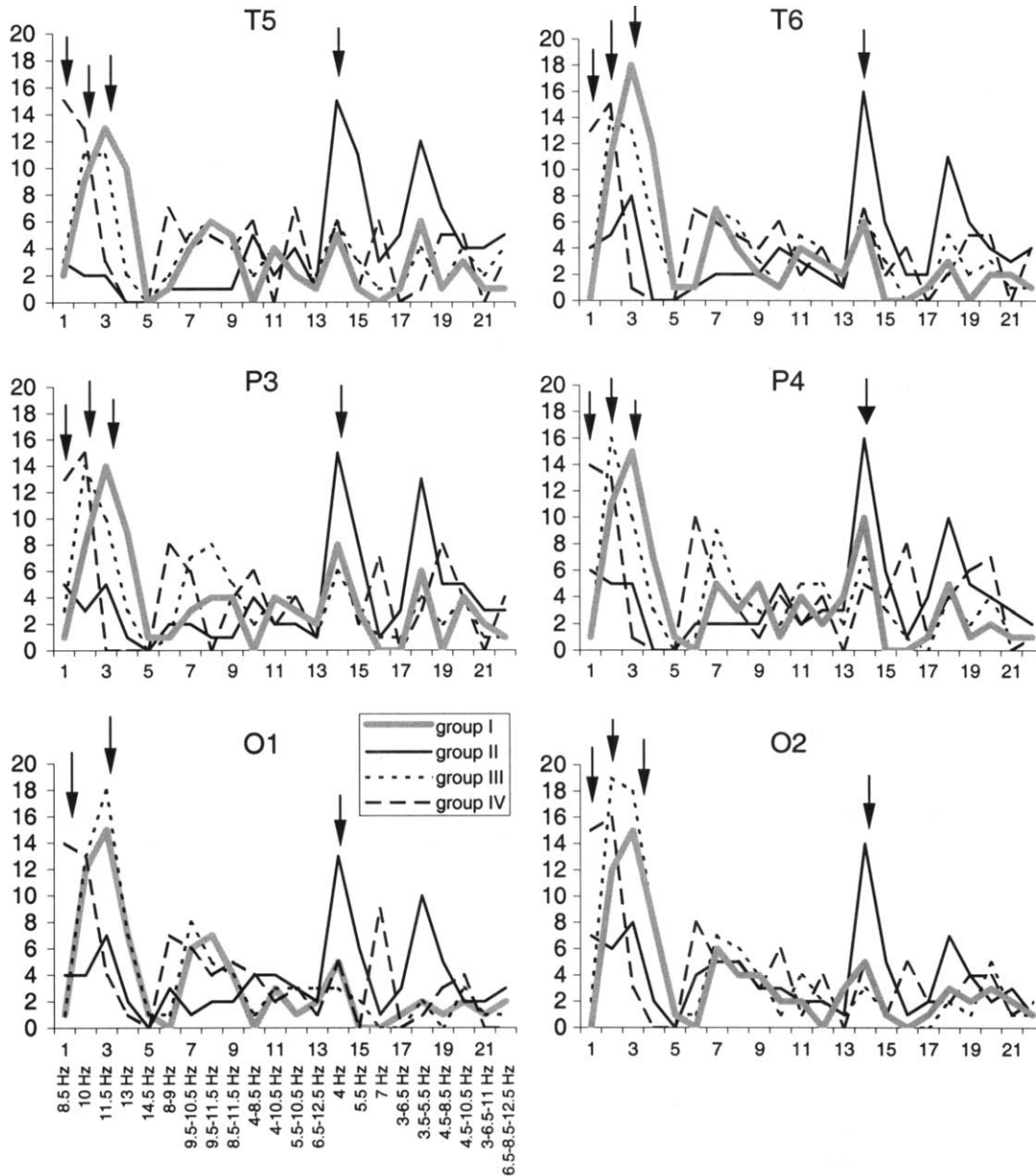


Fig. 2. Mean (for each subgroup separately) probability classification profiles (PCPs) of spectral patterns (SPs) calculated for resting period. Only EEG channels, where usual alpha activity is the most pronounced are presented (O1, O2, P3, P4, T5 and T6). The X-axis displays the labels (numbers) of standard SP from 1 to 22 and their main frequency peaks. The Y-axis displays the share of the corresponding SP in the percentage from the total number of the classified SP. A line graphic was chosen instead of a bar for the ease of comparison. (Note that X-axis consists of 22 discrete values, all the in-between values are meaningless.) Arrows indicate the dominant peaks in PCPs, which reflect the most probable SP type for the trials for resting period.

same memory task periods showed the opposite picture (Fig. 4). Thus, mean spectral power either not changed or changed in the opposite direction as compared with probability index. This means that the PCP index was independent of the averaged spectral power.

The main effect described above was pronounced in various EEG channels for different memory task periods in all subgroups. At the same time, this effect was detected only in 3–39% for alpha activity and 8–43% for theta oscillations (different subgroups and EEG channels) of all trials (Fig. 3).

3.4. Topological characteristics of PCP transformations

As can be seen in Fig. 5, each subgroup was characterized by its own topological picture of PCP transformations. To some extent, the differences between the subgroups might be explained by dominant frequency differences in the ongoing EEG structure (Table 1, Fig. 2) and possibly by individual memory strategies while performing the task. All changes of PCP in different subgroups occurred in various stages at dominant EEG frequency for each subgroup (Fig. 3).

