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SYSTEMATIC RULES UNDERLYING SPECTRAL PATTERN VARIABILITY: EXPERIMENTAL RESULTS AND A REVIEW OF THE EVIDENCES

Alexander A. Fingelkurts[1,2]*, Andrew A. Fingelkurts[1,2], Christina M. Krause[2],
Alexander Ya. Kaplan[1].

1. *Human Brain Research Group, Human Physiology Department, Moscow State University, 119899 Moscow, Russian Federation*
2. *BM-Science Brain & Mind Technologies Research Centre, P.O. Box 77, FI-02601 Espoo, Finland*
3. *Cognitive Science Department of Psychology University of Helsinki PB 9, 00014 University of Helsinki, Finland*

Abstract: On the basis of three different experiments: oddball task (visual, auditory and audio-visual stimuli), modified Sternberg's and multistage memory tasks, it was shown that: a) there was not a single typical spectral pattern type that would characterized the majority of the trials; b) the total number of the different spectral pattern types was limited; c) different spectral pattern types had different importance to the brain - their occurrence was less or more probable; d) the total number and the number of the most probable spectral pattern types was dependent on the functional brain state; e) actual spectral pattern variability during rest with closed eyes was relatively high (around 65% from the maximum possible rate), but significantly less than stochastic spectral pattern variability. It is suggested that identical sensory events can potentially trigger a limited number of several different alternative reaction patterns in EEG/MEG, depending on the situational context.

Keywords short-term spectral patterns, variability, memory task, oddball task, electroencephalogram (EEG), megnetoencephalogram (MEG)

INTODUCTION

Recent research emphasizes that cognition is not stimulus driven in a reflex-like manner, but is to a large degree based on expectations derived from previous experience, and on generalized knowledge stored in the architecture of cortical and subcortical networks (see reviews, König & Luksch, 1998; Alexandrov, 1999; Engel et al., 2001).

One group of evidences for this came from single-trial studies. Single-trial analysis showed that cortical activity evoked by sensory stimulation is extremely variable. This has been shown for both single units (Gur et al., 1997) and macro-level (evoked potentials) (for review, see Childers et al., 1987). Such single-trial variability is commonly explained by a model in which random ongoing background activity is linearly combined with a stereotyped evoked response (ERP) (Dawson, 1954; McGillem & Aunon, 1987; Arieli et al., 1996). Nevertheless, several reports have shown that ERPs are neither stable nor wholly independent of the "background" EEG (Basar, 1980; Jansen & Brandt, 1991), and therefore, the response of the brain to stimuli is not fully captured in the ERPs (Makeig, 1993). Moreover, there are evidences that post-stimulus ERPs are not sums of a sequence of brief fixed-latency, fixed-polarity potential events, as often assumed, but originate from the phase resetting of ongoing EEG activity. This was shown for auditory (Sayers, 1974) and visually (Makeig et al., 2002) evoked responses. Kisley & Gerstein (1999) also reported that "the ongoing EEG activity was found to modulate both amplitude and shape (including latency) of evoked local field potentials and evoked unit activity in a manner not predicted by linear superposition of background activity and a stereotyped evoked response".

The brain often does not respond in the same way to repeated stimuli, even though cortical neurons are able to respond with remarkable temporal accuracy (Mainen & Sejnowski, 1995). Hence, variability of general brain state can lead to variability of the so-called "repeatable" response (for the review, see Coenen, 1995).

Taken together, these findings suggest that induced activity in the cortex and the resulting behavioral responses exhibit a large variability to repeated presentations of the same stimulus. In this context it is interesting and important to study the degree of diversity of induced brain activity during the same and different functional states and/or experimental tasks. Thus, several major questions arise: Is the number of induced brain activity classes infinite or limited? If it is limited – then in which range? Do all induced brain activity classes have the same importance? Is the number of induced brain activity classes dependent of functional state? In order to face the questions posed above, we assessed in this paper the induced brain activity classes by means of the adaptive classification technique for short-term spectra of spontaneous and task related EEG/MEG (Kaplan et al., 1999, Fingelkurts et al., 2003a). Later this technique was applied for single-trial analysis (Fingelkurts et al., 2002; Fingelkurts et al., 2003b, in preparation). From the stimulus concept viewpoint, a post-stimulus EEG interval contains stimulus context information rather than merely the physical, static features of the stimulus (for the review, see Näätänen & Winkler, 1999). Hence, the initial access to a cortical representation might be reflected in evoked potentials, whereas induced post-stimulus activity may mirror processes related to active memory in reverberating cell assemblies following their stimulus-triggered initial activation (Pivermuller et al., 1999).

Some researchers refer to long, slow induced effects accompanying higher cognitive processing (Kutas & Hillyard, 1980). Thus, the available experimental data suggests that in the post-stimulus interval a unitary sensory stimulus representation of the full stimulus event is completely formed. In connection to this, it seems reasonable to examine the post-stimulus EEG/MEG intervals (free from the direct influences of ERP and/or event-related desynchronization -ERD-/event-related synchronization -ERS- effects).

However, the identification of components with very long latencies (more than 400 ms) is technically difficult, because their effects become submerged in the ongoing EEG/MEG field complex. At the same time, estimations of short-term spectral patterns (SP) – that are induced by stimulus events and based on Short-Time FFT – provide a sufficient measure to EEG/MEG patterns with long latencies (Fingelkurts et al., 2002; Fingelkurts et al., 2003b, in submission). Using the single-trial classification technique, the dependence between the probability of occurrence of induced SPs of a particular type which reflect ‘internal’ events and repetitive ‘external’ events – such as the presentation of a stimulus – is estimated. In this framework, each post-stimulus interval is represented by a particular type of SP.

In the present study, complex stimuli were used in order to assess the activity of high-level sensory neurons (Touryan & Dan, 2001). Moreover, in two experiments (see Methods section) complex stimuli consisted of natural stimuli (words and biological faces) which are defined as the stimuli that are behaviorally relevant and are found within the human’s sensory environment (Touryan & Dan, 2001). It is suggested that because sensory circuits evolve and develop in the natural environment, they may be specifically tuned for efficient coding of natural stimuli (Olshausen & Field, 1996; Nelken et al., 1999).

As the frame hypothesis of the present paper, the variability of spectral patterns (SP) induced by the same stimuli reflects the variability of the cognitive context which comprises the changes in the functional brain state, dynamics of ongoing EEG activity and changes in the immediate environment (see review, Engel et al., 2001). It was supposed that by using the adaptive classification technique (Kaplan et al., 1999; Fingelkurts et al., 2003a), it may be possible to detect the systematic rules underlying the SP variability. Two main paradigms: oddball task (for visual, auditory and audio-visual stimulus modalities) and memory task (multistage memory task and modified Sternberg’s memory task) were chosen to study the functional variability of short-term SPs. Hence, the aim of this paper was to investigate the regularities of the variability of the SPs during the different brain functional states/tasks: a) to identify the number of SP types, b) to estimate the probability of each SP type, c) to study the dependence between the number of SP types and the brain states/tasks.

