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Structural (operational) synchrony of EEG alpha activity during an auditory memory task

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Abstract

Memory paradigms are often used in psycho-physiological experiments in order to understand the neural basis underlying cognitive processes. One of the fundamental problems encountered in memory research is how specific and complementary cortical structures interact with each other during episodic encoding and retrieval. A key aspect of the research described below was estimating the coupling of rapid transition processes (in terms of EEG description) which occur in separate cortical areas rather than estimating the routine phase-frequency synchrony in terms of correlation and coherency. It is assumed that these rapid transition processes in the EEG amplitude correspond to the "switching on/off" of brain elemental operations. By making a quantitative estimate of the EEG *structural synchrony* of alpha-band power between different EEG channels, it was shown that short-term memory has the emergent property of a multiregional neuronal network, and is not the product of strictly hierarchical processing based on convergence through association regions. Moreover, it was demonstrated that the dynamic temporal structure of alpha activity is strongly correlated to the dynamic structure of working memory.

Keywords: Structural or operational synchrony; Binding problem; Short-term memory; Sternberg task; Alpha activity; EEG

Introduction

Interpreting brain activity in terms of putative global mechanisms (Wright and Liley, 1996; Tononi et al., 1998; Haken, 1999; Nunez, 2000) provides an impetus for conducting experiments to test the idea of large-scale integration during cognitive processes. In psycho-physiological experiments memory paradigms have often been used in order to understand cognitive processes (Sternberg, 1996, 1975; Rojas et al., 2000). For instance, the Sternberg memory search paradigm (Sternberg, 1966) has been extensively used for studying short-term memory encoding, scanning and retrieval (Atkinson and Shiffrin, 1968; Sternberg, 1969; Jensen and Lisman, 1998; Rojas et al., 2000; Wolach and Pratt, 2001). In this task a memory set consisting of discrete items is presented to the subjects. A few seconds later, a target item (probe) is presented, and the subject must respond quickly whether the target was among the items presented in the original set or not (positive versus negative probes).

Traditionally, working memory (WM) has been divided into two types of processes: executive control (the encoding manipulation and retrieval of information) and active maintenance (keeping information available "on line") (Cohen et al., 1997). It has been also proposed that the frontal regions along with the posterior parietal and superior temporal areas play a role in WM processes (Smith and Jonides, 1997; Elliott and Dolan, 1999; Gruber and von Cramon, 2001) and are recruited in different ways during encoding, retrieval,

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and keeping information in mind (Raichle et al., 2001; Simpson et al., 2001; Gruber and von Cramon, 2001). However, the *relative contribution* of the frontal, midbrain, and temporal cortical regions for WM processes is still uncertain (Vincent et al., 2001). Moreover, for short-term memory tasks, the specific and complementary *interrelations between different cortical areas* during episodic encoding and retrieval processes are only partially understood.

Electrophysiological studies have revealed that memory encoding, retrieval and retention differ from each other also in terms of EEG oscillations (Nakamura et al., 1992; Krause et al., 1996; Klimesh, 1999; Klimesh et al., 1999; Newman and Grace, 1999; Krause et al., 2001, Basar et al., 2001). For example, it has been shown that during a Sternberg-type auditory memory task, encoding elicits ERS whereas retrieval elicits ERD in the broad alpha-frequency band (Krause et al., 1996).

The role of large-scale synchronous oscillations in the brain (Gordon and Haig, 2001) has been the subject of considerable recent interest. Evidence has been put forward to show that oscillations which are synchronous across distributed cortical regions may represent a crucial mechanism by which the brain binds or integrates spatially distributed activity (Gray and Singer, 1989; Basar et al., 1997, 2001).

Prior to recent developments, coherence was the main methodology used in electrophysiological studies to assess the degree of synchronization between brain signals. However, in a strict sense, the coherence value indicates only the linear statistical relationship between signals in a frequency band. They therefore only characterize (in the framework of the "symphonic" metaphor of EEG; Nunez, 1995) similarities between sets of "orchestral instruments" being used by neuronal ensembles of cortical areas and not how these ensembles cooperate to perform a common functional or behavioral act (for a more detailed discussion, see Kaplan et al., 1997; Nunez, 2000). Several new methods for detecting functional connectivity between cortical areas have recently been published: partial directed coherence (Baccala and Sameshima, 2001), dynamic imaging of coherent sources (Gross et al., 2001), and phase synchrony (Tass, 1999). However, all these methods have several limitations in that they do not take into account the nonstationary nature of the data, require long periods of analysis, and use linear mathematical models of the signal which for the brain is not typically the case (Landa et al., 2000).

To overcome these problems, an emphasis was put in the present study on estimating the coupling of EEG *segments* (it is supposed that they underlie the inherent elementary operations; Fingelkurts and Fingelkurts, 2003) which occur in different EEG channels, rather than applying a routine phase-frequency synchrony analysis in terms of correlation and coherence (Kaplan et al., 1995; Fingelkurts, 1998; Kaplan and Shishkin, 2000). It has been suggested that sharp transformation moments, or more precisely *rapid transition processes* (RTP), in the amplitude of the EEG form the boundaries of EEG segments and correspond to particularly informative "events" of brain systems dynamic, in other words to their "switching" from one microstate to another (Basar, 1983; Lehmann et al., 1995; Nunez, 2000). This means that on the EEG level, successive operations of behavioral or psychological acts can be traced in the palette of segment dynamics on corresponding EEG rhythmic components (Kaplan and Shishkin, 2000). If this holds true, then the simultaneous occurrence of the RTPs generated by different brain systems (observed as sharp amplitude changes in multichannel EEG recording) would provide evidence that they participate in the same functional act (Kaplan et al., 1997). A quantitative description (see Materials and methods) of this type synchrony—the *structural synchrony* (SS)—provides a possible means for new insights into the cooperation of different cortical brain structures (for details, see recent reviews by Kaplan and Shishkin, 2000; Fingelkurts and Fingelkurts, 2001). From a qualitative perspective, the SS process corresponds to the phenomenon of *operational synchrony* (OS) (Fingelkurts and Fingelkurts, 2003).

In our initial effort to link the SS to discrete, concrete functional acts, we showed that spatial configurations of functionally connected cortical areas vary significantly within relatively short time intervals. Such dynamics depended on the functional state of the subjects and also on the memory processes (Fingelkurts, 1998; Fingelkurts et al., 2000). It has also been shown that the segmental structures of alpha1 (8–10 Hz) and alpha2 (10–13 Hz) bands are synchronized during memory performance (Fingelkurts, 1998). The fact that both alpha-frequency bands respond in a similar manner during an auditory memory task was also demonstrated using the ERS/ERD paradigm (Krause et al., 1996): the presentation of the memory set (auditory *encoding*) elicits a significant ERS in both alpha-frequency bands. In contrast, the presentation of the probe (auditory *retrieval*) elicits a significant ERD also in both alpha-frequency bands (Krause et al., 1996). This finding has been reproduced (Krause et al., 1999, 2001).