There were great reorganizations of the PCP topological maps during the transition from one memory task period to another. The changes in the probability of the occurrence of alpha SPs occupied more EEG channels in the right hemisphere than in the left (Fig. 5). The maximum number of active EEG channels (in terms of significant changes in PCP) was observed during the identification period for subgroups I and II. For subgroup IV this parameter was typical for the keeping-in-mind stage. Additionally, three subgroups (I, II, and IV) showed activation in F7 channel during the identification period, which corresponded to the post-retrieval interval (Fig. 5).

3.5. *The relationship between the pre-/post-stimulus intervals and the ERD/ERS responses*

In order to study the relationships between the EEG signal obtained during pre-/post-stimulus intervals and the ERD/ERS responses, the present results were compared with ERD/ERS responses registered during the same memory task (Krause et al., in preparation). It has been shown that auditory encoding (corresponding to the encoding period in this paper) elicits alpha ERS, whereas alpha ERD was evoked during memory retrieval (corresponding to the interval between keeping-in-mind and identification periods in this paper). In the theta frequency range, auditory encoding elicits an early appearing ERS, and retrieval elicits theta ERS which is of greater magnitude than the ERS evoked by encoding (Krause et al., in preparation).

The comparative analysis showed that changes in the probability of the occurrence of the trials with particular SP type are in the same direction as the event-related EEG phenomena (Fig. 4). This testifies that EEG effects (in terms of PCP values) could be the post-reactions of the ERD/ERS responses for the encoding, keeping-in-mind and identification periods of memory task.

However, according to PCP, the occurrence of alpha- and theta-trials is the most probable, but not frequent enough to characterize all the trials (Table 2). Alpha- and theta-ERD/ERS responses during memory task performance are not typical for all trials. They reflected EEG changes only in 3–39% for alpha activity and 8–43% for theta oscillations (different subgroups and EEG channels) of all trials.

4. Discussion

The principal finding from the present study was the significant increase (encoding, keeping-in-mind periods) and decrease (identification period) of the probability of the occurrence of trials with alpha SPs, and the opposite behavior of the trials with theta SP. It is interesting that all changes in the EEG occurred at the dominant frequency, which was already present in the resting period. The cognitive task involving encoding and retrieval of auditory stimuli not bringing new any specific SPs. This finding might be explained by the limitation in frequency diapason

(3–15 Hz), which reduced the number of standard SPs, which were used for adaptive classification. On the other hand, one of the reasons for this may be the relatively easy task (see Section 3.1), which may permit the brain to use the ongoing activity without requiring a change to a specific regimen of the work.

A simultaneously conducted conventional estimation of the EEG spectral power changes showed the independence of PCP estimates from average spectral power for all subgroups. Thus, in the two different types of analyses, the tendencies of the changes in PCP and mean power of the same EEG frequency bands appeared to be opposite, indicating that the sensitivity of PCP values was not just a derivative of the changes in the mean level of the EEG spectral power. The average power spectrum is determined by the particular number of trials with a particular frequency and the amplitude of this frequency.

For example, one memory stage is characterized by 5 alpha-trials with high amplitude, whereas another memory stage is characterized by 10 alpha-trials with low amplitude. As the result, they may give very similar averaged power spectra. Thus, averaged power spectrum constitutes a ‘static’ picture which eliminates dynamic aspects (piecewise stationary characteristics) of EEG transformations. In contrast to conventional spectral analysis, PCP values demonstrate probability variations in the number of trials with particular frequency activity, and this is more sensitive for revealing even weak changes in brain activity (Fingelkurts, 1998).

The comparative analysis of PCP values and ERD/ERS responses suggests that the ERD/ERS responses might be influenced by the EEG characteristics in the pre-stimulus interval (Doppelmayr et al., 1998), and the ERD/ERS responses have a strong influence on the EEG in the post-stimulus interval. Lehman and colleagues (Lehman et al., 1994), investigating pre-stimulus EEG intervals, also concluded that subtle changes in the brain’s spontaneous momentary functional microstate influence event-related information processing.

It has been repeatedly observed that the encoding of auditory stimuli mainly elicits an increase in alpha amplitude (Weiss and Rappelsberger, 1998), whereas memory retrieval elicits a decrease in the amplitude (Krause et al., 1996; Karrasch et al., 1998). As with the alpha ERS usually observed during encoding of auditory information, the increase in the probability of the occurrence of alpha-trials most probably reflects the increase in the probability of the occurrence of ‘idling’ – state for those brain areas which are not specifically involved in the encoding of auditory information (Pfurtscheller, 1992). Information retrieval on the other hand activates ‘semantic’ representations and comparative mental processes, and involves more cortical areas (see keeping-in-mind and identification periods; Fig. 5). Strong decrease in the probability of the occurrence of alpha-trials and increase of theta-trials was detected after the presentation of the frame set (identification or post-