METHODS

General aspects

We tested the above hypothesis by classifying the SPs which characterize different functional states and post-stimulus single-trial EEG/MEG activity induced by complex/natural stimuli. Three experiments were carried out.

First experiment (see details in Fingelkurts et al., 2003c)

306-channel MEG was recorded for seven healthy, right-handed adult subjects (mean age 28) during the auditory, visual and audio-visual stimulation (talking face) using an oddball task.

The stimuli consisted of meaningless disyllables (vowel-consonant-vowel) uttered by a female speaker. Stimulus sequences consisted of frequent (p = 0.85) congruent stimuli (standards) and infrequent deviant congruent (p = 0.05) and incongruent (p = 0.05) stimuli for audio-visual stimulation. Target congruent stimuli (p = 0.05) were presented to be able to check that subjects were consciously attending to the stimuli. The visual stimulation contained only the visual parts of these stimuli and auditory stimulation contained only the auditory parts.

The magnetoencephalogram (MEG) were recorded continuously in a magnetically shielded room with a 306-channel whole-head device. The data were digitized at 300 Hz. The passband of the MEG recordings was 0.06-100 Hz. About 100 responses of the subjects to each deviant stimulus and about 2000 responses to standard stimuli were collected. MEG epochs containing artifacts due to eye blinks, significant muscle activity, or movements were automatically rejected. The presence of an adequate signal was determined by visually checking each raw signal on the computer screen after automatic artifact rejection. Gradiometer signals from 64 MEG locations which roughly correspond to the extended EEG 10-20 International system: $AF_{7/8}$, $AF_{3/4}$ (4 MEG locations), AFz, $F_{9/10}$, $F_{7/8}$, Fz, $F_{5/6}$, $F_{3/4}$, $FT_{9/10}$, $FT_{7/8}$, $FC_{5/6}$, $FC_{3/4}$, $T_{5/6}$ (4 MEG locations), $T_{3/4}$ (4 MEG locations), $CP_{5/6}$, $CP_{3/4}$, $CP_{1/2}$, CPz (2 MEG locations), $C_{5/6}$, Cz (2 MEG locations), $C_{3/4}$, $C_{1/2}$, Pz (2 MEG locations), $P_{5/6}$, $P_{3/4}$, $P_{1/2}$, Oz (2 MEG locations), $O_{1/2}$ (6 MEG locations) were analyzed with a converted sampling rate of 128 Hz.

Prior to the spectral analysis, each MEG sequence (corresponding to different stimulus conditions) was bandpass filtered in the 3-30 frequency range. This frequency range was chosen because several studies have indicated that approximately 98% of the energy of human biomagneitc field lies between 0 and 30 Hz (Thatcher, 2001).

In the present study we examined post-stimulus MEG data (still face, no sound), which is assumed not to be influenced by any artifact of the stimulus-events themselves. Categorized data (post-stimulus intervals) were extracted with respect the preceding stimulus (belonging to post-standard, or post-deviant-congruent, or post-deviant-incongruent intervals). The output of this procedure was sequence of concatenated MEG data, sorted stimulus-wise. Thus, the full MEG streams were split into 3 distinct segments for audio-visual conditions: AV(S) for standard stimuli, AV(C) for deviant congruents, and AV(I) for deviant incongruents; and into 2 distinct segments for auditory and visual conditions: A(S), V(S) for standard stimuli, A(D), V(D) for deviant stimuli correspondently.

Second experiment (see details in Fingelkurts et al., 2002)

Twenty-channel EEG was recorded for nine healthy, right-handed adult subjects (aged 20-29) during the modified Sternberg’s memory task. The memory set (encoding) consisted of four auditorily presented stimuli. The frame set (retrieval) size was kept constant and consisted of one stimulus.

The stimuli consisted of 24 auditory verbs (spoken with a female voice). A total of 192 four-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 four-stimulus block. In total, there were 192 trials, which were presented to the subjects in a pseudorandomized order.

The experiment was designed in such a way that it was possible to test resting, waiting, encoding, keeping-in-mind and identification short-term periods of memory task.

Sixteen Ag/AgCl electrodes placed bilaterally on the subject's scalp using the 10/20 system: $F_{7/8}$, Fz, $F_{3/4}$, Cz, $C_{3/4}$, $T_{3/4}$, $T_{5/6}$, $P_{3/4}$, $O_{1/2}$ were selected for analysis. Vertical and horizontal electro-oculograms were recorded. All electrodes were referred to linked ears. The data was recorded using a sampling rate of 200 Hz. Due to the technical requirements of the tools to be later used for data processing EEG signal was re-sampled with a converted sampling rate of 128 Hz.

Raw EEG signals were recorded with a frequency band of 0.3 to 70 Hz. The impedance of the recording electrodes was always below 5 kΩ. The presence of an adequate EEG signal was determined by visual inspection of the raw signal on the computer screen.

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. Each EEG sequence (corresponding to different periods) was bandpass filtered in the 3-15 frequency range.

Third experiment (see details in Fingelkurts et al., 2003a)

Eight-channel 1-min EEGs were recorded for twelve healthy, right-handed adult subjects (males, aged 19-26) during resting condition (closed eyes) and the multistage memory task (waiting, memorizing of the actual matrix object, and retention of the perceptual visual image). Each stage of the memory task was 20-sec duration.

The visual stimuli presented in front of the subjects to memorize were non-verbalizable matrices composed of nine square elements presented on a matrix screen. The combination of the squares was selected quasi-randomly and presented on the screen for 20-sec by lighting with bottom-mounted red light diodes. Therefore, three distinct short-term (20-sec) periods were tested: before, during, and after the stimulus exposure.

Eight Ag/AgCl electrodes were placed bilaterally on the subject's scalp using the 10/20 system of electrode placement at $F_{3/4}$, $C_{3/4}$, $P_{3/4}$, $O_{1/2}$. Vertical and horizontal electro-oculograms were recorded. All electrodes were referred to linked ears. Raw EEG signals were amplified and filtered in 0.5-30 frequency range and digitized at a sampling rate of 128 Hz by a 12-bit analog-to-digital converter. The impedance of the recording electrodes was always below 5 kΩ. The presence of an adequate EEG signal was determined by visual inspection of the raw signal on the computer screen.