Basar et al. clearly indicate the functional correlates of alpha activity and emphasize the reemerging role of alphas in understanding brain functions (Baser et al., 1997, 2001). In this connection it seems a reasonable next step to examine the structural synchrony of distributed alpha oscillations during memory performance. A memory task is a very convenient tool for such a study because of the way memory reflects a distributed property of large-scale cortical systems (Fuster, 1997; McIntosh, 1999; Basar et al., 2001). Thus, one of the aims of the present study was to investigate the rapid transition processes in alpha activity during an auditory memory task. Another aim was to examine the spatial coupling of such RTPs as a function of the encoding, retrieval, and retention during a short-term auditory memory task. We assumed that the existence of EEG structural synchrony in the form of concrete combinations of cortical areas would indicate selective channeling of information to different operations, concurrently executed in different brain areas.

Materials and methods

Subjects

Nine healthy, right-handed adult volunteers (four males and five females ranging from 20 to 29 years (mean = 24 years, SD = 2.9)) participated in the experiment. The handedness of the subjects was verified with help of an unpublished Finnish version of the Boston V.A. Handedness Questionnaire, which comprises 12 questions about the use of hand and feet in a variety of everyday tasks such as handwriting, kicking a ball, and lighting a match.

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

Stimulus materials

The stimuli consisted of 24 auditory Finnish verbs uttered by a female. The mean length of the stimuli was 6.72 letters (SD = 0.93). The mean stimulus lasted 764 ms (SD = 82). These stimuli were selected because according to psychological cognitive models, processing in STM is primarily phonological, i.e., auditory and lexical in nature and involves a phonological loop of rehearsal in the working memory (Baddeley, 1990). Moreover, recent electrophysiological studies support phonological processing in STM (Wolach and Pratt, 2001).

The auditory stimuli were recorded onto the hard disk of a Macintosh IIFX computer using the Digidesign sound tools software package. Thereafter, the digitized stimuli were stored in a Neuroscan Stim file format (within and in the beginning of a time window of 1000 ms). The length of each auditory stimulus window was 1000 ms, and the auditory stimuli in all cases were located at 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 earphones (10 Ω) and played at a comfortable sound pressure level ($\sim$70 dB). The intensity of the stimulus 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 (Krause et al., 1996; Sternberg, 1966). The memory set (*encoding*) consisted of four auditory stimuli and the frame set (*retrieval*) size was kept constant and consisted of one stimulus. The memory set always consisted of four items because of the risk that supraspan lists (i.e., > 5) might engage long-term memory encoding processes (Durgerian et al., 2001). A total of 192 four-verb memory sets were constructed in such a way that each of the verbs occurred with equal frequency and only once in the same memory set. In 50% of cases, the frame set verb was among the previously presented four-stimulus block. In total, there were 192 trials which were presented to the subjects in a pseudo-randomized order.

Procedure

After electrodes were placed on the subject's head and the instrumentation was calibrated, the subject was seated in a comfortable chair in a dimmed registration room and the procedure of the experiment was explained. To reduce muscle artifacts in the EEG signal, the subject was instructed to assume a comfortable position and to avoid movement. The subject was instructed to look at a TV screen placed in front of him/her (at a distance of 1.5 m) and to avoid unnecessary eye movements. The behavior of the subject was observed on a TV monitor throughout the experiment.

Each trial began with a 3500 ms intraexperimental reference condition. An invisible reference mark indicates 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 the *waiting* period (**W**). After 1500 ms, the 7000 ms four-verb memory set was presented (four 1000 ms auditory stimuli with three ISIs of 1000 ms). The *encoding* period (**E**) consisted of three ISIs. At an interval of 2000 ms after the presentation of the four-verb memory set was the *retention* period (**Re**), after which the frame set (one 1000 ms auditory stimulus) was presented. The subject then had to decide whether the fifth verb had appeared in the memory set or not. A time period of 1500 ms after the presentation of the probe verb was the *test* period (**T**), after which a green spot appeared on the TV screen, marking the end of the T period and reminding a subject to respond by pressing either the "yes" or "no" button on a response pad (see Fig. 1A). The next trial began when a subject had given his/her answer on the response pad. There were 192 trials in all. The total registration time was about 60 min.

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, Pz, P4, T6, O1, Oz, and O2. Additionally, two EOG electrodes were placed on the outer side of the eyes and all electrodes were referred to linked ears, which also served as the ground electrodes. Although it is sometimes claimed that using linked earlobes as a reference can cause scalp distribution distortions, we have shown through modeling experiments that the values of the SS index are sensitive to the morpho-functional organization of a cortex rather than to the volume conduction (Fingelkurts, 1998; Kaplan et al.,

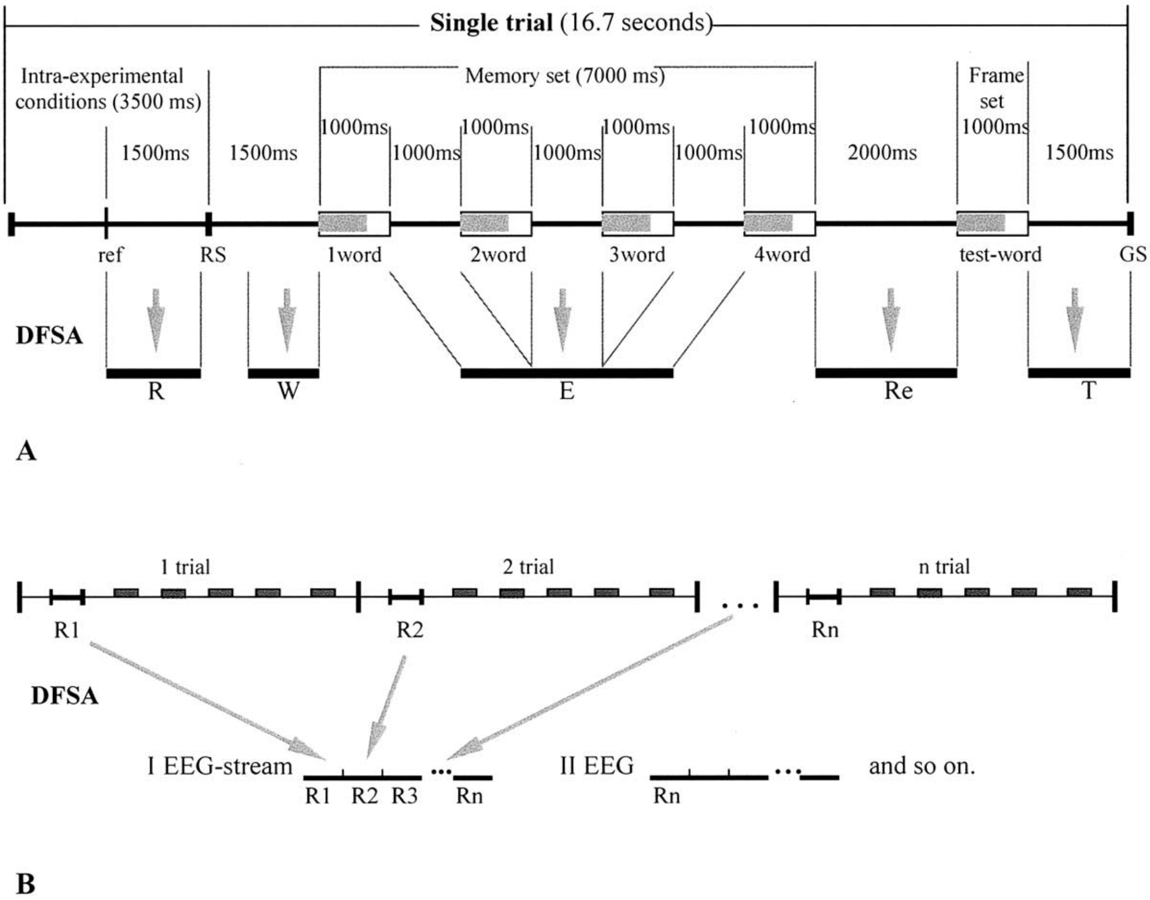

Fig. 1. The scheme of the experimental paradigm (A) and data processing (B, example for resting period is presented). Ref, reference moment; RS, red spot; GS, green spot; DFSA, adapted model of the Deterministic Finite State Automaton; R, resting period; W, waiting period; E, encoding period; Re, retention period; T, test period. 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)). It means that there were no direct influences of ERD/ERS on interstimulus intervals.