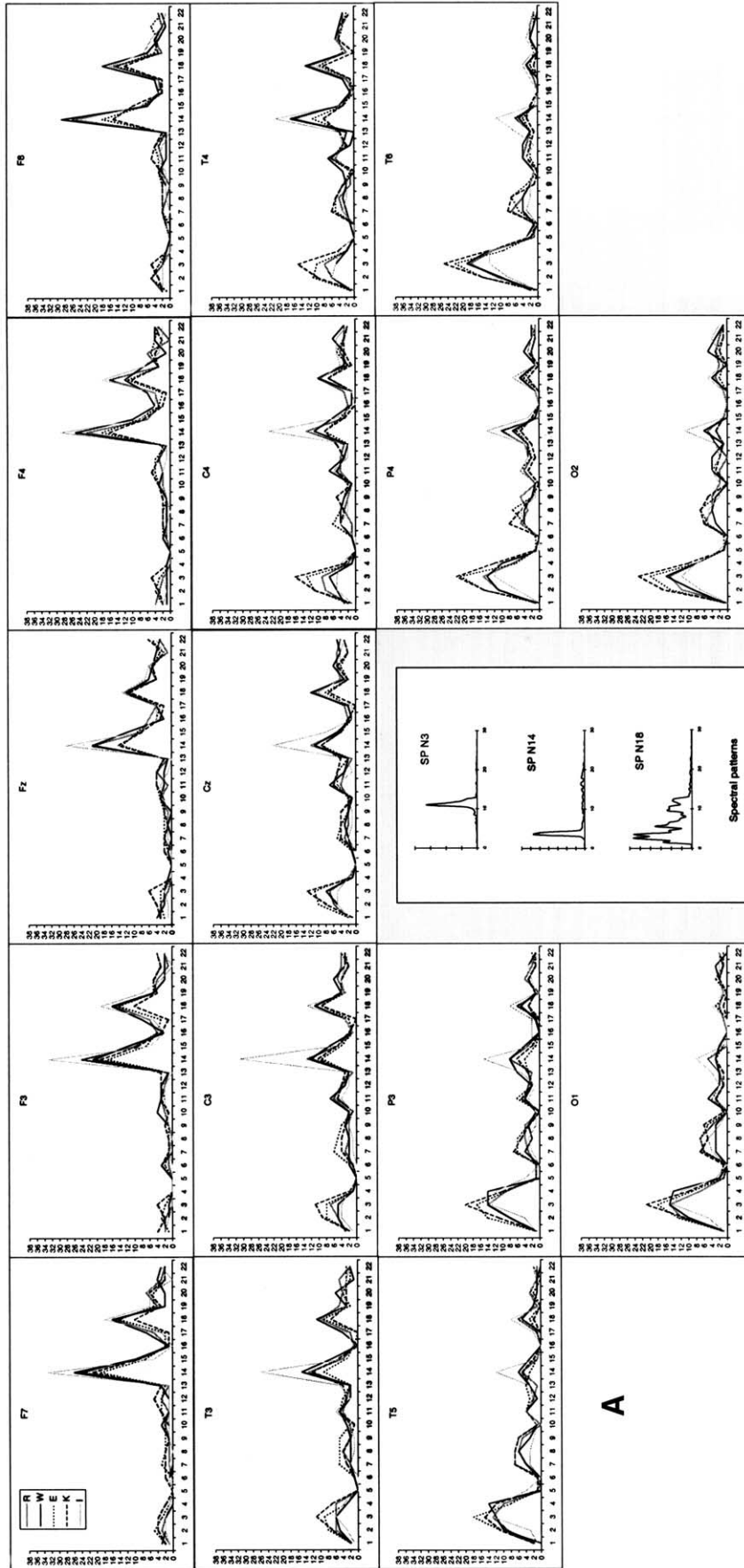


Fig. 3. (continued opposite)