Data processing

Individual power spectra were calculated in the range of 0.5–30 Hz with 0.5-Hz resolution (61 values), using FFT with 2-sec Hanning window shifted by 50 samples (0.39-sec) for each selected EEG/MEG location. These values revealed the best results in disclosing temporal patterns from the signal (according to a previous study). In the case of MEG (first experiment) spectral analysis was performed separately for each of the two gradiometers. Then, the power spectra for the two gradiometers in each location were averaged separately. As a result, individual power spectra with a 0.5-Hz step were calculated for post-stimulus intervals in oddball task (first experiment), for each stage of the modified Sternberg's memory task (second experiment), for three consecutive 20-sec fragments of the 1-min EEG during multistage memory task and for 1-min EEG during resting conditions (third experiment). Individual spectral patterns (SP) were obtained for each subject and each EEG/MEG location separately. These SPs formed the multitude of the objects for further classification procedure.

The parameters of variability within SPs during different functional states and experimental tasks were estimated at two stages. At the first stage, the adaptive classification of sequential single EEG/MEG spectra was performed in each EEG/MEG channel separately by reference to a set of standard SPs. Details of this procedure can be found in Fingelkurts et al., (2003a). This algorithm (SCAN-M software, Moscow State University; Kaplan et al., 1999) results in *m* classes of SPs. Considering that a single EEG spectrum illustrates the particular integral dynamics of tens and hundreds of thousands of neurons in a given cortical area at a particular point in time (Dumermuth & Molinari, 1987), the SPs within each class can be considered effectively generated by the same dynamics, with the same driving force. Whereas SPs from different classes can be considered to have had different driving forces and therefore have been effectively generated by different dynamics (Manuca & Savit, 1996). Each SP can be labeled by the index of the class to which it belongs. Thus, a sequence of SP labels that represents the sequence of EEG/MEG patterns through which the system passes can be obtained. Each channel of each EEG/MEG was reduced to the sequences of classified SPs.

At the second stage, the probability classification profiles (PCP) of SPs for each EEG/MEG location in each subject and for the group of subjects as a whole were calculated. An index was calculated as the number of cases of SP type as a percentage of the total amount of all SPs in any given EEG/MEG location.

PCPs were averaged for each subject separately for each EEG/MEG location and condition (type of stimulation, stage of the memory task). After this, the data for each condition was averaged across those subjects which show similar results.

Minor variations of the basic procedure for data analysis can be found in Fingelkurts et al., 2003b (in preparation) (for the first experiment), Fingelkurts et al., 2002 (for the second experiment) and in Fingelkurts et al., 2003a (for the third experiment).

In order to reveal statistically significant changes in SPs variability in accordance with condition changes, Student *t*-test was used as only the difference between pairs of states was of interest. Statistical significance was assumed when $p < .05$. Results are reported as average values with standard deviations. For an appropriate estimation of 5% level of statistical significance of SP type distribution in PCPs, the numerical modeling was held (500 independent trials). As a result of numerical modeling tests the stochastic level of SP type occurrence and upper/lower thresholds were calculated. These values are the estimation of the maximally (by module) possible stochastic rate of SP type distribution in PCPs. Numerical modeling is a stochastic technique and is commonly applied as probing a complex process for non-random nature when the usage of other statistics is not possible.

RESULTS

Oddball task (first experiment)

It has been supposed that the oddball task, which mainly assesses automatic brain functions, permits the obtaining of stereotype brain activity (brain response) induced by the same stimulus. However, in the present study, single-trial analysis revealed that the same stimulus induced different MEG patterns which altogether were characterized by a set of spectral pattern (SP) types (Fig. 1). Figure 1 presents the total and the most probable number of SP types for auditory, visual and audio-visual stimulation within the oddball task. It can be seen that there was no one typical SP type which would have characterized the majority of the trials, not even during the presentation of the standard stimuli. At the same time, the total number of the different SP types was limited (up to 14±0.9) and the sets of SPs were typical for each type of the stimuli and each type of stimulus modality (Fig. 1).

The number of the total SP types for the deviant stimuli was lower than for the standard stimuli ($p < .001$) independently of the stimulus modality (Fig. 1, Table 1).

Different SP types had different importance for the brain during the presentation of the same stimulus. Thus, several SP types were the most probable during the presentation of a particular type of the stimuli (Fig. 1). Moreover, the number of most probable SP types was larger for the deviants than for the standards ($p < .001$) (for auditory and audio-visual modalities). While for the visual modality the effect was the opposite ($p < .001$) (Fig. 1, Table 1).

All observed findings were quite similar across all tested MEG locations: coefficient of variation (CV = StD/Mean) was much less than 1 (Fig. 1).