2000). Generally, the linked earlobes reference (A1 + A2) has a minimum number of shortages when compared to other reference schemes and is generally considered as the current standard method in EEG studies (see the recent review by Hagemann et al., 2001).

Raw EEG signals were recorded using the Neuroscan 386 Scan 3.0 data acquisition system with a Braintronics CNV/ISO-1032 amplifier with a frequency band of 0.3 to 70 Hz. The data were recorded using a sampling rate of 200 Hz. The impedance of recording electrodes was monitored for each subject with a Braintronics electrode impedance meter prior to data collection and it was always below 5 kΩ. The presence of an adequate EEG signal was verified through visual inspection of the raw signal on the computer screen.

Data processing

A full EEG stream contained 192 experiment trials and for each raw EEG stream a reference file was created with a chronological sequence of the events of the experiment for all the trials.

An adaptation of the model of a Deterministic Finite State Automaton (DFSA) (Hopcroft and Ullman, 2000) was used to extract and combine data with specific common characteristics belonging to R, W, E, Re, and T. Thus, the full EEG streams were split into 5 distinct segments: R for the resting period, W for the waiting period, E for the encoding period, Re for the retention period, and T for the test (identification) period (Fig. 1B).

Due to the technical requirements of the tools which were later used to process the data, 16 EEG channels (F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, T6, P3, P4, O1, and O2) were analyzed with a converted sampling rate of 128 Hz.

Prior to the nonparametric adaptive segmentation procedure (see below), each EEG sequent (corresponding to the different periods of the memory task: R, W, E, Re, and T) was bandpass-filtered in the alpha-frequency range (7–13 Hz) after which the amplitudes were squared. This frequency band was chosen because the alpha band has a relatively pronounced temporal structure which is highly sensitive to subtle changes in the brain state (Lehmann, 1980). Additionally, we wanted to compare the results of this study with the alpha ERD/ERS responses on the same material (Krause et al., 2001). Many studies which use the STM paradigm have shown that the sensory processing of stimuli is reflected mainly in responses of the broad alpha band (Schack et al., 1999; Newman and Grace, 1999). Additionally, alpha-band responses seem to reflect attention and semantic processes (Klimesch, 1999).

Adaptive level segmentation of EEG

It has been suggested that an observed piecewise stationary process like an EEG can be seen as being "glued" from several strictly stationary segments (Brodsky et al., 1999). It is assumed that these segments measured by the EEG may be a reflection of the discrete operations of the brain (Kaplan and Shishkin, 2000; Fingelkurts and Fingelkurts, 2001, 2003). The aim of the segmentation was to divide the EEG-signal into stationary segments by estimating the intrinsic points of "gluing." These instants within the short window when EEG amplitude significantly changed were identified as rapid transition processes (RTP) (Kaplan et al., 1997). The variability in the amplitude is indeed the main contributor to temporal modulation of the variance and power of the EEG signal (Truccolo et al., 2002).

The method for identifying RTPs (SECTION software, Moscow State University) is based on the automatic selection of level conditions in accordance with a given level of probability of "false alerts" and carrying out simultaneous screening of all EEG recordings. A more detailed explanation of the most current version of this methodology and the procedure for segmentation can be found in recent publications (Fingelkurts and Fingelkurts, 2001; Fingelkurts et al., 2003b). In order to estimate RTPs, comparisons were made between the ongoing EEG amplitude absolute values averaged in the test window (6 points = 39 ms) and the EEG amplitude absolute values averaged in the level window (120 points = 930 ms). These values yielded the best results in revealing segments within the signal (according to a previous study; Fingelkurts, 1998). The decision to use short-time windows was based on the need to track nonstationary transient cortical processes on a subsecond time scale. With this technique, the sequence of RTPs with statistically proven ($P < 0.05$, Student t test) time coordinates has been determined for each EEG channel individually.

Calculation of the index of EEG structural synchrony

Thereafter, the synchronization of rapid transition processes (the index of structural synchrony) was estimated. This procedure (JUMPSYN software, Moscow State University) reveals the functional (or operational) interrelationships between cortical sites as distinct from those measured using correlation, coherence, and phase analysis (Kaplan and Shishkin, 2000). Each RTP in the reference EEG channel (the channel with the minimal number of RTPs from any pair of EEG channels) was surrounded by a "window" (from -3 to $+4$ digitizing points on each side of the RTP point) of 55 ms. It was taken that any RTP from another (test) channel coincided if it fell within this window. This window of 55 ms provides 70–80% of all RTP synchronizations (Fingelkurts, 1998). The index of structural synchrony (ISS) for pairs of EEG channels was estimated using this procedure (see Appendix A and Fingelkurts and Fingelkurts, 2001; Fingelkurts et al., 2003b).

Using pair-wise analysis, structural synchrony (SS) was identified in several channels (more than two). These are described as operational modules—OM (Fingelkurts and Fingelkurts, 2001, 2003). OM means that the set of the cortical areas participated in the same functional act during the period analyzed. The criterion for defining an OM was a set of EEG channels in which each channel forms a pair combination (with high values of ISS) with all other EEG channels in the same set. The number of cortical areas recruited in OM was described as "*the order of areas recruitment*."

In order to reduce the amount of data and to select the highest values of ISS (i.e., those with the strongest functional connections), an analysis threshold for SS estimation equaling two was chosen. By applying this threshold:

1. only connections occuring in 59–95% of all the trials (i.e., reflected the actual "principal" process over a total of the trials) were left; in this case the higher the ISS value, the more often a particular connection appeared;
2. only those connections which exceeded the stochastic upper/lower level of ISSstoh were left, i.e., −50% of all the connections;
3. randomly coinciding RTPs which may have occurred in the places of gluing were eliminated.

Separate computer maps of the ISS values were created for each subject and for each EEG stream during different stages (R, W, E, Re, and T) of the memory task. The problem of multiple comparisons between maps cannot easily be overcome due to the large number of electrode pairs (Rappelsberger and Petsche, 1988) employed in the OS maps. This problem is common to all studies which require multiple comparisons between maps (Weiss and Rappelsberger, 2000; Razoumnikova, 2000). The comparisons that have been made should therefore be considered descriptive rather than confirmatory (Stein et al., 1999). For the present study, changes to the maps were only considered relevant if these changes consistently appeared in a majority of the trials and subjects (75–100%) at the same stages of the memory task (a validation of the results obtained is further examined in Appendix B).

Results

Subject performance

All the subjects performed well in the retrieval task. The mean percentage of incorrect answers was 4.4 (SD = 1.97).