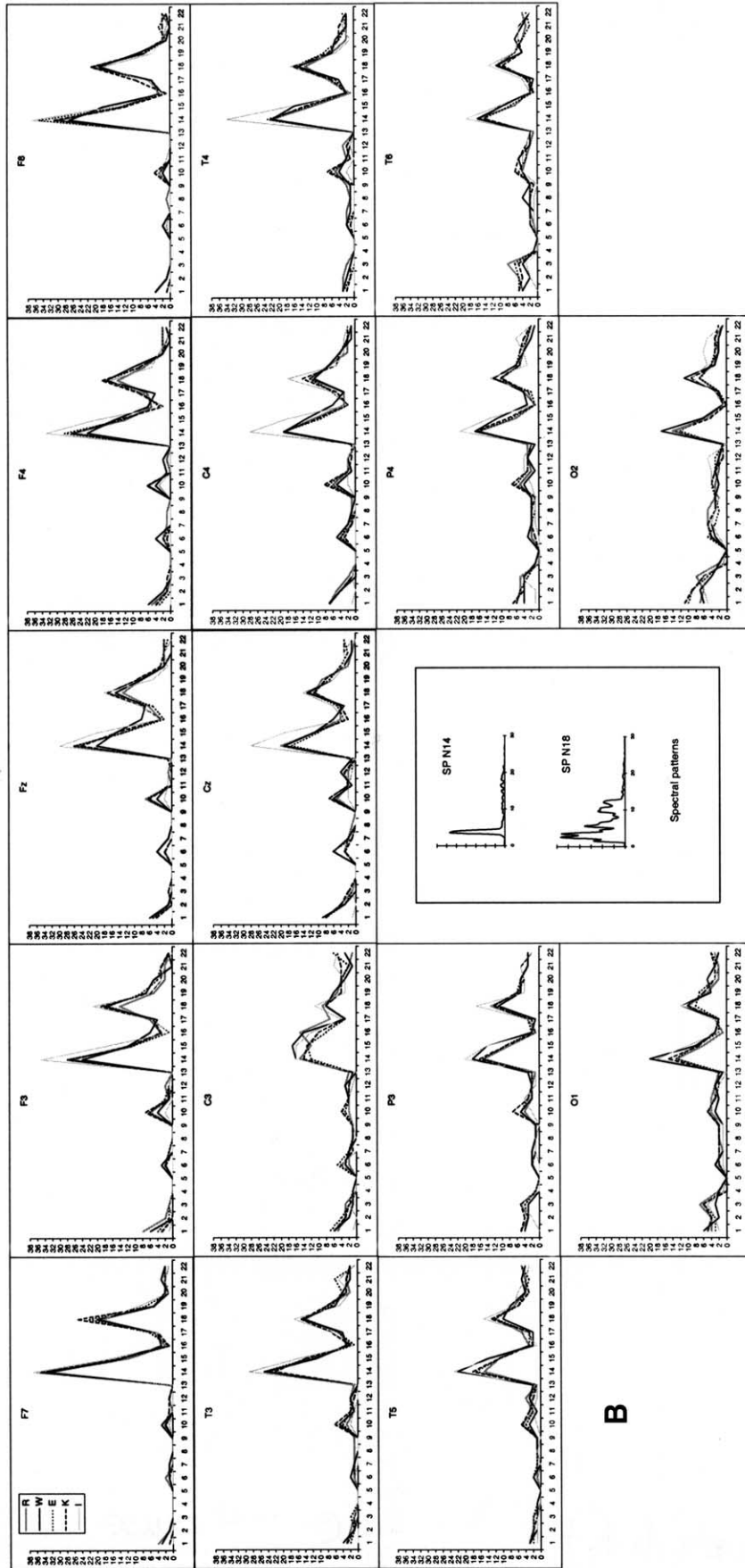


Fig. 3. (continued overleaf)

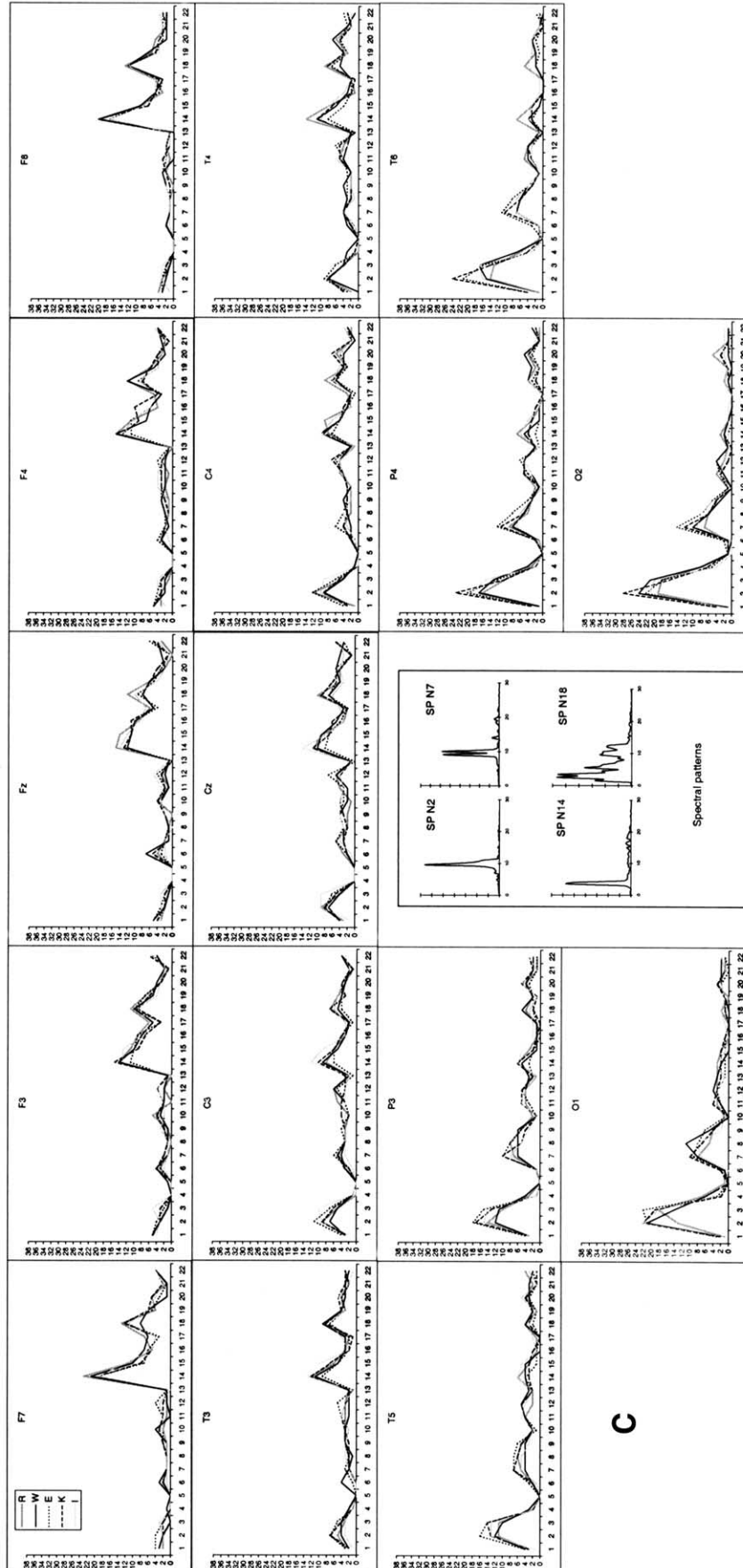


Fig. 3. (continued)