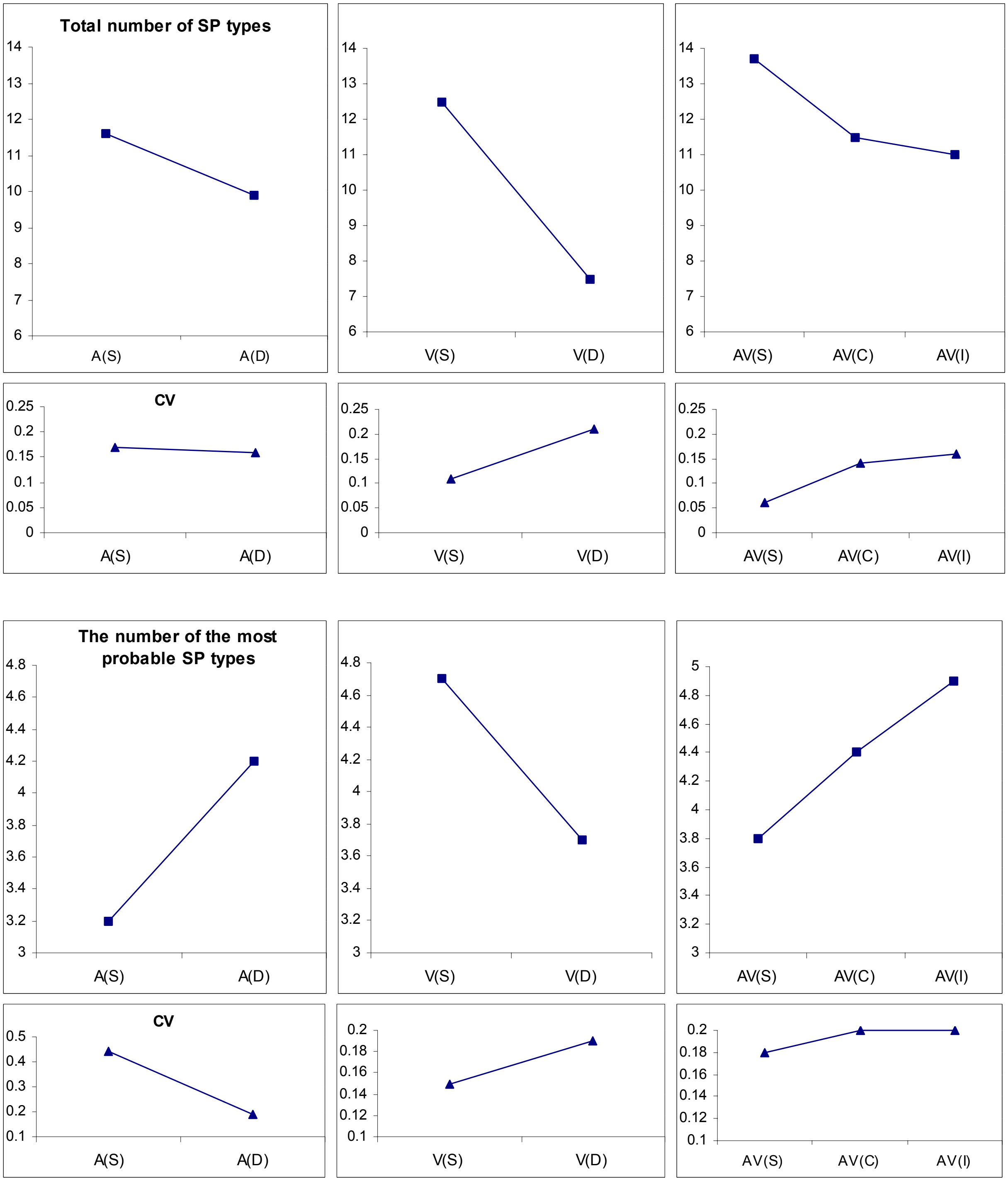

Fig. 1. Total number and the number of the most probable spectral pattern types for the oddball task during standard (2000 trials) and deviant (100 trials) stimulation. Data averaged across 64 MEG locations for all subjects.
A(S) – auditory standard stimuli; A(D) – auditory deviant stimuli; V(S) – visual standard stimuli; V(D) – visual deviant stimuli; AV(S) – audio-visual standard stimuli; AV(C) – audio-visual deviant congruent stimuli; AV(I) – audio-visual deviant incongruent stimuli; CV – coefficient of variation (standard deviation/mean) for MEG locations.

TABLE 1. Results of statistical analysis for data presented in figure 1.

Total number of spectral pattern types

Comparisons		*Significance*	*t*
A(S)xA(D)	>	$p < .001$	5.3
V(S)xV(D)	>	$p < .001$	18.8
AV(S)xAV(C)	>	$p < .001$	9.6
AV(S)xAV(I)	>	$p < .001$	10.7
AV(C)xAV(I)	n.s.		1.6

The most probable spectral pattern types

Comparisons		*Significance*	*t*
A(S)xA(D)	<	$p < .001$	5
V(S)xV(D)	>	$p < .001$	8.1
AV(S)xAV(C)	<	$p < .001$	4.2
AV(S)xAV(I)	<	$p < .001$	7.2
AV(C)xAV(I)	<	$p < .01$	3

A(S) – auditory standard stimuli; A(D) – auditory deviant stimuli; V(S) – visual standard stimuli; V(D) – visual deviant stimuli; AV(S) – audio-visual standard stimuli; AV(C) – audio-visual deviant congruent stimuli; AV(I) – audio-visual deviant incongruent stimuli; n.s. – non-significant; *t* – Student *t*-test

Numerical experiment

The most probable SPs were interpreted as the most "preferred oscillations" of the brain as a response to a particular stimulus. These, the most probable SPs were estimated as the main/dominant SP-peaks in the probability classification profile (PCP). To test if the existence of the peaks in PCPs were functionally dependent and not occasional, a numerical modeling was performed (500 independent trials – 5% level of statistical significance of SP type distribution in PCPs). As a result of numerical tests the stochastic level of SP type occurrence and upper/lower thresholds were calculated. These values are the estimation of the maximally (by module) possible stochastic rate of SP type distribution in PCPs.

Figure 2 illustrates an example of actual data and numerical testing data for auditory standard stimuli. In the average PCP for 7 subjects for O1 MEG location, 12 different types of SPs were obtained. From actual PCP it can be seen that two SP types (labeled by 4 and 5) were the most probable among the others SPs – the values significantly exceeded ($p < .05$–$p < .001$) the stochastic level (Fig. 2, check $\mathrm{PCP}_{\mathrm{actual}}$ and $\mathrm{PCP}_{\mathrm{stoch}}$). Theoretically, the stochastic rate should be distributed equally among all 12 SP types within PCP_{stoch}; and stochastic measure should be 100% / 12 = 8.33. Numerical modeling showed that stochastic measures fluctuate around value 8.33 and PCP_{stoch} was characterized by the absence of any peaks (Fig. 2). Also, the presence of SP types in PCP_{actual} was significantly different from PCP_{stoch} ($p < .05$–$p < .001$, except SP10). This means that the most probable SP types were not occasional and may have a functional nature. Thus, all SPs that the probability index (peaks in the PCP) significantly exceeded the upper threshold of the stochastic level of SP type occurrence were described as the most probable SPs.

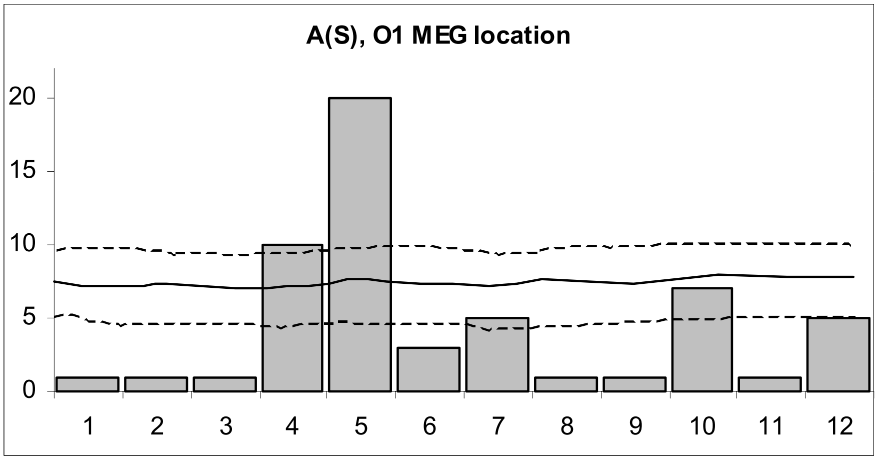

Fig. 2. Example of the probability classification profiles for actual data and numerical testing data for auditory standard stimuli. Data averaged across 7 subjects for O1 MEG location. The X-axis displays the labels of different types of spectral patterns (SP). The Y-axis displays the share of the corresponding SP type as a percentage of the total number of SPs. The continuous line represents the stochastic level of SP types occurrence in the probability classification profile modeled by means of a numerical test (500 independent trials). Dotted lines indicate upper/lower thresholds of the stochastic level. In the insertion, the theoretical stochastic measure (100% / 12 types of SPs) is displayed.

To test whether the SP types change along with the changing of the functional brain state, a second experiment using the modified Sternberg's memory task was chosen. This task permits the examination of the brain activity induced by a single stimulus within short-time intervals.