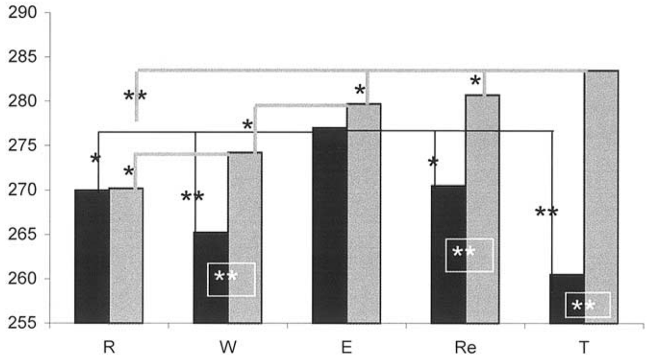

Fig. 2. The average number of RTPs (for alpha-band power) across nine subjects for anterior (gray bars) and posterior (dark bars) EEG channels separately for various memory task stages which were presented in chronological sequence: R, resting period; W, waiting period; E, encoding period; Re, retention period; T, test period. $^*P < 0.01$, $^{**}P < 0.001$ (Student *t* test).

This demonstrates that subjects were attended to the stimuli and responded as instructed throughout the entire experiment. Trials where the subjects showed incorrect performance were not analyzed.

General characteristic of the RTPs occurrence during different stages of memory task

RTPs were successfully found in the alpha-frequency band. A high number of RTPs was found and more than one RTP per second was detected on average.

Quantitative analysis of the number of RTPs revealed certain regularities, and the variation in the number of RTPs between different stages of memory task was evident (Fig. 2). These variations were different for the posterior and anterior EEG channels. A gradual increase ($P < 0.01$–0.001, Student *t* test) in the number of RTPs from the rest stage (R) to the test stage (T) was observed in the anterior EEG channels. At the same time, the highest number of RTPs ($P < 0.01$–0.001, Student *t* test) for posterior EEG channels was detected in the encoding stage (E) and the lowest number of RTPs ($P < 0.001$, Student *t* test) was observed in the test stage (T). The number of RTPs varied as a function of EEG electrode location. Thus, during all the stages of the memory task (except the rest stage), an anterior-posterior gradient was found (Fig. 2). The number of RTPs for the alpha-band power was systematically highest in the anterior EEG channels (a significant difference was found for the W, Re, and T stages, $P < 0.001$, Student *t* test)

The relationship between the number of RTPs and alpha-band power in the posterior-anterior line was found to be opposite. So, a decrease in the alpha-band power from the posterior to the anterior EEG electrodes was accompanied by an increase in the number of RTPs (compare with Table 1).

In addition, no relationship between the number of RTPs and the overall (average) alpha-band power across different stages of the memory task was observed. The mean alpha power did not vary ($P > 0.05$, Student *t* test) as a function of the memory task stage (Table 1, lower part).

RTP synchronization during memory task

From the data obtained, it can be seen that the RTPs in different EEG channels appeared to be temporarily close. Estimating the synchronization of RTPs (see Materials and Methods) between EEG channels could demonstrate the synchrony of operations between different cortical areas (Kaplan et al., 1997; Fingelkurts and Fingelkurts, 2001, 2003). The statistically significant values for the index of

Table 1
Mean spectral power (± mean error) for the alpha-frequency band calculated for each EEG channel averaged for all subjects

EEG channel	R	W	E	Re	T
O1	12.2 ± 2.8	11.9 ± 3.2	12.3 ± 2	11.8 ± 3	12.3 ± 1.8
O2	12.2 ± 1.6	12.1 ± 3.1	12.4 ± 2.7	12.2 ± 3.1	12.4 ± 1.5
P3	11.95 ± 2.4	11.7 ± 3.3	12.1 ± 1.7	11.8 ± 2.8	12.1 ± 1.7
P4	12 ± 2.6	11.95 ± 2.6	12.1 ± 3	11.8 ± 3	12.1 ± 2.6
T5	11.7 ± 3.1	11.7 ± 2.9	12 ± 3.1	11.6 ± 2.1	12 ± 2.7
T6	12.2 ± 1.5	12 ± 3	12.4 ± 3	11.9 ± 2.7	12.3 ± 1.7
C3	10.95 ± 2.8	10.95 ± 1.4	10.94 ± 1.8	10.81 ± 2.8	11 ± 3
C4	10.95 ± 2.6	10.95 ± 2.9	11.2 ± 2.8	10.85 ± 3.2	11.2 ± 2.8
Cz	10.95 ± 3	10.95 ± 2.6	11.31 ± 2.7	10.8 ± 1.8	11.3 ± 2.9
T3	11.12 ± 1.6	10.89 ± 1.7	10.94 ± 2.3	10.85 ± 1.9	10.94 ± 2.7
T4	11.35 ± 1.9	11.25 ± 3	11.31 ± 2.8	10.74 ± 3.2	11.23 ± 1.9
F3	10.56 ± 2.7	9.93 ± 1.9	10.1 ± 3	9.88 ± 2.8	10 ± 3
F4	9.8 ± 2.8	10.21 ± 2.5	10 ± 3.1	9.81 ± 2.9	10.12 ± 2.8
Fz	9.9 ± 2.8	10.1 ± 2.8	10 ± 3.2	9.85 ± 1.9	10 ± 3
F7	9.75 ± 3	9.67 ± 2.9	9.65 ± 2.8	9.76 ± 3	9.8 ± 1.9
F8	9.75 ± 3.1	9.65 ± 3	9.76 ± 2.8	9.74 ± 2.8	9.87 ± 2
Mean	11.08 ± 0.9	10.92 ± 0.8	11.2 ± 1	11.12 ± 0.9	10.88 ± 0.9

In the lower part of the table the mean spectral power (± mean error) for the alpha-frequency band calculated for all EEG channels and for all subjects is presented. R, resting period; W, waiting period; E, encoding period; Re, retention period; T, test period of the memory task.

