Clinical Neurophysiology 111 (2000) 1719–1732

www.elsevier.com/locate/clinph

A new strategy involving multiple cognitive paradigms demonstrates that ERP components are determined by the superposition of oscillatory responses

S. Karakaş[a,b,*], Ö.U. Erzengin[a,b], E. Başar[b,c]

[a]Department of Experimental Psychology, Hacettepe University, Beytepe 06532, Ankara, Turkey
[b]TÜBİTAK Brain Dynamics Research Network, Ankara, Turkey
[c]Institute of Physiology, Medical University, Lübeck, Ankara, Turkey

Accepted 7 July 2000

Abstract

Objectives: The goal of the present paper was to study the contribution of the delta and theta responses to two components of the event-related potential (ERP) waveform, the N200 and P300, which were recorded from 3 topographical sites of the brain.

Methods: This contribution was studied using a set of systematically varying experimental paradigms. Such a strategy enabled the demonstration of the variations in the event-related potentials and the event-related oscillations as task conditions and respective cognitive operations systematically changed. The study employed easy oddball, hard oddball, mismatch negativity and single stimulus paradigms and it was conducted on 42 healthy adults (age range 19–30 years, 26 females, 16 males) from the university student population. Data were analyzed with electrophysiological (selective averaging, amplitude frequency characteristics, digital filtering) and statistical methods (analysis of variance, multivariate step-down regression).

Results: The data showed that the morphology of the ERP components for different experimental paradigms represented a specific pattern of superposition of the delta and theta oscillatory responses.

Conclusions: The cognitive correlates of the oscillatory responses were discussed and the results were evaluated on the basis of the superposition principle and the theory of oscillatory neural assemblies.

Keywords: Event-related potentials; Event-related oscillations; Delta response; Theta response; Superposition principle; Degrees of consciousness

1. Introduction

The present work studied the contribution of two event-related oscillations (EROs), delta and theta, to two event-related potential (ERP) components, N200 and P300, which were recorded from 3 topographical sites of the brain. This contribution was studied using a set of systematically varying experimental paradigms that involved 4 different task conditions. The utilization of the multiple paradigms approach enabled the study of the variations in the pattern of the ERP/ERO relationship that took place as task conditions and, thus, cognitive operations changed. No study has been encountered until the present that has combined the utilization of multiple ERP paradigms and two frequency windows when trying to unravel the way the brain functions.

In a recent review (Başar et al., 1999a,b) it was argued that during functional states, EROs of various frequencies interact to give way to the ERP waveform and that this process is realized through communication networks of large populations of neurons. This argument principally rests on the principle of superposition according to which the morphology of the compound ERP waveform and the components on this waveform are determined by the superposition of oscillatory responses. The approach that the principle of superposition represents is basically the 'paradigm change' that Mountcastle (1992) mentioned when he claimed the testability of the statement concerning the active role of the slow wave events for signal transmission in the brain. A possible neural mechanism for this has recently been discussed by Sannita (2000); according to this view, the oscillatory responses in the 20–80 and 100–600 Hz frequency ranges pace neurons selectively to the physical properties of the stimulus and are thus closely related to sensory information processing.

However, the only systematic demonstration of the superposition principle had been achieved by the original study

* Corresponding author. Tel./fax: +90-312-2992100
E-mail address: skarakas@hacettepe.edu.tr (S. Karakaş).

1388-2457/00/$ - see front matter
PII: S1388-2457(00)00418-1
CLINPH 2000508

(Başar and Ungan, 1973) and this demonstration was based on the transient characteristics of solely the evoked potential (EP) waveform. Subsequent studies only indirectly demonstrated the principle as they studied the oscillatory responses under discrete experimental paradigms (Başar, 1980, 1998; Başar et al., 1975, 1999a; Başar-Eroğlu et al., 1992; Demiralp et al., 1999; Robinson, 1999; Stampfer and Başar, 1985).

The prevailing literature on the association between cognition as a behavioral phenomenon on the one hand and ERPs and EROs on the other hand can be considered in 3 groups. The first group has predominantly been related to the P300 component and this complex relationship has usually been studied under a limited number of experimental conditions. These studies emphasized the relevancy of the delta response to the P300 component and to the cognitive operations of matching and decision-making (Başar-Eroğlu et al., 1992; Duncan-Johnson and Donchin, 1979; Pfefferbaum et al., 1986; Schürmann et al., 1995; Stampfer and Başar, 1985).

The second group of studies again studied mainly the P300 component, this time emphasizing the relevancy of the theta oscillation (Demiralp and Başar, 1992; Klimesch et al., 1994). In the study by Yordanova and Kolev (1998), the late theta (300–600 ms) at Fz and Pz was found to be affected by the active oddball condition in single sweeps with respect to amplitude, phase-locking and enhancement against pre-stimulus activity. The study demonstrated a strong association between P300 and the late theta oscillation and this finding led the authors to conclude that single theta responses can be used for revealing the functional differences between passive and oddball conditions.

The third group involved a smaller number of studies. This group investigated the association between ERP, ERO and cognition on the basis of both the delta and the theta responses. Stampfer and Başar (1985) and Başar et al. (1984) showed that the P300 is characterized by enhancement and prolongation in theta oscillation and delay of the delta oscillation. In an omitted stimulus paradigm study, the P300 component was accompanied by 40 Hz oscillation. Both of these were recorded most markedly from the CA3 region of the cat hippocampus (Başar-Eroğlu and Başar, 1991).

The alpha oscillation, its prolongation and the post-stimulus blocking would also merit special consideration in the study of cognitive processes (Başar et al., 1997; Klimesch, 1999). However, the time course of ERPs is dominated mainly by the delta and theta oscillations (Başar, 1998, 1999); for this reason, the point of emphasis in the present study has also been these specific oscillatory responses.

Cognitive psychophysiology has a number of standard experimental paradigms and studies make use of these paradigms to produce different cognitive states. The oddball (OB) paradigm has two different stimuli and the subject has to count the less frequent, the deviant stimuli. The OB paradigm thus requires the allocation of attention and short-term memory processes or ‘memory updating’ for stimulus recognition and decisions in respect of the response (Donchin and Coles, 1988; Johnson, 1988; Sutton et al., 1965). Another paradigm uses the same stimuli; however, the subject is asked to perform an irrelevant task during the series of stimuli. This paradigm is used in the literature for obtaining the mismatch negativity (MMN) component (Näätänen et al., 1978, 1982) and is thus named in the present study as the ‘MMN paradigm’. The cognitive state of MMN involves sensory memory for change detection; this state involves pre-attentional and pre-conscious processing (Karakaş, 1997; Näätänen, 1990, 1992). In the SS paradigm there is one type of stimulus and the subject performs the task of counting such stimuli. The SS paradigm involves attention allocation, signal detection and decisions in respect of the response (Cass and Polich, 1997; Polich and Heine, 1996; Polich et al., 1994).

The foregoing paradigms thus form a series with respect to the processes that these paradigms/tasks trigger (Table 1). With the exception of the MMN paradigm, all paradigms require focused attention and they further require the operation of recognition and memory processes for effective task performance. Thus, a systematic manipulation of paradigms and, via the experimental paradigms, the respective cognitive states would allow the demonstration of the respective variations in ERPs and EROs. Providing a comparative analyses, such a multiple paradigms approach would be appropriate for investigating the functional or more specifically the cognitive meaning of the EROs. This approach was previously used in investigating the functional correlates of the

Table 1
The description of the experimental paradigms

Paradigm	Stimulus	Task	Respective cognitive/behavioral processes
Easy oddball (OB-ES)	Two types of stimuli: deviants (2000 Hz), standards (1000 Hz)	Count deviants	Sensory process; sensory memory; pre-attentional change detection; focused attention; short-term memory, memory updating; stimulus recognition; decision for response
Hard oddball (OB-HD)	Two types of stimuli: deviants (2000 Hz), standards (1000 Hz)	Count deviants	Sensory process; sensory memory; pre-attentional change detection; focused attention; short-term memory, memory updating; stimulus recognition; decision for response
Mismatch negativity (MMN)	Two types of stimuli: deviants (2000 Hz), standards (1000 Hz)	Perform irrelevant task	Sensory process; sensory memory; pre-attentional change detection
Single stimulus (SS)	One type of stimulus: deviants (2000 Hz)	Count deviants	Sensory process; focused attention; signal detection; short-term memory, memory updating; decision for response

gamma activity (Karakaş and Başar, 1998; Karakaş et al., 2000a). The comparative analyses in these studies led to conclusions that had not been possible in other studies where a single, or at best, a limited number of paradigms were used.

In the present study, it is hypothesized that when experimental paradigms and respective cognitive states are systematically varied, the event-related oscillations will also vary systematically. It is further hypothesized that superposition of the paradigm-specific variations in oscillatory responses will lead to paradigm-specific morphology of the event-related waveform.

2. Materials and methods

2.1. Subjects

A total of 42 paid subjects (16 males, 26 females) volunteered and gave written consent to participate in the study. Subjects were young adults, they were between 19 and 30 years of age and they were from the undergraduate or graduate populations. Subjects were naive to electrophysiological studies. Three were left-handed.