Modified Sternberg's memory task (second experiment)

Figure 3 displays the total number of SP types and the number of the most probable SP types during the modified Sternberg's memory task. The design of this task permits to examine different stages of the memory task in chronological succession. The general results of this experiment reproduced the findings of the first experiment (see above). The brain activity in all single-trials (during each stage of the modified Sternberg's memory task) was characterized not by one type of SPs, but by the set of SP types (up to 13) and only several of them (up to 5) were the most probable (Fig. 3).

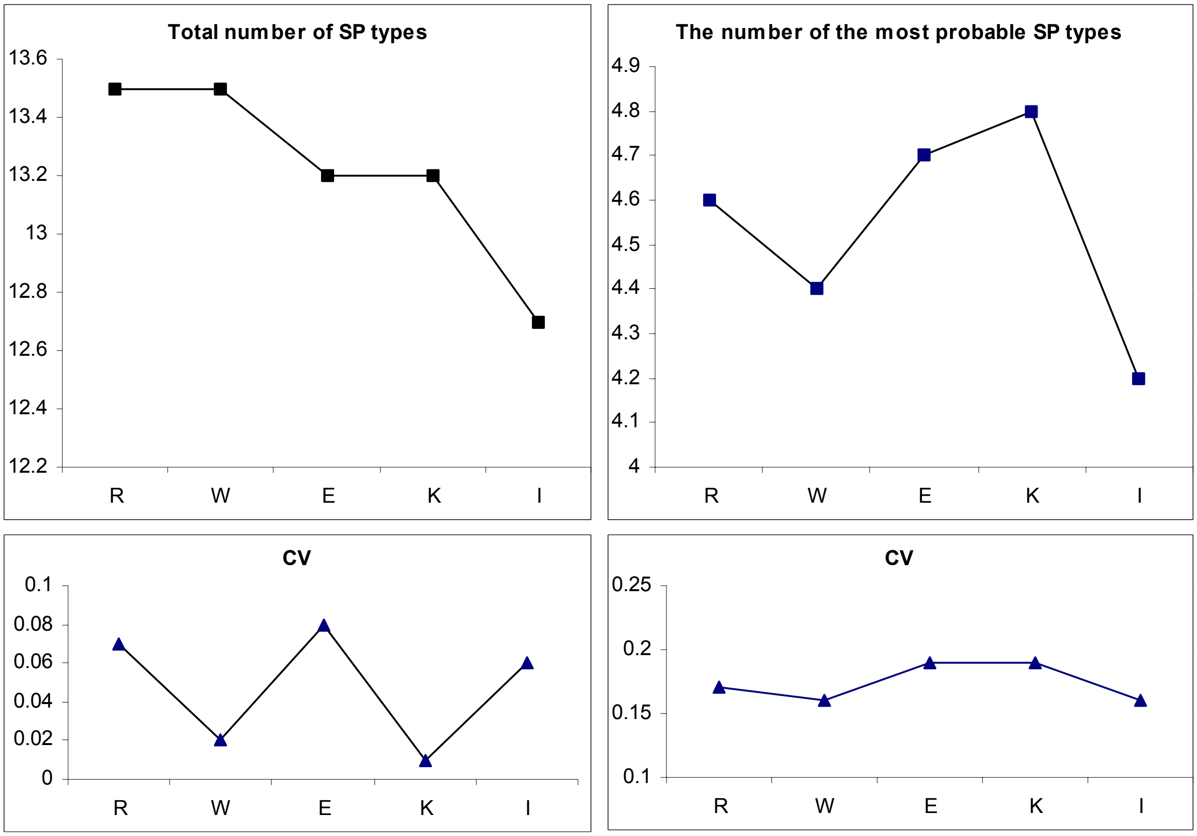

Fig. 3. Total number and the number of the most probable spectral pattern types for all single-trials (*n* = 192) during different stages of modified Sternberg's memory task. Data averaged across 9 subjects and 16 EEG channels. Stages of the memory task presented in chronological order.
R – resting conditions; W – waiting stage of the memory task; E – encoding stage of the memory task; K – keeping-in-mind stage of the memory task; I – identification stage of the memory task; CV – coefficient of variation (standard deviation/mean) for EEG channels.

It can be seen from figure 3 that the changes in the brain functional state (in the chronological sequence of stages of the memory task) were accompanied by changes in the number of the total and the most probable SP types. Thus, the total number of SP types was the largest for the resting and waiting conditions ($p < .05$), medium for the encoding and keeping-in-mind stages ($p < .05$) and the smallest for the identification stage of the memory task (Fig. 3, Table 2). Generally, the total number of SP types which characterized a particular brain state in all single-trials decreased along with the increase in functional loading. At the same time, the number of most probable SP types has a more complex relation with the different stages of the memory task (Fig. 3, Table 2).

TABLE 2. Results of statistical analysis for data presented in figure 3.

Total number of spectral pattern types

Comparisons		*Significance*	*t*
RxW	no diff.		
WxE	>	$p < .05$	2.7
ExK	no diff.		
KxI	>	$p < .05$	2.5
RxE	n.s.		
RxK	n.s.		
RxI	>	$p < .05$	2.6
WxK	>	$p < .001$	5.4
WxI	>	$p < .01$	3.9
ExI	>	$p < .05$	2.5

The most probable spectral pattern types

Comparisons		*Significance*	*t*	
RxW	>	$p < .05$	2.5	(6 subjects from 9)
WxE	<	$p < .05$	2.1	(3 subjects from 9)
ExK	no diff.			(all subjects)
KxI	>	$p < .05$-.01	2.6-4.1	(6 subjects from 9)
RxE	<	$p < .05$	2	(3 subjects from 9)
	>	$p < .05$	2.3	(3 subjects from 9)
RxK	<	$p < .05$	2.4	(1 subject from 9)
RxI	>	$p < .05$-.01	2.5-3.5	(5 subjects from 9)
WxK	<	$p < .05$	2	(1 subject from 9)
WxI	>	$p < .05$-.01	2-2.8	(6 subjects from 9)
	<	$p < .01$	2.8	(3 subjects from 9)
ExI	>	$p < .01$	3.1-3.3	(3 subjects from 9)

R – resting conditions; W – waiting stage of the memory task; E – encoding stage of the memory task; K – keeping-in-mind stage of the memory task; I – identification stage of the memory task; n.s. – non-significant; no diff. – no difference; *t* – Student *t*-test

The observed findings were similar for all tested EEG channels (see the coefficient of variation, Fig. 3).

This experiment involves higher brain functions such as controlled encoding, identification, retention, and retrieval and these are greatly dependent on general functional state and context. However, the duration of the tested stages of the memory task were about one second. This duration is too short to test the variability of ongoing EEG activity during one functional state. Therefore a third experiment with 20-sec functional states was conducted.