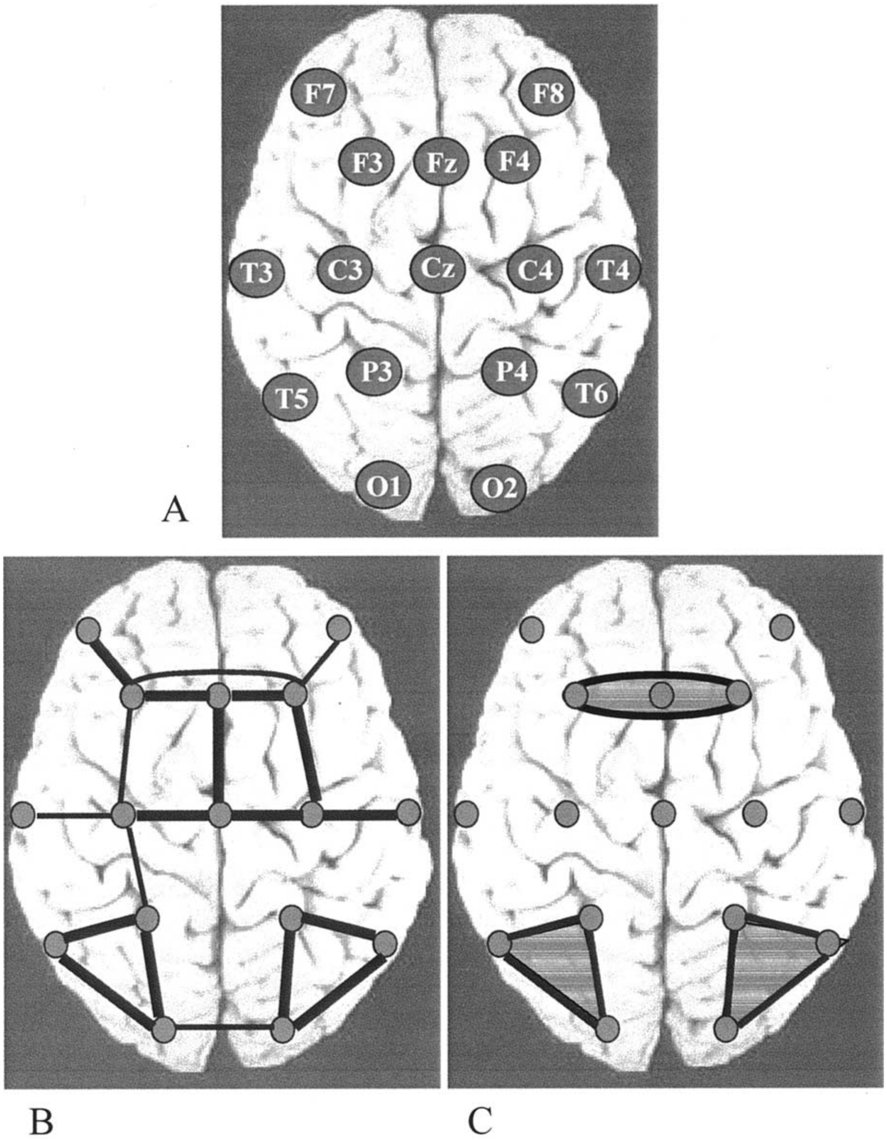

Fig. 3. Computer maps of stable (irrelevant to any cognitive activity) EEG SS combinations for pairs of channel (B) and for operational modules—OM. (C). The statistically significant ($P < 0.05$) values of ISS (ISS > 2) which occur in more than 60% of repetitions across all subjects ($N = 9$) are mapped onto schematic brain maps as connecting lines between the EEG channels involved. The darkened figures show the OMs. (A) The labels and positions of EEG electrodes. Thin lines for B indicate the cases of ISS at $2 <$ ISS < 3; thick lines, ISS > 3.

structural synchrony were mapped onto brain schemata as connecting lines between corresponding EEG channels.

The main finding was that for all subjects there exist (higher than random level, $P < 0.05$) pair and multichannel (corresponding to operational modules) EEG SS patterns in the alpha-band power. Some of these patterns occurred *independently* of the different memory stages and always remained the same, therefore being characterized as *stable.* Stable pair patterns organized the net of EEG structural synchrony relations which involved occipital symmetrical, central, and frontal EEG channels (Fig. 3). The majority of the subjects had two symmetrical occipital OMs with third recruitment order (the number of cortical sites organized in the OM during the analyzed time interval) (Fig. 3).

At the same time, maps *relevant* (specific) to the different memory stages of the intercortical SS (higher than random level, $P < 0.05$) for pairs of areas and OMs were obtained. A reorganization of the EEG SS process was observed during the transition from one memory stage to another.

Fig. 4 illustrates the maps of EEG structural synchrony for pairs of EEG channels and OMs obtained during the different stages of the memory task. A change in cognitive activity (transition from one stage to another during the memory task) resulted in a reorganization in the EEG SS process for all subjects. Significant reorganization took the form of a gradual widening of the coupling occurring between pairs of cortical areas until the encoding stage and then a slow narrowing until the test stage of the memory task (Fig. 4A). In contrast, the diversity of OMs and their

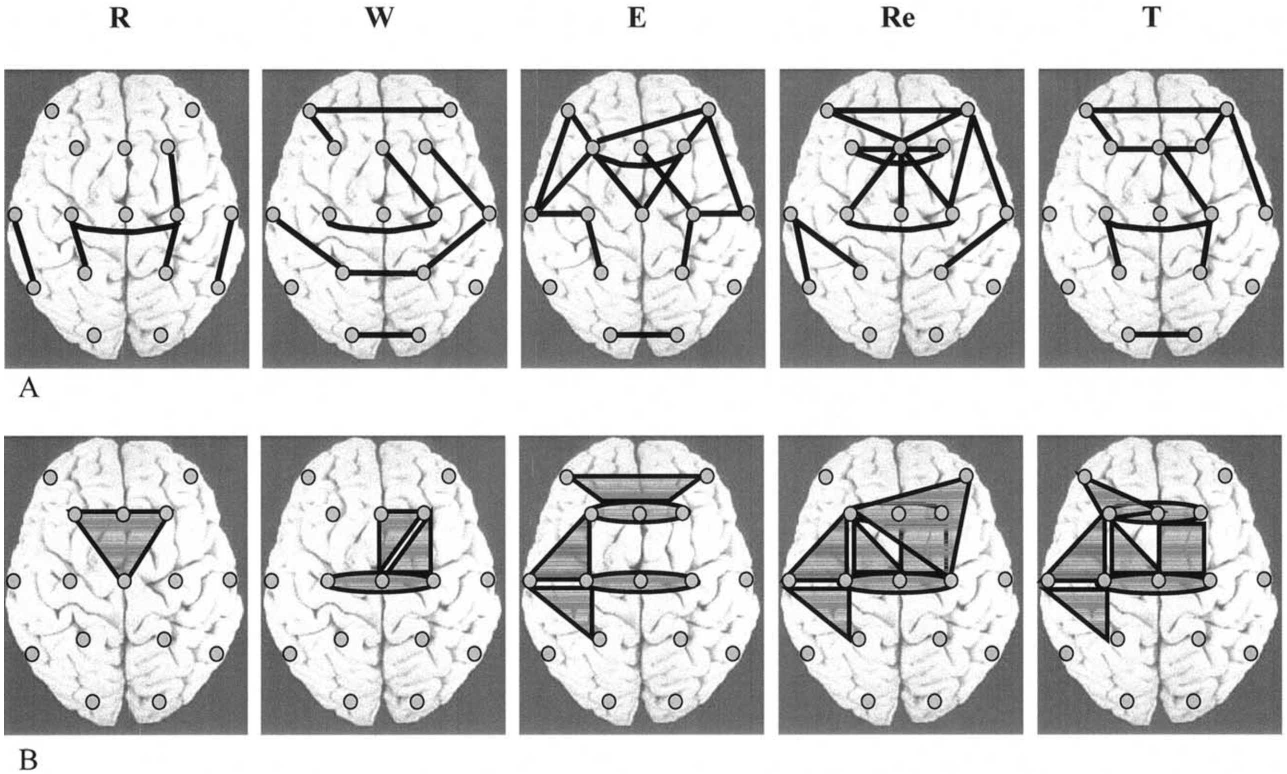

Fig. 4. Computer maps of EEG SS of cortical alpha activity relevant (specific) to memory task stages, which were presented in chronological sequence: R, resting period; W, waiting period; E, encoding period; Re, retention period; T, test period. The statistically significant ($P < 0.05$) values of ISS (ISS > 2) which occur in more than 60% of repetitions across all subjects ($N = 9$) are mapped onto schematic brain maps as connecting lines between the EEG channels involved. (A) SS in pairs of EEG channels; (B) the OMs (darkened figures).