Basic information was collected on each subject using a standard survey sheet. The information consisted of the daily habits (sportive activities, sleeping habits, cigarette smoking, tea, coffee, cola consumption, alcohol consumption) and health condition of each subject. Only those individuals who reported being free of neurological or psychiatric problems were admitted to the study. Individuals who were, at the time of testing, under medication that would affect cognitive processes or who stopped taking such medication were not employed in the study. Hearing levels of potential subjects were assessed through computerized audiometric testing prior to the experimental procedures. Individuals with hearing deficits were also not employed in the study.

2.2. Stimuli and paradigms

The auditory stimuli had 10 ms r/f time, 50 ms duration and were presented through headphones at 65 dB SPL. Two types of stimuli were used: the standards and the deviants. Depending on the experimental paradigm, the standard stimuli were either 1000 or 1900 Hz. Deviants were always 2000 Hz (Table 1).

In all the paradigms, the deviant stimuli were embedded randomly within a series of standard stimuli. The probability of the deviant stimuli was 0.20 and that of standard stimuli 0.80. In the MMN paradigm, there were 51 deviant and 204 standard stimuli. In the other paradigms, the number of deviants varied between 30 and 33 and standards between 120 and 130. The single stimulus paradigm had 31 deviants with silence employed at the time points of the standard stimuli.

The multiple experimental paradigms that the present study employed, their stimulus composition, task requirements and characteristic processes of the paradigms as have been formulated in relevant research are given in Table 1 (Başar-Eroğlu et al., 1992; Donchin and Coles, 1988; Johnson, 1988; Katayama and Polich, 1996; Mertens and Polich, 1997; Polich, 1991, 1994; Polich and Kok, 1995; Polich and Margala, 1997; Näätänen, 1990, 1992; Näätänen et al., 1982; Sutton et al., 1965). Each subject was exposed to all paradigms and related procedures in a single session. Sessions lasted between 310 and 510 s. The details of the paradigms are given below in the order that the paradigms were experimentally presented.

2.2.1. Familiarization phase

EEG recordings under eyes-open and eyes-closed conditions served to familiarize the subject with the experimental environment. Each recording lasted 2.5 min.

During the eyes-open condition and the paradigms that did not involve a visual task, subjects were required to keep their eyes open and try not to move them or blink. They were asked to look at an 'X' sign that was placed on the wall at a distance of 2 m at the approximate eye level.

2.2.2. Mismatch negativity (MMN) paradigm

In this paradigm, the subject was asked to perform an irrelevant task while the 2000 Hz deviant and 1000 Hz standard stimuli were presented through headphones.

In the MMN paradigm the irrelevant task that was used to direct attention away from the auditory stimuli involved digits of ascending or descending order that were printed on an A4 size piece of paper. Every now and then, a digit would be skipped. The task of the subject was to read the digits, count the number of interruptions and to report the number at the end of the session.

At the completion of the procedures for the MMN paradigm, subjects were asked whether they had been aware of the acoustic stimuli and how many kinds of stimuli there were. The subjects reported having experienced auditory stimulation. All reported being unaware of whether there were one or many kinds of sounds.

2.2.3. Single stimulus (SS) paradigm

This paradigm employed no stimulus (i.e. silence) as the standard. Thus, only the 2000 Hz deviant stimuli were presented and the subject was required to count them.

2.2.4. Easy oddball (OB-ES) paradigm

This paradigm employed the stimuli of the MMN paradigm, i.e. the 2000 Hz deviants (targets) and 1000 Hz standards. The subject was required to count the deviant stimuli.

2.2.5. Hard oddball (OB-HD) paradigm

This paradigm employed a shorter frequency separation between the deviants and the standards; while the deviants were again 2000 Hz, the standards were 1900 Hz. Subjects were again required to count the deviant stimuli.

Before the experiments with the OB paradigms, a practice series of stimuli was presented that illustrated the task conditions. The subject was asked to perform the task during the practice session until he/she correctly discriminated the deviant and standard stimuli. The subject was encouraged to perform the counting task accurately during the experimental tasks and they were given feedback on the accuracy of their performance at the completion of the SS and the two OB paradigms.

2.3. Electrophysiological recording

The brain's neuroelectricity was recorded at midline recording sites (Fz, Cz and Pz) of the 10–20 system using a commercial electrode cap system (Electro-Cap) of appropriate size. Electrodes were referenced to linked earlobes with the forehead as the ground. Bipolar recordings were made of electro-ocular (EOG) activity (electrodes at the outer canthus and the supraorbital area of the left eye) and submental electromyographic (EMG) activity. The impedance for all electrode sites was kept at 3 kΩ or less. Neuroelectric activity was amplified (Nihon Kohden Neurofax 4418K) and filtered with a bandpass between 0.16 and 70 Hz (3 dB down, 12 dB octave/slope). The notch filter was not activated. The total recording time was 2000 ms, 1000 ms of which served as the pre-stimulus baseline. The 2000 ms recording time was digitized with a sampling rate of 512 Hz.

Data acquisition, analysis, and storage were achieved by a commercial system (Brain Data 2.80) which also controlled stimulus presentation and automatic rejection of trials in which response amplitude exceeded ±50 μV. This system was used for on-line monitoring of single sweeps and averaged waveforms. The neuroelectric activity was recorded on paper, but both this activity and the dynamic condition of the subject were also simultaneously displayed on the CRT of the Neurofax using a formatter (Nihon Kohden EEG Formatter VY-210BK) and a hi-fi stereo video-cassette recorder. This system made the recording and playback of both the neuroelectric activity and the subject also possible.

2.4. Data analysis

2.4.1. Computation of selectively averaged ERPs

Before the averaging procedure, the epochs that contained artifacts were rejected first by an on-line and later an off-line technique. The on-line rejection was accomplished by the data acquisition software that rejected all epochs where the neuroelectric activity exceeded ±50 μV. This occurred for epochs that contained muscle activity. In the off-line procedure, single sweep EOG recordings were visually studied and trials with eye-movement or blink artifacts were rejected. These artifact-free sweeps were used in the calculation of average ERPs of the subjects and of the sample (grand averages) for each experimental paradigm, stimulus type and electrode site.

2.4.2. Determination of the frequency responses of the system

The frequency responses of the system were determined using two methods: the transient response frequency characteristics (TRFC) method through which the amplitude frequency characteristics (AFC) were computed (Başar, 1980; Röschke et al., 1995) and the method of digital filtering (DF).

The basic experimental procedure for determining the frequency characteristics of a complex signal involves the successive application of sinusoidal stimuli of different frequencies to the system's input. However, since the AFC method requires long experimental times, it is not suitable for studying the brain which is not static as technical systems may be. In the present study, frequency characteristics were computed by the alternative transient response frequency characteristics (TRFC) method. In the TRFC method, the amplitude frequency characteristics, $|G(j\omega)|$, are computed by the application of the Laplace transform (i.e. one-sided Fourier transform) to the transient response, $c(t)$, of the system (Başar, 1998; Brandt and Jansen, 1991; Jervis et al., 1983; Kolev and Yordanova, 1997; Parvin et al., 1980; Röschke et al., 1995; Solodovnikov, 1960).

The AFC is expressed in relative units and it reflects the amplification in studied frequency channels. The presence of a peak in the AFC thus reveals the frequency selectivities of the system and these are interpreted as its most preferred oscillations when responding to stimuli (for details of methodology see Başar and Karakaş, 1998). The AFC method is advantageous because it shows the status of all frequencies in a combined manner; this advantage does not exist in the wavelet analysis which studies phase-locked signals in a given frequency window. However, results from wavelet analysis for selected frequencies have been parallel to those from the AFC for that frequency window (Demiralp et al., 1998). The AFC method was used in the present study for a global description of the frequency selectivities and the frequency limits of these selectivities.

The frequency responses were also determined through the method of digital filtering. In this method, the experimentally obtained transient evoked response, $c(t)$, was theoretically filtered by means of the convolution integral using the weighting function, $g_{KF}(t)$, of the adequately determined ideal filter (for details of methodology see Cook and Miller, 1992; Farwell et al., 1993; Karakaş and Başar, 1998).

Filtering produces visual displays of the time courses of oscillatory components within the frequency limits of the utilized filters. The digital filters are advantageous because they do not produce the phase shifts that electronically designed filters with capacitive-resistive configurations do. Digital filtering was employed in the present study for digital bandpass filtering of the ERPs. This allowed the subsequent demonstration of EROs of different frequency bands.

In the present study where the low frequency delta and theta responses were investigated, the compound ERP waveform was first filtered using a 0.1–30 Hz bandpass filter. The compound ERP waveform was then decomposed into the delta and theta bands. For this a response-adaptive filtering technique was used where the bandpass filter limits for the delta and theta bands were determined from selectivity channels that were displayed in the amplitude frequency characteristics as distinct peaks. In the present study, the remaining oscillations at the higher frequencies were also taken into account as statistical residuals. The low cut-off frequency of these residual frequencies was obtained by adding '0.10 Hz' to the high limit of the theta filter.