Multistage memory task (third experiment)

Figure 4A illustrates the influence of different memory stages (20-sec of duration each) on the SP type sequences. It can be seen that in each memory stage the induced brain activity is characterized by a particular and limited set of SP types (Fig. 4A; Fig. 5: W, E, K). Moreover, the sets of SP types for three stages of the memory task were different (Fig. 4A). Note that the sets of SP types changed in the same moment when the memory task stage changes.

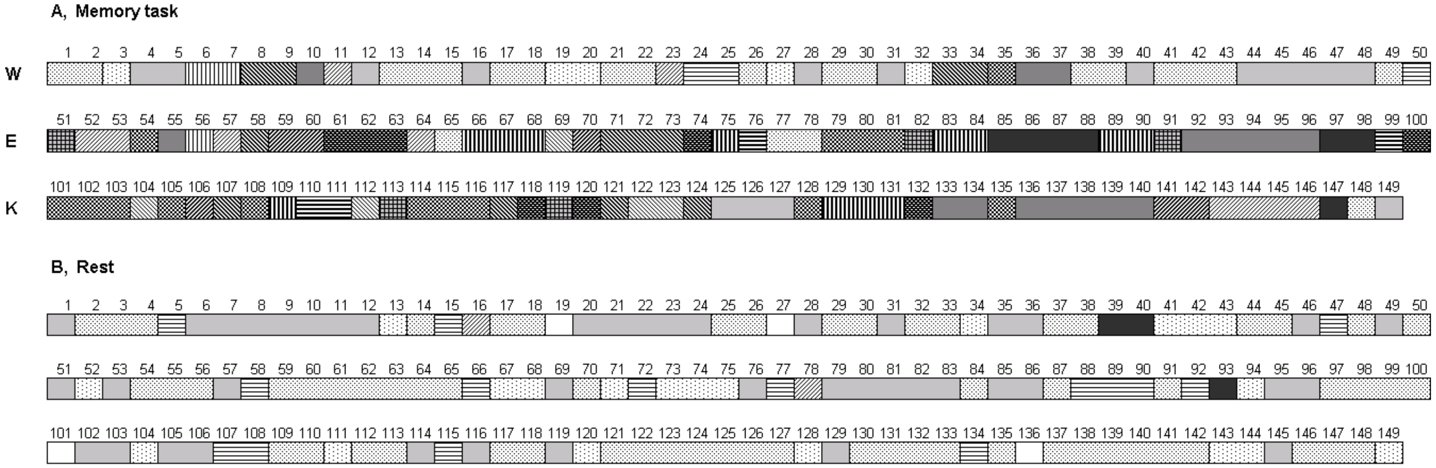

Fig. 4. The sequence of spectral pattern types in O1 EEG channel for the three stages (20-sec duration each) of the memory task and for resting condition (eyes closed) 1-min EEG. Different spectral pattern types are marked in different colors (the same spectral pattern types have the same color). Numbers indicate 149 spectral patterns calculated on 2-sec EEG epochs with 50 points shift (0.39-sec). W – waiting stage of the memory task; E – encoding stage of the memory task; K – keeping-in-mind stage of the memory task.

Simultaneously, the total number of SP types was dependent on the functional state of the brain (resting condition, stages of memory task). Thus, the number of SP types was the largest for the resting condition ($p < .05$), medium for the waiting stage ($p < .01$) and the smallest for the encoding and keeping-in-mind stages of the memory task (Fig. 5, Table 3). Like in the second experiment described above, the total number of SP types, which altogether characterized a particular brain state, decreased along with the increase in functional loading. Also as in the two experiments described above, several SP types (up to 5±0.1) were the most probable for each of the memory task stages (Fig. 5). Note that the increase in functional loading leads to an increase in the number of most probable SP types (*p* < .001, Table 3). These findings altogether were typical for all tested EEG channels (check coefficient of variation, Fig. 5).

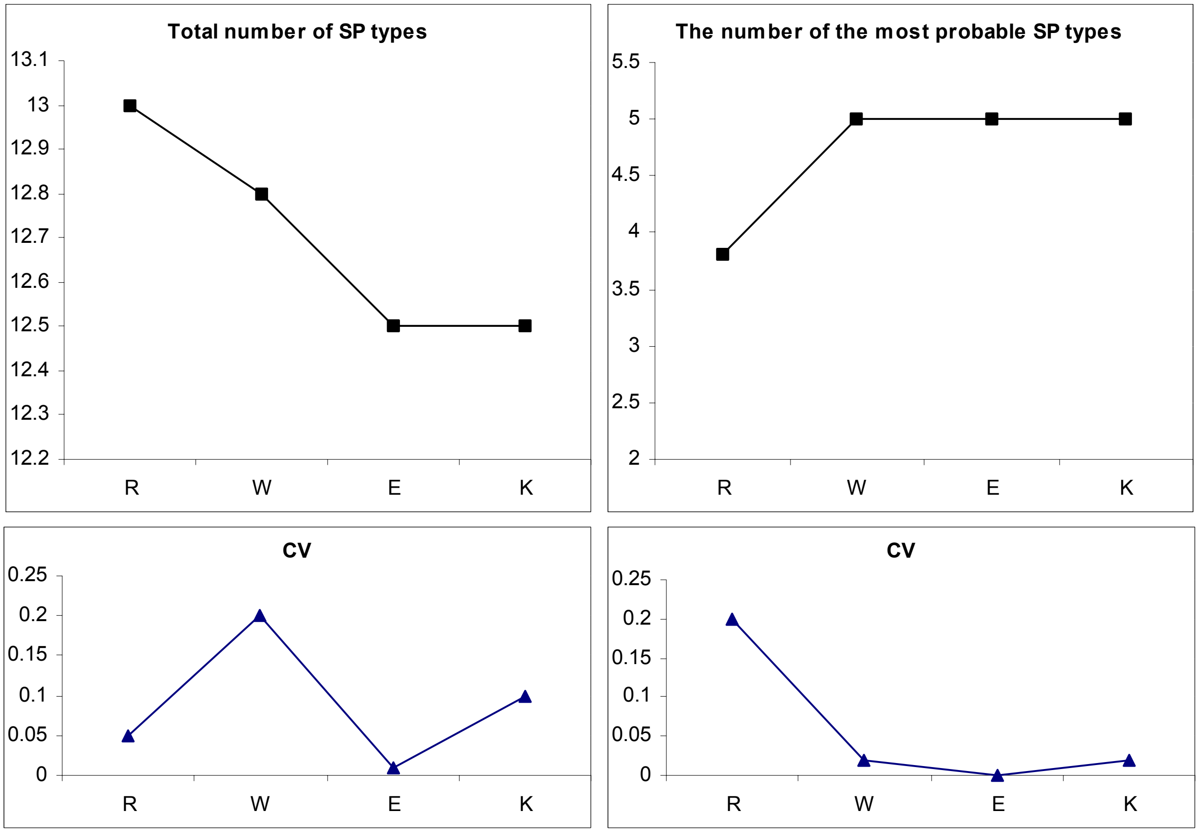

Fig. 5. Total number and the number of the most probable spectral pattern types for multistage memory task (288 EEGs) and resting condition (96 EEGs). Data averaged across 12 subjects and 8 EEG channels. R – resting conditions; W – waiting stage of the memory task; E – encoding stage of the memory task; K – keeping-in-mind stage of the memory task; CV – coefficient of variation (standard deviation/mean) for EEG channels.