"recruitment order" grew at the same time as the cognitive loading increased, and reached its maximum at the retention stage (Fig. 4B). One can see that the main "events" recruited the anterior cortical areas with active participation of left temporal and parietal areas during encoding and identification periods.

The question of whether the peculiarities observed in the EEG structural synchrony process during the memory task are characteristic of the majority of the trials analyzed is examined in further detail in Appendix B.

Discussion

This study concentrated on the temporal and spatial structure of alpha activity during the performance of an auditory memory task. We analyzed the rapid transition processes in the local EEGs and their structural synchronization between different EEG channels. It has been suggested that the process of operational synchrony might be reflected in the values of the SS index (Kaplan et al., 1997; Kaplan and Shishkin, 2000; Fingelkurts and Fingelkurts, 2001, 2003).

The main finding of this study indicates that the segmental dynamics of alpha processes are strongly correlated with short-term memory processes and may be presented in the combination of RTPs within distributed cortical networks. These combinations may be the reflection of the metastable operational brain microstates (Kaplan and Shishkin, 2000; Fingelkurts and Fingelkurts, 2001, 2003).

Analysis of the EEG segments

The rapid transition processes occurring in a continuous EEG mark the boundaries between quasi-stationary segments. It is assumed that each homogenous segment identified using this methodology corresponds to a temporary stable microstate in the brain's activity—an operation (Fingelkurts and Fingelkurts, 2001, 2003). The transitions from one segment to another could reflect the time moments of switching from one neuronal network activity to another (Kaplan et al., 1997).

Variations in the RTP rate across different cortical areas are of particular interest because they help in comparing the degree to which these areas are involved in information processing. The existence of a negative correlation between the number of alpha-activity RTPs and the alpha-power posterior-anterior gradient which was found in this present study (Fig. 2 and Table 1) cannot just reflect the alpha-power gradient but could be determined by "structural" characteristics of alpha-activity dynamics. This finding is in agreement with data obtained in our previous work (Fingelkurts, 1998; Kaplan and Shishkin, 2000) where it was shown that a high level of alpha-power structural synchrony is specific to the anterior brain regions. Most likely the "structure" of alpha activity we registered on the scalp is a result of the superposition of a number of "generators" which produce alpha activity with differing dynamic characteristics and which have different cortical locations (Lutzenberger, 1997; Florian et al., 1998).

We observed a decrease in the number of the RTPs in the posterior EEG channels during the waiting, retention, and test (retrieval) memory stages which indicate a reduction in the number of short segments in the EEG (Fig. 2). Since (mathematically) there is a negative correlation between the number of RTPs and the duration of the segments in the EEG signal, a decrease in the number of the RTPs probably indicates that occipital and parietal areas are performing longer operational acts. By contrast, the anterior cortical areas exhibited many changes in their operations to what was reflected in shorter segments during these same memory periods (Fig. 2). It could be suggested that shortening the duration of brain operations fits the conditions of a more dynamic performance of cooperative activity of the brain—stabilization periods of EEG structural synchrony between several EEG channels during memory retrieval (see the following section). However, during the encoding period, posterior EEG channels demonstrated an increase in the number of EEG segments, probably indicating an increase in the operational activity of these cortical areas.

Another possible explanation for the decrease in RTPs number in the posterior EEG channels and the increase in RTPs number in the anterior EEG channels is that it may simply indicate the fact of a posterior EEG desynchronization (ERD) and an anterior EEG synchronization (ERS) occurring as a result of increased effort of the subjects, and not longer and shorter operations as suggested above. This is, however, highly unlikely since in general the ERD causes the increase in RTP number and ERS causes the decrease in RTPs (Fingelkurts, 1998). But this view is not supported by the results of the experiment and by the topographic peculiarities of ERD/ERS responses obtained for the same subjects' EEGs which were registered under the same experimental conditions (Krause et al., 2001). In contrast to our results (showing a more "active" anterior brain part during encoding and retrieval), it has been shown that the strongest alpha-ERS responses during encoding and alpha-ERD responses during retrieval periods were observed in the posterior part of the brain (Krause et al., 2001). Most likely, ERD/ERS and RTP processes are two different but complementary phenomena and there is no linear dependence between them (see also Kaplan and Borisov, 2003).

Analysis of the EEG structural synchrony

It was shown that the process of EEG structural synchrony within the alpha-band power was reflected in a pair of RTPs coincidences and in the OMs (operational modules) with different numbers of cortical areas involved. Functional couplings which were irrelevant (Fig. 3) and relevant (Fig. 4) to the memory task stages were identified. We described the stable (but irrelevant) configurations as the *basic structure of SS,* and supposed that this basic structure of alpha-band SS probably reflects the basic EEG characteristic or some intrinsic unspecific brain regulations which contribute to ongoing EEG activity which we cannot monitor experimentally (Fingelkurts et al., 2003a).

In addition to irrelevant, it was shown that there are also relevant or specific functional combinations of cortical areas which changed significantly during different stages of the memory task (Fig. 4). The obtained results therefore support our initial supposition. We reasoned that if the operations that subserve memory functions (for example, encoding, scanning, detection, and retrieval) draw upon shared processing resources mediated by the appropriate cortical areas, these brain sites must then synchronize their operations in order to achieve the appropriate functional state for each memory stage. This process in the cerebral cortex may be reflected in the phenomenon of EEG structural synchrony.

In general, the central, frontal, and parietal cortical areas were recruited (Fig. 4) during memory processing. Although the encoding, retention, and test processes shared the same neural substrates, the concrete steady operational modules and their diversity were different in each of the STM stages. Thus, the right and left frontal and prefrontal areas synchronized their operations and organized the OM during the encoding period. Another OM involved the left temporal, parietal, and central cortical areas (Fig. 4, E). These data support the idea that the prefrontal areas play a key role in several functions, including selective attention (Knight and Grabowecky, 1995), working (Goldman-Rakic, 1987), and short-term memory (Ranganath and Paller, 1999). The left prefrontal cortex is differentially more involved in encoding novel aspects of information (Tulving et al., 1994) and the right, in episodic memory (Nyberg et al., 1996). This is most probably the reason why these areas were recruited in the same OM (Fig. 4, E). The left temporal areas, which participated in the same operational modules, are thought to be associated with phonological processing (Domonet et al., 1992).

In the next stages of the memory task (Re and T), the symmetrical prefrontal areas no longer participated in the same OM but were still important for the retrieval process (Xiong et al., 2000), and so participated in other OMs (Fig. 4, E). Additional new OMs appeared. The left cortical areas were involved in several OMs indicating a coupling of these cortical sites during retrieval (Abdullaev and Posner, 1997; Warburton et al., 1996), and providing evidence that the left hemisphere of the brain dominates. The highest number of areas involved in operational modules was achieved during the retention stage of the memory task (Fig. 4, Re). These data are consistent with the results which were obtained in a previous work involving memorizing visual objects (Fingelkurts et al., 2000). However, the diversity of OMs in the visual task was richer when compared with the audio task which indicates more dynamic activity of the cortical structures involved in the process of memorizing visual items. Both findings support the hypothesis (Wolach and Pratt, 2001) that more brain activity is associated with the processing of visual than auditory stimuli (Kotchoubey et al., 1996; Pratt et al., 1994, 1997).