3. Results

The mean correct responses taken across subjects were 31.05 (±0.54) for the SS paradigm, 30.05 (±0.54) for the OB-ES paradigm and 31.55 (±3.12) for the OB-HD paradigm. The total number of possible correct responses had been 31.00 for the SS paradigm, 30 for the OB-ES paradigm and 33 for the OB-HD paradigm. A one-way analysis of variance showed that the numbers of correct responses in the 3 experimental paradigms (SS, OB-ES and OB-HD) were not significantly different. According to this finding, subjects were able to perform the tasks equally well across the experimental paradigms.

3.1. Variations in ERP components according to experimental conditions: average ERPs

In the present study, the N100 latency point was taken as the most negative point within the 70–120 ms latency window, the P200 was taken as the most positive point within the 160–220 ms window, the N200 was taken as the most negative point within the 150–280 ms window, and the P300 was taken as the most positive point within the 260–400 ms window. These time ranges sufficiently included the latency variations of the ERP peaks that were obtained under the experimental paradigms of the study (Figs. 1–3). The present study mainly analyzed the N200 and the P300 components under all paradigms including the 'MMN paradigm'. The term 'MMN' was used in the study for denoting a specific set of experimental conditions; the MMN component was not calculated in this study and no analysis was made regarding this component. The ERP and ERO components were studied for both the deviant and the standard stimuli; however, due to their critical value, only findings for the deviant stimuli are reported in the sections below. (For a detailed study of the responses to the standard stimuli see Karakaş and Başar, 1998.)

Figs. 1–3 show the grand average unfiltered and filtered waveforms for the Fz, Cz and Pz recording sites, respectively. These and the following figures show both the prestimulus EEG that serves as the baseline in the present study and the post-stimulus ERP; this circumstance was abbreviated as EEG/ERP. Qualitative analyses of the waveforms in Figs. 1–3 showed that the experimental conditions produced similar N100 peaks for each recording site. The N200 at the Fz and Cz recording sites was nearly equivalent for the task conditions that involved discrimination (OB-ES, OB-HD) and was higher in amplitude than that obtained under the non-task condition (MMN). The N200 at the Pz recording site was smaller in amplitude than that at Fz; however, the N200 variations at Pz according to the experimental paradigms were similar to those obtained for the Fz site.

The P300 at the Pz recording site was the largest; P300 became smaller as the recording site changed from Pz to Fz. At all sites, P300 gradually grew smaller as the paradigms changed from OB-ES to OB-HD and finally to the MMN paradigm where an irrelevant task was performed throughout stimulation.

Under the SS paradigm, the P300 amplitude from the Pz recording site was comparable, both in amplitude and morphology, to that obtained under the OB-ES paradigm. However, P300 at Fz was not as distinctly obtained; it took place at a broad positivity that also contained an indistinct N200 component.

The effects of the experimental variables were studied using a $4 \times 3 \times 2 \times 2$ analysis of variance (ANOVA) for repeated measures (Table 2). The factors in ANOVA were experimental paradigm (OB-ES, OB-HD, MMN and SS),

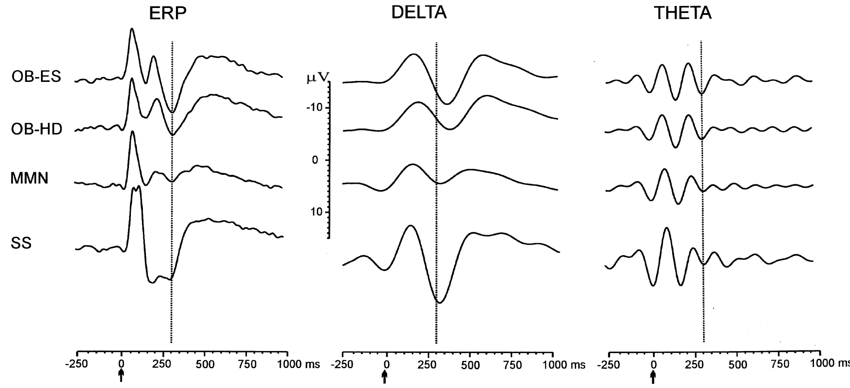

Fig. 1. Grand average (38 subjects) EEG-ERPs, delta responses and theta responses obtained under the OB-ES (846 sweeps), OB-HD (945 sweeps), MMN (1471 sweeps) and SS (891 sweeps) paradigms from the Fz recording site. Stimulation applied at '0 ms' time point.

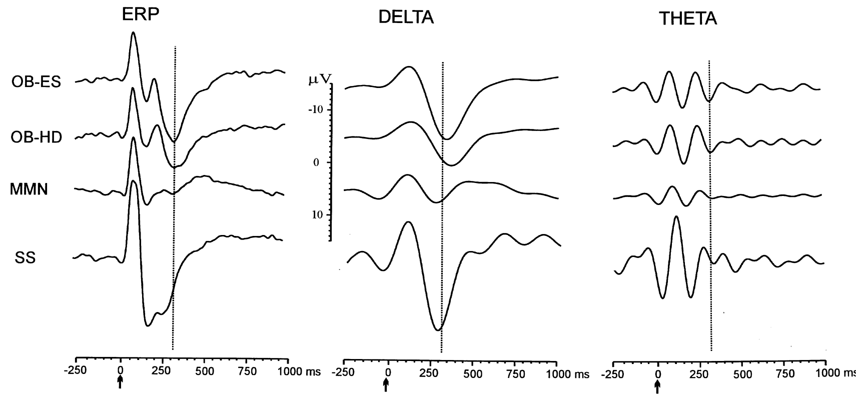

Fig. 2. Grand average (38 subjects) EEG-ERPs, delta responses and theta responses obtained under the OB-ES (846 sweeps), OB-HD (945 sweeps), MMN (1471 sweeps) and SS (891 sweeps) paradigms from the Cz recording site. Stimulation applied at '0 ms' time point.

recording site (Fz, Cz and Pz), selected latency point (N200 and P300), and selected filter limit (delta and theta frequency ranges). The dependent variable was amplitude; the values were obtained from the ERP and ERO waveforms at the N200 and P300 latencies.

ANOVA showed all main effects as significant (Table 2). Accordingly, amplitudes were affected by the experimental paradigm, the site of recording, the selected latency point and the selected filter range. All interaction effects except the recording site × selected latency point were also found to be significant. The significant second and third order interactions showed that the effect of the filter or the contribution of theta and delta oscillations to amplitude varied selectively according to combinations of experimental conditions.

3.2. Variations in EROs according to experimental conditions: amplitude frequency characteristics and filtered waveforms

Fig. 4 depicts the amplitude frequency characteristics (AFC) of the grand average ERPs of different experimental paradigms (OB-ES, OB-HD, MMN and SS) and recording sites (Fz, Cz and Pz) for the 1–100 Hz frequency range. The AFCs in Fig. 4 gave a global idea concerning the frequency selectivities for different experimental conditions of the study. Albeit with varying degrees of prominence, the delta response existed in all the AFC curves. The delta response was distinctly obtained especially at the OB-ES paradigm from the Fz recording site; as the paradigms changed from the OB-ES to OB-HD, SS and finally to MMN, the delta response gradually lost its distinctiveness. The AFCs for the Pz recording site was composed mainly of the delta response; furthermore, this delta did not selectively respond to different experimental conditions.

The theta oscillation was obtained at the AFCs (Fig. 4) of the Fz and Cz recording sites. Within these recording sites, theta activity was distinctly obtained especially in paradigms that involved demanding tasks and high cognitive load (OB-ES, OB-HD). Though the amplitudes were high, the delta and theta responses were not clearly discriminated from each other in the SS and MMN paradigms. The theta oscillation was relatively indistinct at the Pz recording site except for the MMN paradigm where the response was high but not distinctly discriminated from the delta response.

Figs. 1–3 also show the averaged ERP waveforms that had been filtered at the delta and theta frequency ranges. All digitally filtered waveforms demonstrated amplitude enhancement upon stimulation. Such enhancement showed

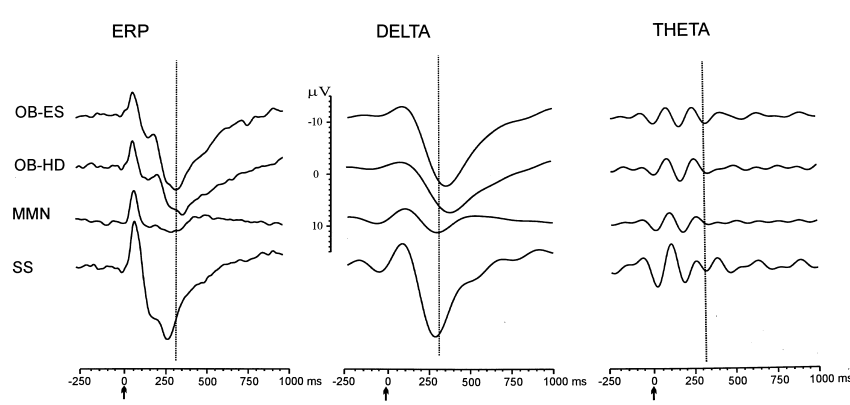

Fig. 3. Grand average (38 subjects) EEG-ERPs, delta responses and theta responses obtained under the OB-ES (846 sweeps), OB-HD (945 sweeps), MMN (1471 sweeps) and SS (891 sweeps) paradigms from the Pz recording site. Stimulation applied at '0 ms' time point.

that the responses were phase-locked to the stimuli since the non-phase locked responses would have been largely attenuated by averaging. All filtered waveforms clearly showed the existence of both the theta and the delta oscillatory responses under all paradigms and recording sites.