One of the factors contributing to the SP variability observed above could be the "natural" fluctuations of ongoing EEG that characterize the basic activity of a particular brain region. Ongoing EEG activity may be considered as context for sensory processing and cannot be ignored in exploration of cognitive processes (Arieli et al., 1996; Engel et al., 2001). Therefore, the SP variability of the ongoing EEG activity during resting condition (eyes closed) was considered.

TABLE 3. Results of statistical analysis for data presented in figure 5.

Total number of spectral pattern types

Comparisons		*Significance*	*t*
RxW	n.s.		
WxE	>	$p < .01$	3.8
ExK	no diff.		
RxE	>	$p < .05$	2.3
RxK	>	$p < .05$	2.3
WxK	>	$p < .01$	3.8

The most probable spectral pattern types

Comparisons		*Significance*	*t*
RxW	<	$p < .001$	4.8
WxE	no diff.		
ExK	no diff.		
RxE	<	$p < .001$	4.8
RxK	<	$p < .001$	4.8
WxK	no diff.		

R – resting conditions; W – waiting stage of the memory task; E – encoding stage of the memory task; K – keeping-in-mind stage of the memory task; n.s. – non-significant; no diff. – no difference; *t* – Student *t*-test

Ongoing activity (third experiment)

Figure 4B presents the sequence of SP types for the O1 channel in a 1-min EEG during the resting condition (eyes closed). It can be seen that the sequence of SPs is far from being homogenous. Even without any type of external stimulation induced by the design of the experiment the brain passes through variations of SP types. The total number of different SP types was limited (up to 13±0.6) (Fig. 5 (R)) and appears to be evenly distributed along 1-min EEG (Fig. 4B). At the same time, and as in the three experiments described above, the SPs had a different importance for the brain during the resting condition (closed eyes). Thus, the number of the most probable SP types was up to 4±0.5 (Fig. 5 (R)). These findings were similar across all tested EEG channels: coefficient of variation (CV = StD/Mean) was much less than 1 (Fig. 5 (R)).

There was a specific set of SPs for each EEG channel or small group of channels, since the number in SP types in all EEG channels taken together was substantially greater (21.2±0.7) than in each individual EEG channel (13±0.6) ($p < .001$, $t = 25$, Table 4). Moreover, if SP types that occurred in less than 2% of the cases were not taken into account, then this number decreases ($p < .001$, $t = 27$) to 12.5±0.6 (Table 4). This indicates that about 50% of the SP types have a very low occurrence; i.e., not more than 2-3 times per 149 analysis epochs in a one-minute EEG! This causes up to 0.54±0.02 values for the relative incidence of the SP type change in the transition between neighboring EEG epochs of the same EEG (Table 4). These values were considerably smaller than the relative rate of SP stochastic alternation in the actual EEG (0.83±0.01) ($p < .001$, $t = 54$). The relative rate of SP stochastic alternation was obtained by randomized mixing of SPs in each channel of the actual EEG (Fingelkurts et al., 2003a).

TABLE 4. Mean (for 12 subjects) parameters of EEG spectral pattern type variability averaged for 8 EEG channels

N	13±0.6
Ns	21.2±0.7
Ns(>2)	12.5±0.6
RI	0.54±0.02
SA	0.83±0.01

N – the total number of spectral pattern types; Ns – the number of spectral pattern types for all EEG channels taken together; Ns(>2) – the same like Ns, but without spectral pattern types, which were presented in probability classification profiles less than in 2% cases; RI – the relative incidence of the spectral pattern type change; SA – the relative rate of spectral pattern stochastic alternation in the actual EEG; "±"– standard deviation

DISCUSSION

We investigated the trial-to-trial SP variability in the oddball task and the modified Sternberg's memory task. Additionally, we assessed the state-dependent modulation of SP variability during a multistage memory task and resting condition. At the general level, perhaps the most important outcome of the analysis presented here is the finding that brain activity was characterized by a "family" of SPs induced by the same stimulus and that the set of SP types was limited (up to 14 types). And also that several SP types from the “family” (up to 5 types) were the most probable and this probability was significantly different from the stochastic estimations. This suggests that the type of brain activity induced by the same stimulus can be different but not “any” type. This was observed for the auditory, visual and audiovisual modalities (standard and deviant stimuli) (Fig. 1) and may suggest the universality of the described effects.

The total number and the number of the most probable SP types were dependent on the type and the modality of the stimuli (Fig. 1, Table 1). Probably top-down factors such as familiarity with the stimulus (Miller & Cohen, 2001) and cross-modal, task-specific influences (Heanny et al., 1989) modulate SP profiles. Indeed the data reviewed in Engel et al. (2001) indicates that top-down processing is associated with the modulation of the temporal structure of both ongoing and stimulus-induced activity. Hence, cognitive processing cannot be separated from the environment in which it occurs (Clancey, 1997).

The findings of the present study (first experiment) and literature data suggest that stimulus events of long latency are intrinsically not reproducible. A cognitive act requires a prior state of readiness that expresses the existence of a goal, a preparation for motor action to position the sense organs, and selective sensitization of the sensory cortices. Their excitability has already been shaped by the past experience that is relevant to the goal and the expectancy of stimuli (Alexandrov, 1999; Freeman, 1999). This means that each moment of the present experience merges with the past experience. Therefore the past experience continually changes following the circular causality rule in which each perception concomitantly is the outcome of a preceding action and the condition for a following action (Freeman, 1999; Beer, 2000).

In this framework it is believed that the high variability of SPs to repeated identical stimuli originates mainly in fluctuations of the subject's cognitive "context" defined by his/her attentive state, spontaneous thought process, and strategy to carry out the task, among others (Lutz et al., 2002). Also factors such as motivation, emotion and mood, including those related to the working memory, novelty-seeking and mental imagery modulate the neural impact of sensory events in a manner that they create a highly “edited” subjective version of the world (see review, Mesulam, 1998).

It has been suggested that immediate context is reflected in ongoing EEG activity (see review, Engel et al., 2001). If so, then changes in the brain functional state should be partially accompanied by changes in SP types which describe this functional state. Also by assuming natural variability of the brain functional state, each single-trial of the same functional state should be characterized by different SP types. The second experiment permits testing such supposition by using chronological changes of brain functional state within single-trial. Thus, single-trials of each stage of the memory task (corresponding to a particular functional state) were characterized by a set of SP types and some SP types were the most probable (Fig. 3). Additionally, in the present study it was shown that SP variability (the total number and the number of the most probable SP types) was dependent on the functional state (Fig. 3, Table 2). Thus, results of the second experiment support the viewpoint that the interplay of multiple internal and external influences on the brain determines a cognitive process.