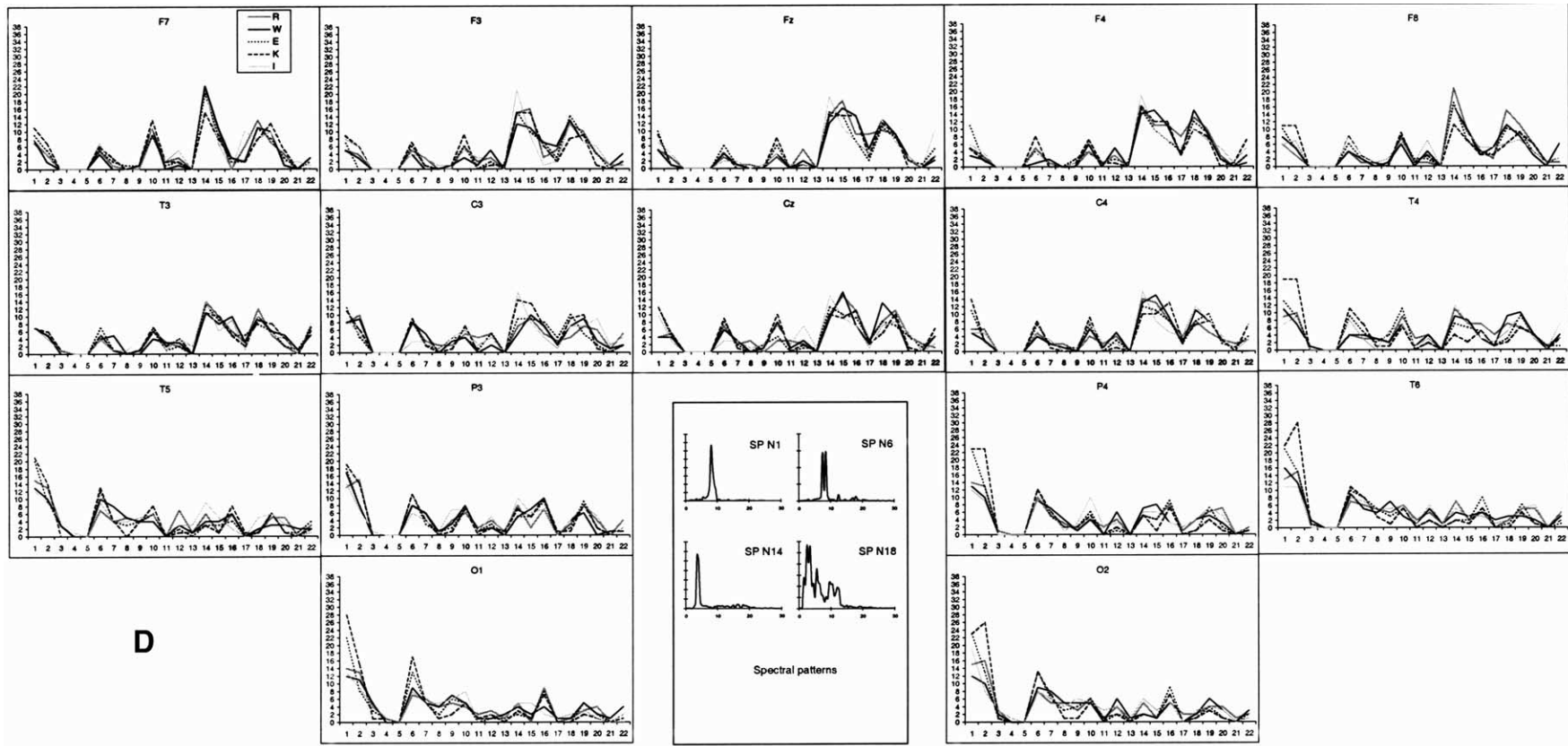


Fig. 3. Mean (for each subgroup separately) probability classification profiles (PCPs) of the spectral patterns (SPs) calculated for 5 periods of memory task. The X-axis displays the labels (numbers) of standard SP from 1 to 22. The Y-axis displays the share of the corresponding SPs in the percentage from the total number of the classified SPs. Sixteen EEG channels are presented. In the insertion at the centre of the figure the SPs, which have the maximum values in the classification profiles are presented. The X-axis of the insertion displays the frequency (Hz), and the Y-axis displays spectral power (μV^2). SP number at the insertion corresponds to the SP number at the PCP. R, resting period, W, waiting period, E, encoding period, K, keeping-in-mind period, I, identification period. (A) I group, (B) II group, (C) III group, (D) IV group.