The highest amplitudes for both the delta and the theta responses were obtained for the SS paradigm. The delta response gradually grew smaller in amplitude through the SS, OB-ES, OB-HD series. The smallest amplitudes for both responses were obtained for the MMN paradigm. ANOVA showed the effect of paradigm × selected filter limit to be significant ($F(9, 216) = 32.39$, $P < 0.001$).

Post-hoc Tukey tests showed that the significant differences for the delta response originated from the difference of the SS paradigm from all other paradigms at both the N200 and P300 latencies and from the difference of the OB-ES paradigm from the OB-HD paradigm at the N200 latency and from the OB-ES and MMN paradigms at the P300 latency. Significant differences for the theta response originated from the differences between the SS and OB-HD, OB-ES and OB-HD paradigms at the N200 latency and between the SS and OB-ES and between OB-HD and MMN paradigms for the P300 latency.

The delta responses in Figs. 1–3 showed latency variations. To facilitate latency comparisons, a reference latency (that for P300 of the OB-ES paradigm) was taken for each recording site and lines were drawn at that latency through unfiltered and filtered waveforms of the experimental paradigms. The figures showed that the positive-going arm of the delta oscillation occurred earliest for the SS paradigm, followed by that for the MMN paradigm. The longest latency was obtained for the OB-HD paradigm. Figs. 1–3 show that the duration of the theta oscillations for the SS and MMN paradigms were comparable. Furthermore, this duration was shorter than that for the two OB paradigms which were comparable within themselves.

The delta response was most enhanced at the Pz recording site; it became lower in amplitude from Cz to Fz recording sites. The theta response showed a frontocentral distribution and had a lower amplitude at Pz. The related recording site × filter limit was significant ($F(6, 144) = 48.52$, $P < 0.001$).

3.3. Relations between EROs and ERPs: bivariate and multivariate statistical analyses

The relationships between ERP and ERO amplitudes and statistical predictability of ERPs from EROs were analyzed through bivariate (Pearson product moment correlation

Table 2
Analysis of variance for repeated measures for component amplitudes as a function of experimental paradigm, recording site, selected latency point and selected filter range

Variables	Sum of squares	d.f.	Mean square	F	Level of significance
Paradigm (A)	6202.62	3	2067.54	31.83	0.001
Error (A)	4676.63	72	64.95		
Recording site (B)	3268.99	2	1634.50	44.84	0.001
Error (B)	1749.86	48	36.46		
Latency point (C)	7438.58	1	7438.58	102.25	0.001
Error (C)	1745.89	24	72.45		
Filter range (D)	6496.77	3	2165.59	35.57	0.001
Error (D)	4384.03	72	60.89		
A*B	307.34	6	51.22	5.64	0.001
Error (A*B)	1308.69	144	9.09		
A*C	1341.96	3	447.32	13.75	0.001
Error (A*C)	2342.01	72	32.53		
A*D	5793.12	9	643.68	32.39	0.001
Error (A*D)	4291.84	216	19.87		
B*C	6.25	2	3.13	0.54	NS
Error (B*C)	276.52	48	5.76		
B*D	3006.26	6	501.04	48.52	0.001
Error (B*D)	1487.06	144	10.33		
C*D	2419.78	3	806.59	43.55	0.001
Error (C*D)	1333.50	72	18.52		
A*B*C	141.78	6	23.63	5.00	0.001
Error (A*B*C)	680.56	144	4.73		
A*B*D	360.62	18	20.03	6.45	0.001
Error (A*B*D)	1341.97	432	3.11		
A*C*D	707.80	9	78.65	8.56	0.001
Error (A*C*D)	1983.92	216	9.19		
B*C*D	104.03	6	17.34	5.87	0.001
Error (B*C*D)	425.17	144	2.95		
A*B*C*D	93.70	18	5.21	2.91	0.001
Error (A*B*C*D)	772.63	432	1.79		

analysis) and multivariate (stepwise multiple regression) techniques.

One of the approaches for studying the relationship and predictability involved the mathematical reconstruction of ERP component amplitudes from the amplitudes at the delta, theta and higher frequency responses at N200 and P300 latencies. The relationship between the recorded and reconstructed amplitudes was studied for each experimental condition that included combinations of the levels of the experimental paradigm, recording site and selected latency point. The relationships were studied by a bivariate technique, the Pearson product moment correlation. The correlation coefficients between recorded and reconstructed amplitudes were found to be 0.99 ($P < 0.001$) for all experimental conditions.

Another approach for studying the predictability of the ERP from the ERO components involved the utilization of the stepwise multiple regression analysis. This technique was applied to each experimental paradigm (OB-ES, OB-HD, MMN and SS), recording site (Fz, Cz and Pz) and selected latency point (N200 and P300). The predictors were the amplitudes at the N200 and P300 latencies on waveforms filtered at delta, theta or the higher frequency ranges. The predicted variables were the N200 and P300 amplitudes on the ERP waveform. A summary of the results is presented in Tables 3–5. The tables include multiple correlations (R), cumulative proportion of explained variances (R^2) and the unstandardized regression weights (β). Since multiple analyses were made on the data set, a Bonferroni type adjustment was made for inflated Type 1 error for each of the recording sites separately. For this, α was assigned the value of 0.05 for each R among a set of Rs, such that α for a set of Rs did not exceed a critical value. The same procedure was also carried out independently for the regression weights (β).

Tables 3–5 show the regression values for Fz, Cz and Pz recording sites, respectively. The values in Tables 3–5 are given after each step of the stepwise regression to allow the evaluation of the amount of explanation that each predictor provided and the change in the amount of explained variance with the sequential addition of each predictor (i.e. delta, theta and higher frequencies) to the regression equation. The tables show that the proportion of explained variances that was obtained for the conditions of the study (recording site and latency point) varied between 0.82 and 0.99. Being in line with the 0.99 correlation coefficients between the amplitudes at the ERP and the reconstructed waveforms, this finding showed that the amplitudes for delta, theta and the residual (higher) frequencies amply account for the amplitudes at N200 and P300 latency points. The contribution of the residual to the proportion of explained variance varied between 0.01 and 0.08. This finding showed that the major contribution came from the additive effect of the two lower frequencies.

The major contributor to the ERP component amplitudes was the delta response (Tables 3–5). The proportion that the delta amplitudes explained varied between 0.57 and 0.94; the maximum was for P300 (at Pz under the SS) and the minimum was for N200 (at Fz under the SS). The increase in the proportion of explained variance by addition of the theta

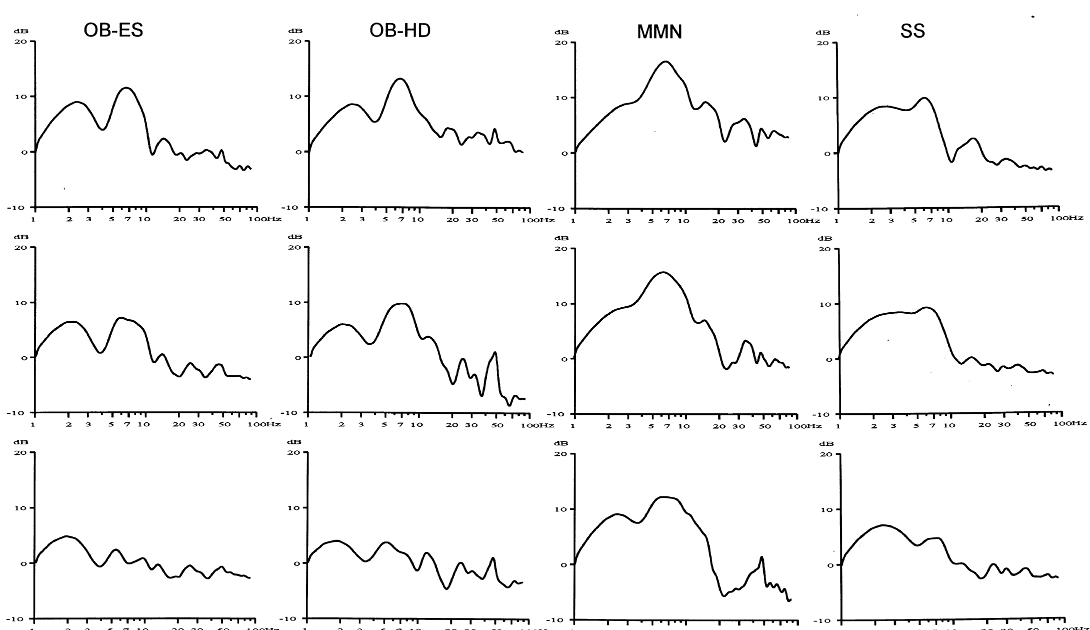

Fig. 4. Amplitude frequency characteristics for the EEG-ERPs of Fz (first row), Cz (second row) and Pz (third row) for the deviant stimuli of the OB-ES, OB-HD, MMN and SS paradigms. Curves are obtained by applying Fourier transform to averaged EEG-ERP curves. Abscissa, frequency in logarithmic scale; ordinate, potential amplitude (gain), $|G(j\omega)|$, in decibels. The curves are normalized in such a way that the amplitude at 0 Hz is equal to 1 (or 20 log1 = 0). For abbreviations see text.