The experimental results prove that the functional lifespan of operational cortical modules within the anterior part of the cortex became shorter (their diversity increased) during the retention and test periods. This reflects the more dynamic performance of synchronized brain operations during retrieval. Notably, the spatially oriented EEG segmentation by Lehmann et al. (1993) is in accord with this suggestion. They demonstrated that stabilization of stationary EEG maps shorten under the influence of nootropic drugs. In contrast, the application of neuroleptics results in a substantial increase in the duration of periods of stabilization of EEG maps (Kinoshita et al., 1995).

Since the overall (average) alpha-band power did not significantly change during the stages of the memory task (Table 1, lower part), its influence on the topological changes of structural synchrony process as a function of memory task stages can be excluded. This, therefore, provides evidence that there is an *actual* difference in the degree of association between the signal structure in the different EEG channels (Fig. 4). This conclusion is in line with previous research into ISS (Fingelkurts, 1998; Kaplan and Shishkin, 2000; Fingelkurts et al., 2000, 2003b) where different types of analysis (inter- and intraindividual) of the relationship between the overall power and the SS of the same band power revealed independent tendencies.

Parallels in the dynamics of alpha activity and the dynamics of the memory task

As discussed above, the dynamic structure of alpha activity underwent a considerable transformation when compared across separate (but chronologically following) brain functional states (Fig. 4). In order to show this dependence clearly, we created a scheme (Fig. 5) onto which the significant changes in the number of SS pairs and OMs together with cognitive loading (stages of the memory task) were mapped. Thus, a significant reorganization ($P < 0.05$, Student t test) was observed in the form of a gradual increase in the number of the coupling between pairs of cortical areas until the encoding stage and then as a slow decrease until the test stage of the memory task (Fig. 5). In contrast, the diversity of OMs and their “recruitment order” were growing simultaneously as the cognitive loading increased and reached its maximum at the retention stage.

These data in general support our previous findings on the alpha oscillations dynamic (Fingelkurts, 1998; Fingelkurts et al., 2000) and also is in keeping with data obtained using coherence analysis in other frequency bands (Weiss and Rappelsberger, 2000; Razoumnikova, 2000). In these studies it was shown that cognitive loading is characterized by greater connectivity between cortical areas.

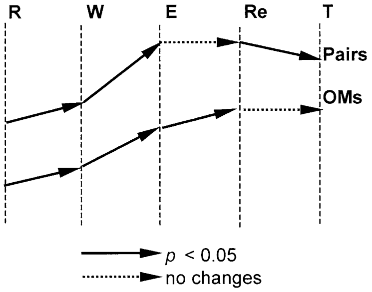

Fig. 5. The scheme of the changes (averaged for nine subjects) in the number of the occurrence of EEG SS pairs and OMs calculated for correspondent five stages of the memory task. The scheme scale is proportional to the real data, which are presented in Fig. 4. At the top of the scheme are the labels indicating the stages of the memory task which were presented in chronological sequence: R, resting period; W, waiting period; E, encoding period; Re, retention period; T, test period. Solid arrows indicate significant ($P < 0.05$, Student t test) changes, and doted horizontal arrows mark the absence of the changes.

Thus, the findings of the present study clarify that there exists an obvious correlation between the dynamic structure of alpha activity and the dynamic structure of the memory task and this is expressed through a gradual increase in the EEG structural synchrony process together with a growth of cognitive loading (Fig. 5).

Conclusion

In summary, the results of the present study showed that there is a strong correlation between the dynamics of alpha processes and the dynamics of short-term memory processes and may be represented in combinations of RTPs within distributed cortical networks. It may be interpreted that functionally distinct regions might be preferentially synchronized and involved in different stages of memory processing such as encoding, retrieval, and retention. More generally, this implies that synchronization of the operations of certain cortical areas (large-scale networks) seems necessary as a basis for the successful performance of complex cognitive processes (Fingelkurts and Fingelkurts, 2003).

It is intriguing that although memory encoding, retrieval, and retention often share common regions of the brain network, the functional integration of these areas is unique for each stage of the short-term auditory memory task. This suggests that the classical understanding of the parietal-frontal activation during short-term memory storage and its passive state during retrieval is oversimplified. The results presented in the present study suggest that cortical regions may play a part in more than one functional network, and that it is the interactions with other brain regions that determine what operations are being served at that time. Most probably, working memory is the emergent property of a multiregional network (functional integration), and is not a strictly hierarchical processing based on the convergence through association regions (McIntosh, 1999; Foucher et al., 2001).

For the purposes of this study, rapid transition processes which reflect the particular temporal structure of the EEG signal were estimated for alpha rhythm. The dynamics of alpha processes in relation to memory processes obtained in the present study provides support to the hypothesis that alpha rhythms may be the "building blocks" (Lehmann, 1989) of brain functions rather than idle processes of the brain (see Basar, 1990; Schurmann and Basar, 2001).

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Appendix A: The estimation of the index of structural synchrony

The ISS was computed as follows:

$$\mathrm{ISS} = m_{windows} - m_{residual}, \text{ where } m_{windows} = 100 * sn_w/sl_w;\ m_{residual} = 100 * sn_r/sl_r$$

sn_w, total number of RTPs in all windows (window for synchronization—55 ms each) in the test channel;

sl_w, total length of EEG recording (in data points) inside all windows in the test channel;

sn_r, total number of RTPs outside the windows (window for synchronization—55 ms each) in the test channel;

sl_r, total length of EEG recording (in data points) outside the windows in the test channel.

The ISS tends toward zero where there is no synchronization between the RTPs and has positive or negative values where such synchronization exists. Positive values indicate "active" coupling of RTPs, whereas negative values mark "active" uncoupling of RTPs.

However, it is obvious that even in the absence of any functional cortical interregional cooperation there should be a certain stochastic level of RTPs coupling, which would reflect merely occasional combinations. The values of such stochastic interarea relations must be substantially lower than in the actual presence of functional interrelation between areas of EEG derivations.

To arrive at a direct estimation of a 5% level of statistical significance of the ISS ($P < 0.05$), numerical modeling was undertaken (500 independent trials). As a result of these tests, the stochastic level of RTPs coupling ($\mathrm{ISS}_{\mathrm{stoh}}$), and the upper and lower thresholds of $\mathrm{ISS}_{\mathrm{stoh}}$ significance were calculated. These values represent an estimation of the maximum (by module) possible stochastic rate of RTPs coupling. Thus, only those values of ISS which exceeded the upper (active synchronization) and lower (active unsynchronization) thresholds of $\mathrm{ISS}_{\mathrm{stoh}}$ have been assumed to be statistically valid ($P < 0.05$). More information about the current version of methodology and theoretical concepts of RTPs synchronization are described elsewhere (Kaplan and Shishkin, 2000; Fingelkurts and Fingelkurts, 2001, 2003; Fingelkurts et al., 2003b).

Appendix B: Methodological aspects (results validation)

Of interest was whether the regularities obtained in the EEG structural synchrony during the memory task would determine the total picture: Would the SS characterize the greater part of the trials analyzed? To answer this question, the index of structural synchrony for each EEG pair must be checked for homogeneity, which means that the rules governing the changes in SS maps are the same throughout the whole experiment. Testing may be accomplished by splitting a whole EEG stream into two or more parts and analyzing these separately. Homogeneity can be assumed when all subparts yield the same result (Martin and Bateson, 1993). This would mean that the data are valid.