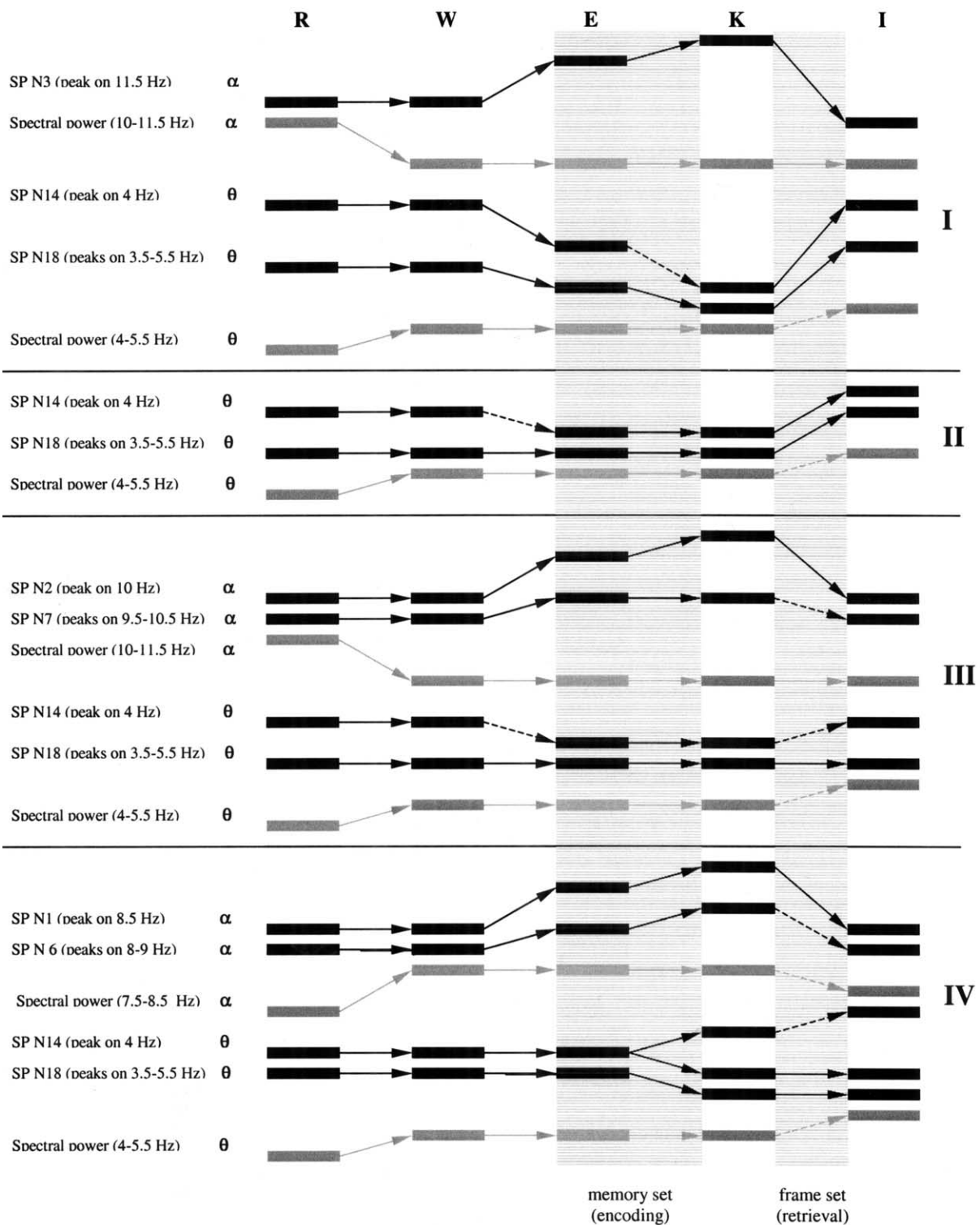


Fig. 4. The scheme of the changes of the probability of the occurrence of alpha- and theta-trials and the changes of the mean spectral power calculated for correspondence frequency bands for the 4 subgroups. The scheme scale is proportional to the real data, which are presented in Fig. 3. At the left side of the scheme there are SP numbers with corresponding main frequency peak(s), and spectral power with correspondent frequency bands. At the right side of scheme, there are the subgroups numbers. At the top of the scheme there are the labels of the memory task periods, which are presented in chronological sequence: R, resting period, W, waiting period, E, encoding period, K, keeping-in-mind period, I, identification period. Solid arrows indicate significant ($P < 0.05-0.001$) changes, and dotted arrows indicate non-significant changes. Horizontal arrows mark the absence of the changes. The gray areas at the scheme mark memory and frame sets of the memory task when ERD/ERS were calculated (Krause et al., in preparation).