Table 3
Stepwise multiple regression analyses with component amplitudes as predicted variable and oscillations as predictor variables for N200 and P300 latencies obtained under the experimental paradigms for the Fz recording site

Paradigm	Variables						
	Predicted	N200			P300		
	Predictor Model	Delta 1	Theta 2	Higher 3	Delta 1	Theta 2	Higher 3
OB-ES	R	0.84	0.96	0.99	0.94	0.98	0.99
	R^2	0.71	0.91	0.99	0.89	0.96	0.99
	β	1.00	1.00	1.00	0.99	0.92	0.97
OB-HD	R	0.77	0.95	0.99	0.92	0.98	0.99
	R^2	0.59	0.90	0.99	0.84	0.96	0.99
	β	0.96	0.90	0.99	0.97	0.95	0.94
MMN	R	0.85	0.94	0.99	0.90	0.97	0.99
	R^2	0.73	0.88	0.99	0.81	0.94	0.99
	β	0.97	0.92	0.98	0.99	0.95	0.93
SS	R	0.76	0.96	0.99	0.91	0.97	0.99
	R^2	0.57	0.93	0.99	0.83	0.95	0.99
	β	0.95	0.95	0.92	0.97	0.97	0.87

Table 5
Stepwise multiple regression analyses with component amplitudes as predicted variable and oscillations as predictor variables for N200 and P300 latencies obtained under the experimental paradigms for the Pz recording site

Paradigm	Variables						
	Predicted	N200			P300		
	Predictor Model	Delta 1	Theta 2	Higher 3	Delta 1	Theta 2	Higher 3
OB-ES	R	0.93	0.98	0.99	0.95	0.98	0.99
	R^2	0.86	0.96	0.99	0.90	0.95	0.99
	β	0.98	0.90	0.84	0.96	1.00	0.93
OB-HD	R	0.91	0.97	0.99	0.96	0.99	0.99
	R^2	0.83	0.94	0.99	0.93	0.97	0.99
	β	0.98	0.90	0.93	1.00	0.93	0.95
MMN	R	0.87	0.96	0.99	0.93	0.97	0.99
	R^2	0.76	0.92	0.99	0.87	0.94	0.99
	β	0.97	0.91	0.98	1.00	0.89	0.94
SS	R	0.85	0.95	0.99	0.97	0.99	0.99
	R^2	0.72	0.91	0.99	0.94	0.98	0.99
	β	0.97	0.94	0.98	0.98	0.99	0.82

amplitude to the regression equation was between 0.04 and 0.36; the maximum was for N200 (at Fz under the SS) and the minimum for P300 (at Pz under SS and OB-HD). For all paradigms and recording sites, the proportion that the delta amplitudes explained was higher for the P300 component (P300: 0.70–0.94; N200: 0.57–0.86). Meanwhile, the increase in the proportion of explained variance by the addition of the theta amplitudes to the regression equations was higher for the N200 component (N200: 0.10–0.36; P300: 0.04–0.20). The proportion of variance that the delta amplitudes explained generally increased toward the posterior recording sites while that for the theta amplitudes increased toward the anterior recording sites.

Fig. 5 shows filtered waveforms superimposed on the unfiltered waveform. The figure was prepared for the Fz recording site and for the different experimental paradigms (OB-ES, OB-HD, MMN and SS).

A collective evaluation of Fig. 5 and Tables 3–5 showed that distinct P300 components were obtained when there was a high delta contribution that was also in-phase with the theta oscillation at the P300 latency point. This criterion held primarily for the OB-ES paradigm, thus the large P300

Table 4
Stepwise multiple regression analyses with component amplitudes as predicted variable and oscillations as predictor variables for N200 and P300 latencies obtained under the experimental paradigms for the Cz recording site

Paradigm	Variables						
	Predicted	N200			P300		
	Predictor Model	Delta 1	Theta 2	Higher 3	Delta 1	Theta 2	Higher 3
OB-ES	R	0.87	0.94	0.99	0.92	0.98	0.99
	R^2	0.76	0.89	0.99	0.86	0.95	0.99
	β	0.99	1.00	1.00	0.96	1.00	0.95
OB-HD	R	0.76	0.94	0.99	0.95	0.99	0.99
	R^2	0.58	0.88	0.99	0.90	0.97	0.99
	β	0.98	0.92	0.99	0.99	0.96	1.00
MMN	R	0.79	0.95	0.99	0.84	0.95	0.99
	R^2	0.63	0.90	0.99	0.70	0.90	0.98
	β	0.96	0.96	0.96	0.98	1.00	0.97
SS	R	0.80	0.98	0.99	0.95	0.99	0.99
	R^2	0.64	0.95	0.99	0.90	0.98	0.99
	β	0.93	0.93	0.83	0.93	0.97	0.78

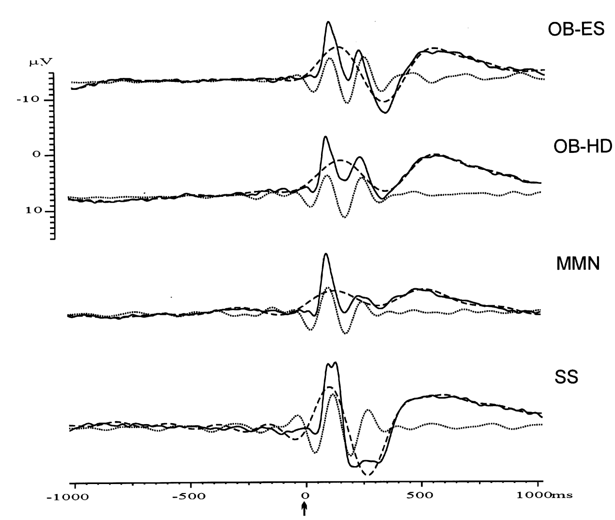

Fig. 5. Superimposed unfiltered grand average EEG-ERPs (continuous line) and filtered waveforms (delta oscillation, discontinuous line; theta oscillation, dotted line) for the OB-ES, OB-HD, MMN and SS paradigms for the Fz recording site. Stimulation applied at '0 ms' time point. Number of subjects and sweeps are as given in Fig. 1.

under this paradigm. The delta and theta responses were also in-phase at the OB-HD and MMN paradigms, but the delta responses were increasingly smaller resulting in the increasingly smaller P300 amplitudes in these two paradigms. Meanwhile, in the SS paradigm, the delta and theta oscillations were not entirely in-phase at the P300 latency; thus, the insignificant P300 takes place with a large positivity that also includes an insignificant N200 component.

4. Discussion

In the present work, a collection of electrophysiological and statistical methods was used to show the contribution of the delta and theta oscillatory responses to the variations in the N200 and P300 ERP components. The methods of electrophysiology included amplitude frequency characteristics and digital filtering; the statistical methods included the univariate analysis of variance, the bivariate correlation analysis and the multivariate stepwise regression. The study employed multiple experimental paradigms; the systematically varying task conditions helped bring out the relations between the neuroelectric responses (ERPs and EROs) and cognition (Table 1).

4.1. ERP components are complex signals: the contribution of EROs to the ERP components

According to the principle of superposition, a complex signal is the result of a particular combination of individual phenomena; according to this principle, analysis of the compound ERP waveform should make use of the constituent oscillatory responses as the unit of analysis (Başar, 1980; Başar and Ungan, 1973).

The present paper statistically confirmed that the morphology of the two ERP components, N200 and P300, is formed by the combination of oscillatory responses at different frequency ranges. The bivariate correlation coefficients between the actual ERP component amplitudes and those of the reconstructed components were close to 1; this showed the close congruity between the morphology of the complex ERP component and its constituent oscillatory responses at different frequency ranges. This basic finding was elaborated through findings of the multivariate technique, stepwise multiple regression, which showed that the combination of the oscillatory responses accounted for close to 100% of the total variance in the amplitude of the complex ERP components, N200 and P300. Findings from the stepwise regression analysis demonstrated the gradual development of the compound ERP waveform and its components.