This interplay should be reflected in SP variability of one continues brain functional state. The third experiment of the present study showed that the brain keeps the state (waiting stage of the memory task) through a particular set of SPs (interim transiency) probably reflecting the fulfillment of micro-operations which are needed to achieve the main goal of this state (Fig. 4A, (W)). Temporal peculiarities of SP variability in EEG during different stages of the memory task are described elsewhere (Fingelkurts et al., 2003a). Studies at the neuronal level (Abeles et al., 1993) also showed that in a given behavioral condition there were usually many different patterns, each repeating several times, and not one (or a few) pattern repeating many times. Although the mechanisms underlying such variability are different, such examples suggest that variability of brain activity within one functional state may be the rule rather than the exception.

When a perturbation is very strong or the goal is achieved (changes of the memory task stage, based on the design of the experiment), the brain shifts from the previous state (waiting stage) to a new state (encoding stage) with its own new set of SPs (Fig. 4A, (E)). And finally, changing of the encoding stage to keeping-in-mind stage also accompanied by changing of the sets of SPs (Fig. 4A, (K)). Perhaps the SP variability within one functional state reflects the poly-operational structure of brain activity.

If ongoing EEG activity reflects ordered states of internally generated activity it should reflect the functional architecture of the networks: traces of the past history and the features of planned behavior. Evidences come from Arieli and co-workers (Arieli et al., 1996; Tsodyks et al., 1999) who showed that even in the anesthetized state, ongoing brain activity is endowed with specific patterning that reflects the functional architecture of the underlying network. These findings suggest that ongoing brain activity contains structured information and therefore has an important role in cortical functioning (Tsodyks et al., 1999).

In the present study it was shown that the resting state (closed eyes, third experiment) was also characterized by a set of SP types and the relative incidence of the SP type change during the transition between neighboring EEG epochs was more than 0.50 (Fig. 4B, Table 4). This is in a strongly overlapping (by 80%) 2-sec analysis epochs. At the same time, the relative incidence of the SP type change was significantly smaller than the relative rate of SP stochastic alternation (Table 4). The relative rate of SP stochastic alternation presents an estimation of the maximum possible rate of relative alteration in the type of SPs for a given EEG. Thus, actual SP variability during rest with closed eyes was relatively high (around 65% from the maximum possible rate), but significantly less than stochastic SP variability. This means that SP variability in the actual EEG reflects non-stochastic processes. The SP types during rest emerge, persist for some time, then disappear and are replaced by other SP types (Fig. 4B). This suggests that ongoing brain activity occurs in discontinuous steps and confirms that the cerebral cortex is continuously active in wakefulness. For details of the SP variability in ongoing EEG activity during resting conditions see (Fingelkurts et al., 2003a).

High variability of the ongoing brain activity during resting condition can be explained by the fact that the brain is situated within a body. As a consequence, the performance of the brain can't be reduced to "just" computing and extracting information from external stimuli (König & Luksch, 1998). In contrast, the brain needs to deal with the internal life providing and controlling vital processes of the organism and mental activity. This brain activity should be reflected in the resting EEG. Thus, it was shown that the alert eyes closed EEG state is very much an active state (Thatcher & John, 1981; Herscovitch, 1994).

Besides the high SP variability (the existence of the sets of SP types) observed in the present study in all three experiments, it was shown that SP types are of different significance. Thus, 3-5 SP types (in each experiment) were the most probable when compared with the others (Fig. 1, 3, 5). It can be explained by the fact that an environment has a variable nature, and only subsets of input signals are relevant for the subject in the particular moment of time. Cognitive systems selectively stabilize representations that are important for the subject (Grossberg, 1980). This perhaps reflects the finite capacity of the brain facing the infinite complexity of the environment. Responses are directed further by information based on the probabilities of occurrence of each event. Thus, probability classification profiles obtained in the present study can be considered as the measure of the variability of the actual environment the subject is submitted to.

Together the results of the present study and the above considerations imply that identical sensory events can potentially trigger one of many different alternative reactions, depending on the peculiarities of the situational context (past experience, present needs and contemplated consequences) and the same goal can be reached through numerous means. Perhaps, this increases brain adaptability which is based on diversity, competition and choice rather than on stereotyped responses (see review, Mesulam 1998). From the biological viewpoint, brain is not primarily designed to give faithful representations of the environment, but to ensure survival of its bearer and its genes (König & Luksch, 1998). Thus, the categorization of input stimuli performed by the nervous system is actually dependent on the changing needs of the organism (Orban et al., 1996). In functional terms, a “compromise” based on the saving of energy resources and on agreement between intrinsic goals and motivational states permits a cognitive system to select only the inputs that are meaningful to accomplish an actual organism’s goal (Fingelkurts et al., 2002). The various influences compete for stable, resonant states of the involved cell populations that would express a successful match of the input to the predicted constellation (Engel et al., 2001). The solution to the cognitive problem or task is therefore defined as the settling of the entire system into a metastable state of best fit (for the review, see Fingelkurts & Fingelkurts, 2001; Fingelkurts et al., 2002).

Thus, to capture and understand the full complexity of brain performance, organisms should not be regarded as information processing devices, but rather as actively exploring subjects that adapt the neuronal analysis of their internal and external environment according to their needs and their life history (Engel et al., 2001). The operational synchrony (Kaplan et al., 1997) at different spatial-temporal scales and the metastability process with multivariability of its operational elements (Kaplan, 1999; Kaplan & Shishkin, 2000) and also, feedback interactions (Grossberg, 1980; Mesulam, 1998; Engel et al., 2001) are the mechanisms supporting this processing (for the review see Fingelkurts & Fingelkurts, 2001).

PRACTICAL ASPECTS

It is important to note several aspects of the approach presented in this paper that are generally applicable. One significant advantage of being able to identify different types of SPs is that subsets of EEG/MEG segments sharing the same dynamics can be grouped together thereby improving the statistics and one's ability to model and to make predictions. Also ontologically (from the viewpoint of EEG/MEG phenomenology) it is more correct to obtain, for example, ERPs and ERD/ERS by averaging only those EEG/MEG segments which share the same dynamics. In that case, the "family" of the ERP and/or ERD/ERS types would characterize a particular stimulus. Comparisons of brain reactions to different stimuli should be done by comparing their ERPs and/or ERD/ERS families.

Another practical advantage is that probability classification profiles of SPs can be used as a measure of the degree of the actual context variability. Also, the suggested approach permits the revealing of new response properties such as typicality and probability, and distinguishing them from each other (Fingelkurts et al., 2002; Fingelkurts et al., 2003b, in preparation).

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