Therefore, we evaluated the index of structural synchrony profiles for pairwise coupling (120 possible pair combinations available from the 16 EEG channels) for 5, 10, and 20 s of EEG (for different stages of the memory task (R, W, E, Re, and T)), and compared the results with the 60-s profile of the same EEG (for details about EEG-stream construction see Materials and methods and Fig. 1). The $\mathrm{ISS}_{\mathrm{stoh}}$ and its upper/lower thresholds (distribution of $\mathrm{ISS}_{\mathrm{stoh}}$) were estimated also.

By way of example, Fig. 6 illustrates this analysis for the resting period of memory task (segment R). The profile of SS already existed at 5-s EEG interval, and remained almost the same as for the whole 60-s EEG (which corresponds to *all trials* of the memory task for segment R). The main positive peaks (which correspond to concrete EEG pair combinations) coincided precisely at 5- and 60-s EEGs (Fig. 6). Although we cannot be sure about the statistical significance of a 5-s profile, because the ISS values lay inside the threshold of $\mathrm{ISS}_{\mathrm{stoh}}$, it is important that the SS profile (main peaks) practically for all 5-s EEG intervals coincided pre-

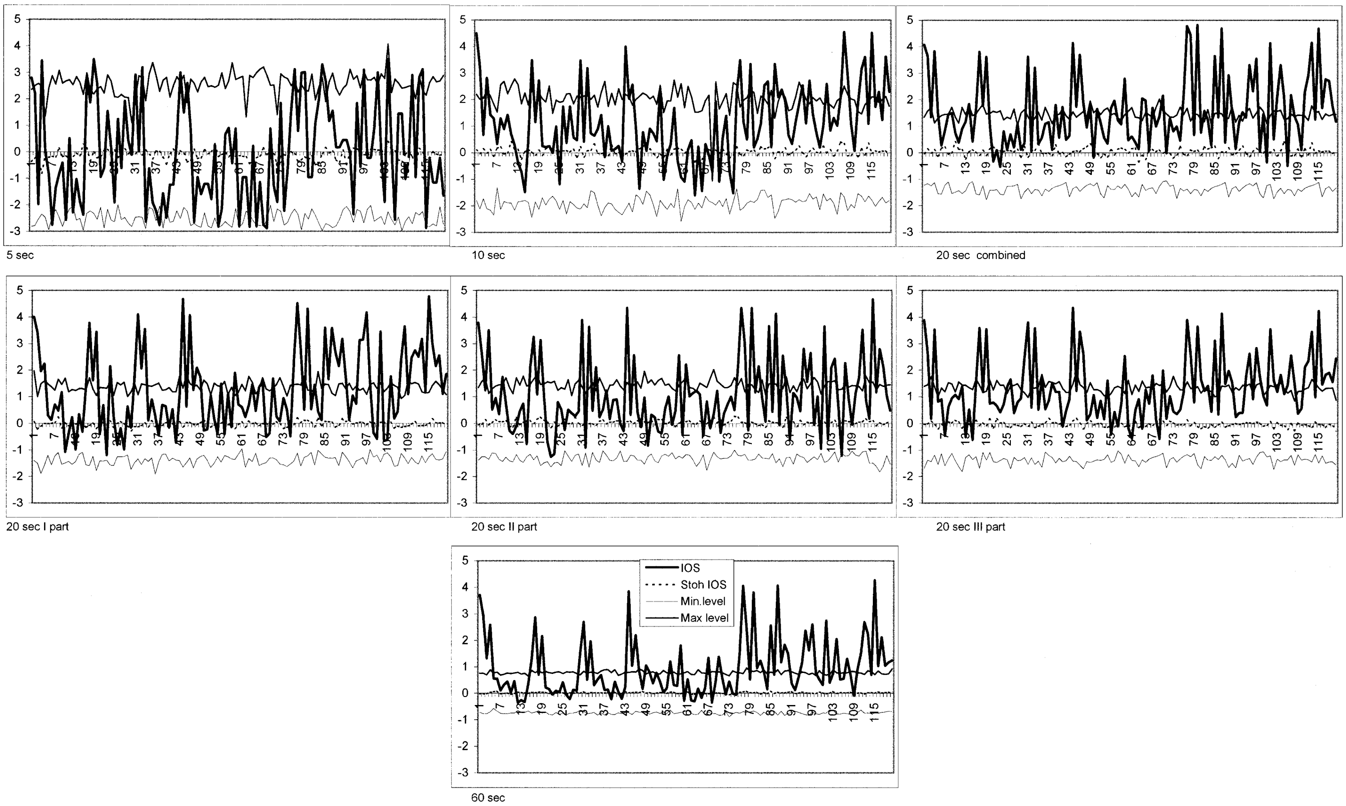

Fig. 6. Structural synchrony of cortical alpha activity for different time intervals. The *Y* axis displays the ISS values. The *X* axis displays the 120 possible pair combinations of 16 EEG channels (1 = O1–O2, 2 = O1–P3, 3 = O1–P4, 4 = O1–T5, ··· 115 = F4–Fz, 116 = F4–F7, 117 = F4–F8, 118 = Fz–F7, 119 = Fz–F8, 120 = F7–F8). A line was chosen instead of a bar for ease of comparison. Explanations are located in the text.

cisely with the 60-s EEG. The SS profile for the 10-s EEG interval was more stable and the main peaks reached the level of statistical significance ($P < 0.05$). The first, second, and third 20-s EEG intervals did not differ from each other significantly (correlation coefficient (CC) = 0.97, $P < 0.05$ for I–II; CC = 0.87, $P < 0.05$ for I–III; CC = 0.81, $P < 0.05$ for II–III) and were very similar to the whole 60-s EEG profile (CC = 0.84 ± 0.12, $P < 0.05$). Moreover, the all pair combinations which exceeded the threshold two (threshold of analysis) were the same for each of 20-s EEG intervals and whole 60-s EEG (Fig. 6). The results obtained showed that the functional relationships between EEG recordings were stable and characterized the vast majority of the analyzed trials. The evidence became stronger if we take into consideration the results of analysis of the 20-s EEG interval, which was artificially constructed from 1-s EEG intervals taken 20 times randomly during the 60-s EEGs (see Fig. 6). This SS profile was similar to any other SS profile on 20-s EEGs (CC = 0.88, $P < 0.05$; CC = 0.92, $P < 0.05$; CC = 0.81, $P < 0.05$; correspondingly to I, II, and III 20⅟m EEG intervals) and almost the same as the SS profile at the 60-s EEG (CC = 0.78, $P < 0.05$). At least all peaks, which exceeded the threshold of analysis, coincided precisely (Fig. 6).

Thus, the splitting-test reliabilities (estimated by CC) of the map parameters between the different parts of data were very high which confirmed the validity of the findings. Reliability measures minimize both Type I and Type II errors and eliminate the need for multiple comparisons because “by definition chance findings do not replicate” (Duffy et al., 1994, p. XI). Altogether these findings clarify that we can consider changes in SS maps relevant for the analysis since these changes appeared consistently in a majority of the trials (60–95%) during the same stages of the memory task.

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