The multiple paradigms approach of this study (Table 1) enabled the systematic variation of the task conditions and thus the cognitive states (Başar-Eroğlu et al., 1992; Donchin and Coles, 1988; Johnson, 1988; Katayama and Polich, 1996; Mertens and Polich, 1997; Polich, 1991, 1994; Polich and Kok, 1995; Polich and Margala, 1997; Näätänen, 1990, 1992; Näätänen et al., 1982; Sutton et al., 1965). As such, the approach is suitable for studying whether oscillatory activity selectively responds to experimental conditions. Oscillatory activity should respond selectively to conditions of the experiment since it might otherwise be argued that when complex signals are digitally filtered or are decomposed, there would always be some oscillatory activity. The findings of the present study showed that the contributions of the different frequencies to the ERP waveform varied according to the conditions of the experiment. The pattern of the contributions is detailed in Table 3, Fig. 5 and the respective sections. In summary, the delta oscillation explained a higher proportion of the variance in the P300 component. Furthermore, regardless of the ERP component, the explanatory power was higher at the Pz site. Parallel to this finding, the P300 component was also larger at the Pz recording site. Meanwhile, the secondary contribution of the theta oscillation explained a higher proportion of the variance in the N200 component with higher explanatory power at the Fz site. Parallel to this finding, the N200 component was especially obtained at the Fz and Cz recording sites; the component attained its largest amplitude at Fz.

In the condition of a high delta contribution and an in-phase relationship between delta and theta oscillation, the explanatory value of EROs might be underestimated. In fact, the proposition that EROs are the building blocks of ERP components might even be considered a tautology. The essential nature of the brain's oscillatory responses as the level of discourse to be taken in understanding the ERPs was strongly highlighted in the findings from the SS paradigm where the delta and theta oscillations were not exactly in-phase.

According to the principle of superposition, the existence of different peaks does not necessitate the existence of different functional structures; similarly, disappearance of peaks does not necessarily show that the functional groups have ceased their activity (Başar and Ungan, 1973; Başar, 1980). The findings of the present study on the SS paradigm are a clear demonstration of these statements. In the SS paradigm, indistinct N200 and P300 components were obtained at Fz and Cz recording sites; these components took place on a broad positivity at the ERP waveform that in fact mimicked the well-known N1-P2 component of the evoked potential waveform. In this circumstance, should the conclusion be that the cognitive processes that are ascribed to the N200 and P300 components (Başar-Eroğlu et al., 1992; Donchin and Coles, 1988; Karakaş, 1997; Näätänen, 1990; Näätänen and Picton, 1986; Polich, 1991, 1994, 1997) did not exist under the SS paradigm? Such a conclusion would be challenged by the processes that the SS task involves, i.e. attention and performance of a signal detection task (Table 1). It would also be empirically challenged; Polich and colleagues (Cass and Polich, 1997; Polich and Heine, 1996; Polich et al., 1994) demonstrated that the P300 components in the SS and the OB paradigms are analogous with respect to cognitive characteristics.

The SS paradigm ranked highest with respect to its amplitude and contribution of the delta response to the P300 component. So the contributor to the P300 component did exist at the SS ERP. However, neither the P300 nor the N200 was clearly observable at the ERP waveform; Fig. 5 demonstrates how this occurred. The indistinct ERP components were due to the counter-phase relationship between the theta and delta oscillations at N200 and P300 latencies. In fact, when the delta and theta oscillations were not entirely out of phase at that latency, as in the Pz recording site, a distinct P300 component was obtained. The amplitude of this P300 was comparable in amplitude and morphology to that obtained for the OB-ES paradigm (Fig. 3).

The above findings and discussions show that the ERP components represent an interplay between mainly the theta and the delta oscillations. The morphology and the amplitudes of the ERP components are a result of a specific superposition of these oscillatory responses. These findings show that the adequate unit of analysis of the brain's event-related neuroelectricity should not be the resultant ERP morphology but the constituent oscillations.

4.2. The cognitive correlates of the EROs

Amongst the multiple experimental paradigms of the study, all except the MMN required attention allocation and within the larger group, tasks required the operation of recognition and memory for effective task performance. This multiple paradigm approach allowed a comparative analysis when discussing the functional or more specifically the cognitive meaning of the ERO components.

The delta response was principally obtained from the Pz recording site (at AFCs the only response was at Pz; in digitally filtered waveforms the largest amplitudes were at Pz). The delta responses existed only when the task required detection or discrimination of stimulus and also task performance. Digitally filtered waveforms allowed a more detailed analysis. The amplitude of the delta oscillation was higher under SS and OB-ES where target recognition was easier. When stimulus discriminability was low, as in the OB-HD paradigm, or the mode of processing was reduced to one of pre-conscious detection (Näätänen, 1992) as in the MMN paradigm, delta amplitudes decreased. Meanwhile, as the cognitive functions changed from pre-conscious detection in MMN to the easy and finally the harder target recognition in the OB-HD paradigm, the latency of the peak on the positive-going arm of the delta response systematically increased.

The largest contribution of the delta response was to the P300 amplitude; thus, the P300 amplitude was large when the delta was large. The delta amplitude congruently varied in amplitude with task-relevant responding that necessitates conscious stimulus evaluation and memory updating. The delta response thus represents cognitive efforts that involve stimulus-matching and decisions with respect to the response to be made (Başar, 1999; Başar-Eroğlu et al., 1992). Other studies also emphasized the relevancy of the delta response to the P300 component and to cognitive operations of matching and decision-making (Başar-Eroğlu et al., 1992; Duncan-Johnson and Donchin, 1979; Pfefferbaum et al., 1986; Schürmann et al., 1995; Stampfer and Başar, 1985). The relationship of the delta response to cognitive efforts was also demonstrated with threshold experiments; in such studies, the waveform was mainly in the form of the delta response (Parnejford and Başar, 1999). However, although with much lower amplitudes, the delta response was also obtained under the MMN paradigm. These findings led the authors (Karakaş et al., 2000b) of a recent study to propose a working hypothesis to the effect that the distinction between the OB and MMN paradigms can be boiled down to a continuum of consciousness and the delta response taken as an index of the degree of consciousness.

The AFCs and the digitally filtered waveforms showed that the theta responses were principally obtained from the Fz and Cz recording sites. As with the delta response, the theta response was obtained under all cognitive paradigms. The response was largest under SS and smallest under MMN paradigms. However, under all paradigms and at all recording sites, the oscillation terminated before P300 occurred (Figs. 1–3). The duration was shorter under the SS paradigm which required merely signal detection and the MMN which required pre-attentional change detection than under the two OB paradigms, both of which involved higher cognitive loads for effective task performance.

Contributing principally to the amplitude of the N200 component and congruently varying in amplitude and also in duration as attentional demands that are a prerequisite to stimulus encoding increase, the theta response represents a complex set of cognitive processes whereby selective attention becomes focused on a task-relevant template that is maintained in short-term memory (Başar-Eroğlu et al., 1992; Demiralp and Başar, 1992; Karakaş, 1997; Klimesch, 1999). This early theta was also observed by Yordanova and Kolev (1998) under the active and passive oddball conditions. This early theta is the 'attentional' theta. The review by Miller (1991) of the relevant studies had shown that theta activity is closely related to orientation, alertness and attentive postures. Theta response was obtained to the fourth attended stimulus in omitted stimulus paradigms with repetitive stimuli and to the omitted stimulus itself where the task of the subject was to estimate the time of occurrence of such stimuli (Başar et al., 1999a,b,c; Başar-Eroğlu and Başar, 1991; Demiralp and Başar, 1992; Demiralp et al., 1994). These findings and those of the present study converge on the conclusion that theta is attention-related. The contribution of the present study to the cognitive meaning of theta response was the following: theta shows systematic variations in various response parameters as the attentional demands vary. However, it is also obtained, though in low amplitudes and short durations, under the paradigm that does not require focusing of attention. All these show that the theta response has the potential of showing not only different amounts of attention but also different forms of it (Posner, 1975), providing the critical parameters are observed.

4.3. From data to theory: prospects

According to the parallel distributed processing (PDP) or the connectionist model (McClelland et al., 1986; Rumelhart et al., 1986) of cognitive psychology, information processing takes place through the interactions of a large number of simple processing elements. The connections between the elements of information can be active at the same time and this enables the system to manipulate a large number of cognitive operations all at once.

The PDP model conjectured that parallel distributed processing should occur through a network distributed across incalculable numbers of locations in the brain. The hypothesis on the parallel sensory-cognitive processing by Goldman-Rakic (1988), distributed processing in large-scale neurocognitive networks by Mesulam (1990), cortical memory by Fuster (1995) and theory of oscillatory neural assemblies by Başar (1998, 1999) are psychophysiological counterparts of the PDP model.

In Başar's formulation, parallel distributed processing is based on the oscillatory activity, the EEG and EROs of various frequencies (Başar, 1998, 1999; Başar and Karakaş, 1998; Quiroga and Schürmann, 1999). According to this formulation, each oscillation represents multiple functions and, conversely, a given function is represented by multiple oscillations. The cognitive functions are represented by the integrative activity of neuroelectric oscillations that occur in parallel.