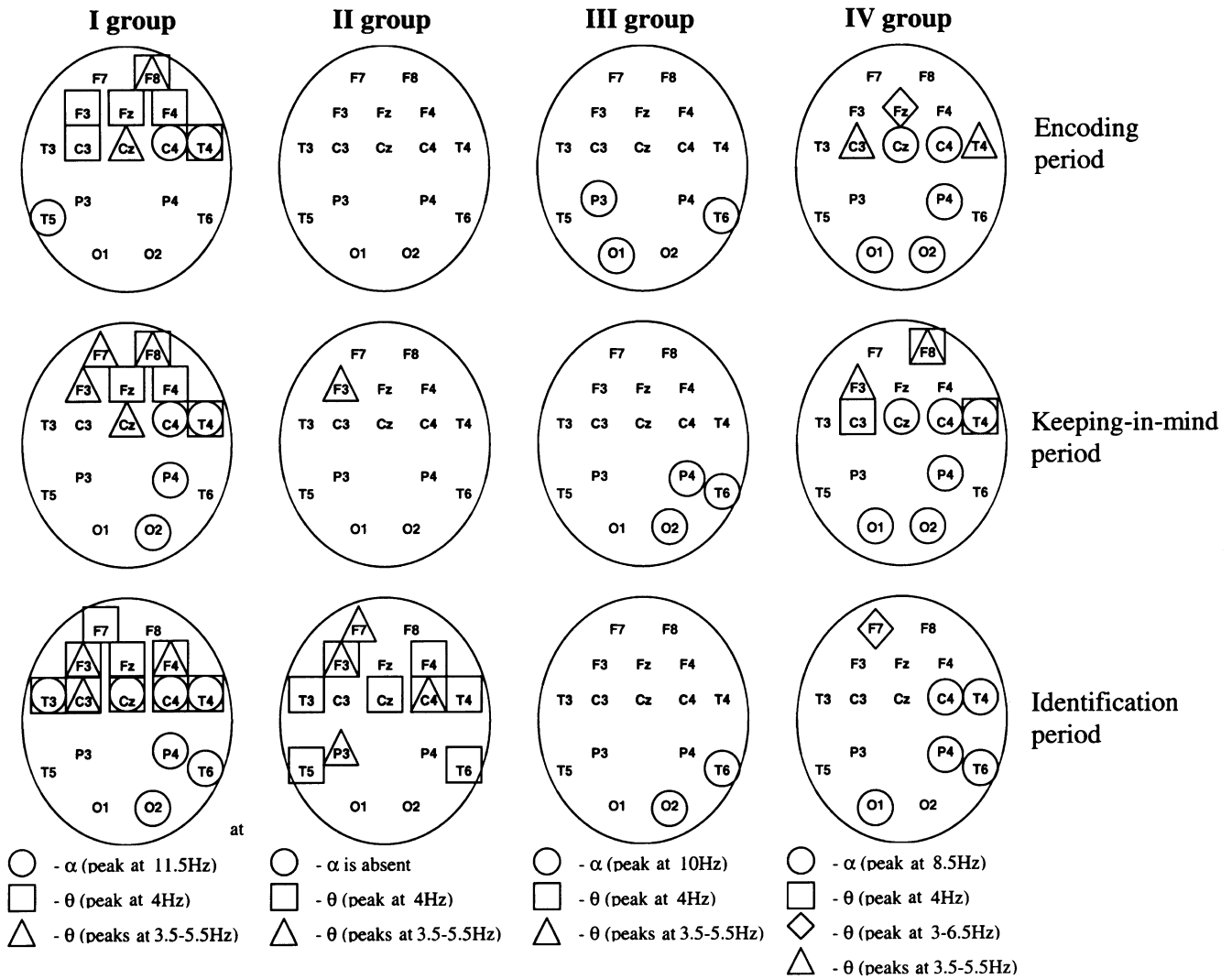


Fig. 5. Brain maps of PCP changes for all subgroups during the transition from resting/waiting period to encoding, then-to keeping-in-mind and to identification periods. Only statistically significant changes ($P < 0.05-0.001$) of PCP are presented. Changes in the probability of the occurrence of particular SP are shown by different symbols. The main frequency peaks of SP are given in the brackets.

retrieval period). This finding is well in line with previous observations indicating that an EEG theta power increase is associated with a simultaneous alpha power decrease (Klimesch et al., 1997). Also it was shown that event-related theta oscillations are highly correlated with retrieval process (Basar et al., 2001a,b). Most likely, the above-mentioned changes in the probabilistic values of the occurrence of the trials with particular SP reflected the scanning of the memory set.

At the same time, during the encoding period, the probability of the occurrence of theta-trials was decreased (Fig. 4), but theta ERS was detected (Krause et al., in preparation). It means that the observed theta ERS reflects theta synchronization, which occurred not in all of the trials. In reality, the number of trials with theta activity was decreased as compared to the resting and waiting stages.

When inspected over all electrode locations and subgroups, the PCP changes were most prominently

detected at the anterior and central electrode locations (Fig. 5). According to Cabeza and Nyberg (1997), attention and working memory processes generally activate frontal and parietal cortices. Note that special responsiveness of the frontal lobes was in theta frequency range. This is in agreement with some previous findings (Basar, 1999; Basar et al., 2001a). Basar et al. pointed out that theta increases in frontal areas are related to large theta enhancements during selective attention processes, short-term memory retrieval and performance. We can add here that in terms of PCP the effect of increased frontal theta is provided not only by theta enhancements, but also by the increasing of the probability of the occurrence of the theta-trials. Moreover, it has been proposed that EEG theta activity would be induced into cortical networks via hippocampo-cortical neural loops (Miller, 1991; Klimesch, 1996b). Changes in the probability of the occurrence of the theta-trials observed in this study might reflect the probability changes of those neuronal

Table 2
Occurrence of alpha- and theta-trials as a percentage of the total number of trials for each EEG channel^a

EEG channels	E		K		I	
	Alpha	Theta	Alpha	Theta	Alpha	Theta
O1	31	10	32	11	25	15
O2	34	8	39	10	28	13
P3	26	14	26	15	20	22
P4	28	14	30	14	22	20
T5	23	14	21	15	17	21
T6	32	12	33	11	23	18
C3	12	16	11	20	9	27
C4	13	21	12	21	9	31
Cz	11	21	11	22	10	31
T3	9	25	9	25	5	33
T4	9	24	12	23	8	33
F3	3	32	4	23	4	40
F4	4	31	4	31	4	37
Fz	4	30	4	28	4	37
F7	4	41	4	41	4	43
F8	4	38	5	35	4	42

^a E, encoding period; K, keeping-in-mind period; I, identification period of memory task.

networks involved in conscious stimulus identification and/or retrieval from working memory, including the hippocampus and associative prefrontal cortices (Klimesch et al., 1994; Braver et al., 1997). At the same time, within the framework of current concepts on the operational architectonics of cognitive activity (Kaplan and Shishkin, 2000; Fingelkurts and Fingelkurts, 2001), attention and working memory, although closely interrelated, are based on different morphological and functional principles (Mishkin and Appenzeller, 1987) and also neurophysiological mechanisms (Posner, 1992; Polich and Squire, 1993).

Findings from different investigations support the idea that prefrontal brain areas play an important role in selective attention (Pribram, 1973; Knight and Garbowecky, 1995) and working memory (Jonides et al., 1998; Ranganath and Paller, 1999; Krause et al., 2000). Moreover, it has been shown that especially the left inferior frontal cortex is activated by word retrieval, particularly verbs (Warburton et al., 1996). This finding being in good agreement with the data here where significant changes in PCP at electrode F7 for three subgroups during the identification period were observed. This corresponds to the post-retrieval interval (in this task, verbs were used as stimuli).