The present study has shown that the studied EROs selectively respond to variations in response to specific task conditions; however, they exist as time-locked activities under all paradigms and, further, at both the N200 and P300 latencies. Stampfer and Başar (1985) and Başar et al. (1984) showed that the P300 is characterized by enhancement and prolongation in theta oscillation and delay of the delta oscillation along the time axis. In an omitted stimulus paradigm, a P300 component was recorded accompanied by a 40 Hz oscillation most markedly from the CA3 region of the cat hippocampus (Başar-Eroğlu and Başar, 1991). Close inspection of the findings of this study showed that P300 is formed by an interplay of the delta and theta oscillatory responses. Yordanova and Kolev (1998) mention an early theta which shows enhancement and strong phase-locking under both the active and the passive oddball paradigms. Had these authors concurrently studied the N200 ERP component, they would probably have concluded that this early theta which took place in the 0–300 ms time period is related not only to the later P300 component but also to the N200 component. These studies support the theoretical position that cognitive functions are represented by the integration of multiple oscillations.

In fact, this parallel functioning is also implied in the ERP literature; the amplitude variation at the P300 latency point is accepted as being proportional to attentional resources engaged during task performance (Kramer and Strayer, 1988). However, the same variations also index working memory and memory updating (Donchin and Coles, 1988; Johnson, 1988; Polich and Margala, 1997). Similarly, the MMN response is hypothesized to be the index of pre-attentive or pre-conscious processing (Näätänen, 1992). However, Näätänen et al. (1993) have shown that the MMN component originates through learning and furthermore there are individual differences in how well the sensory trace regarding the MMN component develops.

The present study was a comprehensive investigation of the variations that the oscillatory responses showed to task and thus to cognitive variations. The study described these variations and showed that the EROs underlie the ERP components. The study discussed the cognitive correlates of the delta and theta responses and opened an avenue for a more detailed analysis of the cognitive and physiological mechanisms that lie behind these oscillations.

There is ample evidence in the literature regarding the relationship between the oscillations in the pre-stimulus activity (the EEG) and oscillatory responses in the post-stimulus activity (the EROs of different frequency ranges). Some examples are as follows: the study of the relationship of the overall power of the background EEG particularly in the slower bands and the individual variability of P300 (Polich, 1997); the study of the parameters of pre-stimulus alpha to amplitude and latency of the ERP components (Jasiukaitis and Hakarem, 1988; McDonald, 1964; Romani et al., 1988; Brandt and Jansen, 1991; Brandt et al., 1991); the influence of the pre-spectral EEG patterns as reflecting the CNS activation level (Fruhstorfer and Bergström, 1969; Pritchard et al., 1985; Romani et al., 1988; Jansen and Brandt, 1991); and finally, the effect of presentation of stimuli during stages of low pre-stimulus alpha or theta (Başar et al., 1989, 1998; Rahn and Başar, 1993). The present study did not specifically address the extensively studied relationship between the spontaneous oscillations (EEG) and the event-related oscillations (EROs). A specific oscillation was referred to as the delta or the theta response when that oscillation was in the delta or the theta frequency range with no intention made for comparing oscillatory responses with spontaneous responses. However, future work on the pattern of relations between the EEG and ERP delta or the EEG and ERP theta under the multiple paradigms approach of the present study may help to strengthen scientific knowledge on EEG/ERO relations.

4.4. Concluding remarks

The investigation of the effect of multiple cognitive paradigms on the delta and theta responses at N200 and P300 latencies suggests the following conclusions.

- The event-related delta and theta oscillations vary in response to task requirements and recording site.

- Two working hypothesis that emerged from the present study are the following: the theta response represents different amounts and forms of attention and the delta response represents degrees of consciousness.
- The delta and theta oscillations underlie both the N200 and P300 components. ERP components are the end-products of a specific superposition of oscillations in various frequency bands. Thus, the basic phenomenon of brain neuroelectricity is not the ERP but the brain's oscillatory responses, EROs.
- If not an epiphenomenon, ERP component morphology may be a neuroelectric response of the brain that represents a molar manifestation of the underlying ensemble of oscillatory responses.
- The critical importance of understanding the ERP waveform on the basis of its frequency responses is clearly demonstrated in the ERP and ERO waveforms for the SS paradigm. The frequency decomposition shows the functional equivalence of the SS and OB paradigms and demonstrates that SS can conveniently be used particularly in clinical studies where rapport with the patient is usually problematic.
- The brain's event-related oscillations are multifunctional and they comprise a parallel processing system of information processing in the brain.

Acknowledgements

We are grateful to Emine D. Çakmak for excellent technical assistance. We thank Marion Engin for proofreading and Belma Bekçi for careful reading of the manuscript. This work was supported by The Scientific and Technical Research Council of Turkey (Grant TBAG-Ü 17-2) and Jülich, DFG Grant.

References

Başar E. EEG-brain dynamics: relation between EEG and brain evoked-potentials, Amsterdam: Elsevier, 1980.

Başar E. Brain function and oscillations: I. Brain oscillations. Principles and approaches, Heidelberg: Springer-Verlag, 1998.

Başar E. Brain function and oscillations: II. Integrative brain function. Neurophysiology and cognitive processes, Heidelberg: Springer-Verlag, 1999.

Başar E, Karakaş S. Toward a theory of brain oscillations (Chapter 19). In: Başar E, editor. Brain function and oscillations: I. Brain oscillations. Principles and approaches, Heidelberg: Springer-Verlag, 1998.

Başar E, Ungan P. A component analysis and principles derived for the understanding of the evoked potentials of the brain: studies in the hippocampus. Kybernetik 1973;12:133–140.

Başar E, Gönder A, Özesmi Ç, Ungan P. Dynamics of brain rhythmic and evoked potentials. II. Studies in the auditory pathway, reticular formations and hippocampus during the waking stage. Biol Cybern 1975;20:145–160.

Başar E, Başar-Eroğlu C, Rosen B, Schütt A. A new approach to endogenous event-related potentials in man: relation between EEG and P300-wave. Int J Neurosci 1984;24:1–21.

Başar E, Başar-Eroğlu C, Röschke J, Schütt A. The EEG is a quasi-deterministic signal anticipating sensory cognitive tasks. In: Başar E, Bullock TH, editors. Brain dynamics, Berlin: Springer, 1989.

Başar E, Hari R, Lopes Da Silva FH, Schürmann M, editors. Brain alpha activity: new aspects and functional correlates. Int J Psychophysiol 1997;26:353–368.

Başar E, Rahn E, Demiralp T, Schürmann M. Spontaneous EEG theta activity controls frontal visual evoked potential amplitudes. Electroenceph clin Neurophysiol 1998;108:101–109.

Başar E, Başar-Eroğlu C, Karakaş S, Schürmann M. Are cognitive processes manifested in event-related alpha, theta and delta oscillations in the EEG? Neurosci Lett 1999a;259:165–168.

Başar E, Başar-Eroğlu C, Karakaş S, Schürmann M. Oscillatory brain theory: a new trend in neuroscience. IEEE Eng Med Biol 1999b;18(3):56–66.

Başar E, Demiralp T, Schürmann M, Başar-Eroğlu C, Ademoğlu A. Oscillatory brain dynamics, wavelet analysis and cognition. Brain Lang 1999c;66(1):146–183.

Başar-Eroğlu C, Başar E. A compound P300-40 Hz response of the cat hippocampus. Int J Neurosci 1991;60:227–237.

Başar-Eroğlu C, Başar E, Demiralp T, Schürmann M. P300-response: possible psychophysiological correlates in delta and theta frequency channels. A review. Int J Psychophysiol 1992;13:161–179.

Brandt ME, Jansen BH. The relationship between prestimulus alpha amplitude and visual evoked potential amplitude. Int J Neurosci 1991;61:261–268.

Brandt ME, Jansen BH, Carbonari JP. Pre-stimulus spectral EEG patterns and the visual evoked response. Electroenceph clin Neurophysiol 1991;80:16–20.

Cass M, Polich J. P300 from a single-stimulus paradigm: intensity and frequency effects. Biol Psychol 1997;46:51–65.

Cook III EW, Miller GA. Digital filtering: background and tutorial for psychophysiologists. Psychophysiology 1992;29:350–367.

Demiralp E, Başar E. Theta rhythmicities following expected visual and auditory targets. Int J Psychophysiol 1992;13:147–160.

Demiralp E, Başar-Eroğlu C, Rahn E, Başar E. Event-related theta rhythms in cat hippocampus and prefrontal cortex during an omitted-stimulus paradigm. Int J Psychophysiol 1994;18:35–48.

Demiralp T, Ademoğlu A, Schürmann M, Başar E. Wavelet analysis of brain waves (Chapter 5). In: Başar E, editor. Brain function and oscillations: I. Brain oscillations. Principles and approaches, Heidelberg: Springer-Verlag, 1998.

Demiralp T, Ademoğlu A, Schürmann M, Başar-Eroğlu C, Başar E. Detection of P300 in single trials by the wavelet transform (WT). Brain Lang 1999;66:108–128.

Donchin E, Coles MGH. Is the P300 component a manifestation of context updating? Brain Behav Sci 1988;11:357–374.

Duncan-Johnson CC, Donchin E. The time constant in P300 recording. Psychophysiology 1979;16:53–55.

Farwell LA, Martinerie JM, Bashore TR, Rapp PE, Goddard PH. Optimal digital filters for long-latency components of the event-related brain potential. Psychophysiology 1993;30:306–315.

Fruhstorfer H, Bergström RM. Human vigilance and auditory evoked responses. Electroenceph clin Neurophysiol 1969;27:346–355.

Fuster JM. Memory in the cerebral cortex: an empirical approach to neural networks in the human and nonhuman primate, Cambridge, MA: MIT Press, 1995.

Goldman-Rakic PS. Topography of cognition: parallel distributed networks in primate association cortex. Annu Rev Neurosci 1988;11:137–156.

Jansen BH, Brandt ME. The effect of the phase of prestimulus alpha activity on the averaged visual evoked response. Electroenceph clin Neurophysiol 1991;8:241–250.

Jasiukaitis P, Hakarem G. The effect of prestimulus alpha activity on the P300. Psychophysiology 1988;25:157–165.

Jervis BW, Nichols MJ, Johnson TE, Allen E, Hudson NR. A fundamental investigation of the composition of auditory evoked potentials. IEEE T Bio-Med Eng 1983;BME-30:43–49.

Johnson R. The amplitude of the P300 component of the event-related potentials: a review and synthesis. In: Ackles P, Jennings JR, Coles MGH, editors. Advances in psychophysiology: a research annual, 3. Greenwich, CT: JAI Press, 1988.

Karakaş S. A descriptive framework for information processing: an integrative approach. In: Başar E, Hari R, Lopes Da Silva FH, Schürmann M, editors. Brain alpha activity: new aspects and functional correlates. Int J Psychophysiol 1997;26:353–368.

Karakaş S, Başar E. Early gamma response is sensory in origin. A conclusion based on cross-comparison of results from multiple experimental paradigms. Int J Psychophysiol 1998;31(1):13–31.

Karakaş S, Başar-Eroğlu C, Özesmi Ç, Kafadar H, Erzengin ÖU. Gamma response of the brain: a multifunctional oscillation that represents bottom-up with top-down processing. Int J Neurosci 2000a in press.

Karakaş S, Erzengin ÖU, Başar E. The genesis of human event-related responses explained through the theory of oscillatory neural assemblies. Neurosci Lett 2000b;285(1):45–48.

Katayama J, Polich J. P300 from one-, two-, and three-stimulus auditory paradigms. Int J Psychophysiol 1996;23:33–40.

Klimesch W. EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. Brain Res Brain Res Rev 1999;29:169–195.

Klimesch W, Schimke H, Schwaiger J. Episodic and semantic memory: an analysis in the EEG theta and alpha band. Electroenceph clin Neurophysiol 1994;91:428–441.

Kolev V, Yordanova J. Analysis of phase-locking is informative for studying event-related EEG activity. Biol Cybern 1997;96:229–235.

Kramer AF, Strayer DL. Assessing the development of automatic processing: an application of dual-track and event-related brain potential methodologies. Biol Psychol 1988;26:231–267.

McClelland JL, Rumelhart DE, PDP Research Group, editors. Psychological and biological models. Parallel distributed processing. Explorations in the microstructure of cognition, vol. 2. Cambridge, MA: MIT Books, 1986.

McDonald M. A system for stabilizing evoked potentials obtained in the brain system of the cat. Med Electr Biol Eng 1964;2:417–423.

Mertens R, Polich J. P300 from single stimulus: modality and response effects. Electroenceph clin Neurophysiol 1997;104:488–497.

Mesulam MM. Large-scale neurocognitive networks and distributed processing for attention, language, and memory. Ann Neurol 1990;28(5):597–613.

Miller R. Cortico-hippocampal hippocampal interplay and the representations of contexts in the brain, Berlin: Springer, 1991.

Mountcastle V. Preface. In: Başar E, Bullock TH, editors. Induced rhythms of the brain, Berlin: Birkhauser, 1992.

Näätänen R. The role of attention in auditory information processing as revealed by event-related potentials and other brain measures of cognitive function. Behav Brain Sci 1990;13(2):201–288.

Näätänen R. Attention and brain function, London: Lawrence Erlbaum Associates, 1992.

Näätänen R, Picton T. N2 and automatic versus controlled processes. In: McCallum WC, Zappoli R, Denoth I, editors. Cerebral psychophysiology, Studies at event-related potentials (EEG Suppl 38). Amsterdam: Elsevier, 1986.

Näätänen R, Gaillard AWK, Mantysalo S. The orienting reflex and the N2 deflection of the event-related potential. In: Gaillard AWK, Ritter W, editors. Endogenous potentials of the brain. Amsterdam: North Holland, 1978.

Näätänen R, Simpson M, Loveless NE. Stimulus deviance and evoked potentials. Biol Psychol 1982;14:53–98.

Näätänen R, Schröger E, Karakaş S, Tervaniemi M, Paavilainen P. Development of a memory trace for a complex sound in the human brain. NeuroReport 1993;4:503–506.

Parnejford R, Başar E. Evoked delta oscillations on the hearing threshold. In: Başar E, editor. Brain function and oscillations: II. Integrative brain function. Neurophysiology and cognitive processes, Heidelberg: Springer-Verlag, 1999.

Parvin C, Torres F, Johnson E. Synchronization of single evoked response components: estimation and interrelation of reproducibility measures. In: Pfurtscheller G, Busser P, Lopes Da Silva F, Petsche H, editors. Rhythmic EEG activities and cortical functioning, Amsterdam: Elsevier, 1980.

Pfefferbaum A, Christensen C, Ford J, Kopell BS. Apparent response incompatibility effects on P3 latency depend on the task. Electroenceph clin Neurophysiol 1986;64:424–437.

Polich J. P300 in clinical applications: meaning, method and measurement. Am J EEG Tech 1991;31:201–231.

Polich J. P300 from a single auditory stimulus. Electroenceph clin Neurophysiol 1994;92:253–261.

Polich J. On the relationship between EEG and P300: individual differences, aging, and ultradian rhythms. Int J Psychophysiol 1997;26(1–3):299–317.

Polich J, Heine M. P300 topography and modality effects from a single stimulus paradigm. Psychophysiology 1996;3:747–752.

Polich J, Kok A. Cognitive and biological determinants of P300: an integrative review. Biol Psychol 1995;41:103–146.

Polich J, Margala C. P300 and probability: comparison of oddball and single stimulus paradigms. Int J Psychophysiol 1997;25:169–176.

Polich J, Eischen SE, Collins GE. P300 from a single auditory stimulus. Electroenceph clin Neurophysiol 1994;92:253–261.

Posner M. The psychobiology of attention. In: Gazzaniga M, Blakemore C, editors. Handbook of psychobiology, New York: Academic Press, 1975.

Pritchard WS, Brandt ME, Shapell SA, O'Dell TJ, Barratt ES. P300 amplitude/prestimulus EEG power relationships. Psychophysiology 1985;22:609–610.

Quiroga RQ, Schürmann M. Functions and sources of event-related EEG alpha oscillations studied with the wavelet transform. Clin Neurophysiol 1999;110(4):643–654.

Rahn E, Başar E. Prestimulus EEG activity strongly influences the auditory evoked vertex responses: a new method for selective averaging. Int J Neurosci 1993;69:207–220.

Robinson DL. The technical, neurological and psychological significance of 'alpha', 'delta' and 'theta' waves confounded in EEG evoked potentials: a study of peak latencies. Clin Neurophysiol 1999;110(8):1427–1434.

Romani A, Callieco R, Cosi V. Prestimulus spectral patterns and the evoked auditory vertex response. Electroenceph clin Neurophysiol 1988;70:270–272.

Röschke J, Mann K, Riemann D, Frank C, Fell J. Sequential analysis of the brain's transfer properties during consecutive REM periods. Electroenceph clin Neurophysiol 1995;96:390–397.

Rumelhart DE, McClelland JL, PDP Research Group, editors. Foundations. Parallel distributed processing. Explorations in the microstructure of cognition, vol. 1. Cambridge, MA: MIT Press, 1986.

Sannita WG. Stimulus-specific oscillatory responses of the brain: a time/frequency related coding process. Clin Neurophysiol 2000;111(4):565–583.

Schürmann M, Başar-Eroğlu C, Demiralp T, Başar E. A psychophysiological interpretation of theta and delta responses in cognitive event-related potential paradigms. In: Kruse P, Stadler M, editors. Ambiguity in mind and nature, Springer series in synergetics, 64. Berlin: Springer-Verlag, 1995.

Solodovnikov VV. Introduction to the statistical dynamics of automatic control systems, New York: Dover, 1960.

Stampfer HG, Başar E. Does frequency analysis lead to better understanding of human event-related potentials? Int J Neurosci 1985;26:181–196.

Sutton S, Braren M, Zubin J, John ER. Evoked potential correlates of stimulus uncertainty. Science 1965;150:1187–1188.

Yordanova J, Kolev V. A single sweep analysis of the theta frequency band during auditory oddball task. Psychophysiology 1998;35(1):116–126.