We mentioned above the dependence of the ERD/ERS responses of the EEG in the pre- and post-stimulus intervals. A comparative analysis of PCP and ERD/ERS suggests the evidence that alpha- and theta-ERD/ERS responses and corresponding alpha- and theta-trials are the most probable, but not frequent enough to characterize all the trials (Fig. 4, Table 2). This data is consistent with our previous work, where it was shown that the main part of EEG individual segments (85–90%) keeps its contribution constant in EEG

classification profile during the changes of cognitive loading (Fingelkurts, 1998; Kaplan et al., 1999a).

Hence, ERD/ERS responses reflect the total picture of a given frequency band power transformations, but they not characterize all of the analyzed trials. The power changes may be strongly dependent on the current combination of uncontrolled factors (which determine piece-wise stationary EEG structure). Moreover, the power increase in averaged response may be not only due to amplitude increase in single trials but to increased synchronization of the waves. This was clearly shown in superposition of single sweeps by Schurmann and Basar (2001). Thus, averaging of such estimates will most likely show the balance of diverse task-related EEG changes rather than actual ‘principal’ processes over all trials. It seems reasonable to keep in mind that if the signal of a poorly understood nature is non-stationary (like the EEG), any of its characteristics may appear to be non-stationary. This means that any averaged estimate of the EEG must be used with caution. Thus, it is difficult to interpret ERD/ERS data without knowing what occurred in the EEG during the pre- and post-stimulus intervals.

These findings imply that obtaining of averaged ERD/ERS responses face the same problem of calculation of averaged ERPs.

The data presented here demonstrates that the usage of a technique of calculation of PCP of SPs, which describe the EEG characteristics of single trials, opens the way for more differential EEG analyses. First, individual pre-/post-stimulus intervals of each trial can be accurately described. Second, it is possible to study temporal relationships between (a) pre-/post-stimulus intervals for each EEG channel separately; (b) pre-/post-stimulus intervals and trials for each EEG channel separately; (c) pre-/post-stimulus intervals for all EEG channels simultaneously, and (d) pre-/post-stimulus intervals and trials for all EEG channels simultaneously.

One could characterize the pre-/post-stimulus intervals of each trial by SPs as the type of EEG pattern forming the background against which the ERD/ERS are formed. In future studies, it might be of interest to pre-select particular trials according to their spectral descriptions before the calculation of ERD/ERS. On the other hand, each of the observed ERD/ERS responses can be individually/separately characterized by features in their background i.e. pre-/post-intervals. Both of these ways of analyses may reveal some relations between the EEG background activity and the instance of its change. In the present study, it was impossible to recalculate ERD/ERS responses accordingly with PCP, thus, the main advantages of noted above PCP and ERD/ERS integration remain for further investigations.

At the same time, data presented in the present paper do not allow to decide whether the reported percentage of EEG changes are typical for all ERD/ERS studies or it is the matter of the present subjects’ sample.

On the other hand, in a previous study, it has been shown that only half of detected SPs, were functionally active.

These exact functionally active SPs provided significant changes in EEG during different memory task periods (Fingelkurts 1998; Kaplan et al., 1999a,b). It seems that the brain's strategy in each trial depends on immediate situation in piece-wise stationary structure of ongoing EEG (pre-/post-stimulus intervals). In order to save energy, the human brain might use the active resources for fulfilling the task. For instance, some ongoing activity may already feed the task, so in these trials there would be no considerable EEG changes. It may also be that another ongoing activity demands significant transformations in order to fulfill the task – here ERD/ERS can be detected. Thus, when the task is novel and, more importantly, conflicts with a more habitual response to the presented stimulus, major changes can occur in the brain systems allocated to the task (Krause et al., 2001). This is in agreement with Basar's concept of the EEG as an active signal in the brain where 'the spontaneous EEG is regarded as a signal that determines or governs the responses of the brain' (Basar et al., 2001b). Such a view is consistent with other studies (Rahn and Basar, 1993a,b; Arieli et al., 1996; Brandt, 1997) which showed that visual and auditory evoked responses qualitatively depending on the frequency content of the pre-stimulus activity. If the assumptions here are correct, it might be possible to attribute the ERD/ERS responses new meanings - perhaps ERD/ERS reflect conflict situations between ongoing EEG and presented stimuli rather than stimulus processing? The latest work of Krause et al. (2001), in which the test–retest consistency of ERD/ERS was studied, gives support to this viewpoint. In that study (Krause et al., 2001), in all studied EEG frequency bands, differences were observed between the ERD/ERS responses elicited during an auditory memory task between the first and second registration (mean test–retest interval 9 days), when examined as a function of relevant experimental factors. However, further tests and analyses are needed in order to make any definitive conclusions.

If the assumptions from previous paragraph are correct, then the significant EEG changes, which are reflected as ERD/ERS, might occur randomly among all the trials. Simultaneously, responses reflecting the habituation of the cellular activity to certain types of stimuli, which is not random, may exist (Fruhstorfer et al., 1970; Cacace et al., 1990).

In conclusion, the results from the present study demonstrate that the technique of calculation of PCP of SPs might be a substantial supplement for the investigation of generalized cortical phenomena of EEG desynchronization–synchronization as the marker of functional cerebral activation–deactivation accompanying cognitive activity in man.

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