Theta rhythmicities following expected visual and auditory targets

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Evoked (EPs) as well as event-related potentials (ERPs) were recorded from two groups of 10 healthy, voluntary subjects in auditory and visual modalities. For ERP recordings ‘the omitted stimulus paradigm’ was employed, in which the subjects were expected to mark mentally the onset time (time prediction task) of the omitted stimulus (target). The standard auditory (AEP) and visual (VEP) evoked potentials and auditory and visual ERPs to the preceding stimuli of the omitted ones were analyzed in time and frequency domains. In the time domain the time prediction task induced increases of the amplitudes of waves existing in standard EPs; however, an additional wave or component could not be detected. Analysis of amplitude frequency characteristics (AFCs) revealed, however, selective, significant increases of the theta (3–6 Hz) frequency components of the responses concerned. These theta increases were especially evident in the frontal and parietal recording sites. Our findings suggest an association between the theta frequency components of transient evoked responses, the association areas of the brain and cognitive performance. The neurophysiological basis of scalp recorded ERPs are discussed in relation to the findings of animal studies with EEG and single unit recordings from cortical and subcortical structures.

INTRODUCTION

In the last two decades investigations showed that event-related potentials (ERP) consist of ‘exogenous’ and ‘endogenous’ components (Picton and Hillyard, 1974; Hillyard and Picton, 1979; Picton and Stuss, 1980; Bağar and Stampfer, 1985; Näätänen 1988). The term ‘exogenous component’ stands for a feature or component of the ERP which correlates with changing physical parameters of the stimuli and ‘endogenous component’ means a component which varies only in relation to the tasks given to the subject, which probably modulate intrinsic brain mechanisms in perceptual processes. During the development of this type of research, the endogenous components which correlate with higher hierarchical levels of information processing like attention, expectation or short as well as long term memories have been mostly differentiated from exogenous components in time and space.

Although a late ERP component following the early exogenous potentials with a latency shift of 250–400 ms called the P300 wave is the first important example of this kind of potential, there is evidence for faster endogenous components which probably cannot be detected in most paradigms used because they overlap with early exogenous components (Picton and Stuss, 1980; Desmedt et al., 1983; Näätänen, 1988; Bağar et al., 1991). Many solutions have been proposed to isolate spatiotemporally overlapping components (for a review see Picton and Stuss, 1980). According to the authors, isolation through experimental
Manipulation and factor analysis have been the most commonly used methods which have yielded objective results. However, these methods lack the physiological interpretability of the isolated components.

The central aim of this study is to detect the endogenous components of ERP which may not necessarily differ from the exogenous components in time and space by means of a method which is sensitive to changes in frequency components of the ERPs.

Başar et al. (1989) carried out a series of ERP studies on human subjects by applying a modified form of the omitted stimulus paradigm of Sutton et al. (1967). The paradigm consisted of auditory or visual stimulation having regular interstimulus intervals where some stimuli were omitted in a random or regular order with various degrees of probability. The subject's task was to mark mentally the time of the omitted stimulus. With this type of paradigm, especially when the stimulus omission occurred in a regular manner (for example every 4th stimulus was omitted), quasideterministic, reproducible patterns of EEG signal occurred anticipating the omitted stimulus. The subjects reported that they had paid attention to the rhythm of preceding stimuli to be able to fulfill the task.

In the present study we applied the same paradigm to test whether event-related changes occurred in different brain areas to the stimuli which precede or follow the omitted stimulus.

We show that the frequency analysis approach may differentiate responses to the stimuli which are coupled with a cognitive task from the standard EPs, detecting some specific changes in frequency components, whereas time domain analysis of the same responses shows no prominent differences.

METHODS

Subjects

The experiments were carried out with two different groups of subjects each consisting of 10 right-handed, healthy volunteers, mostly medical students 19–21 years of age, who had neither any known neurological deficit nor took any medica-ments known to affect the EEG.

Environment

The subject sat in a soundproof and echo-free room which was dimly illuminated. The room was also shielded to attenuate environmental electromagnetic noise effects. After electrode placement the subject was given a few minutes of rest to become familiar with the environment.

Data acquisition and equipment

The data were derived with Ag-AgCl disc electrodes placed on the frontal, vertex, parietal and occipital (F3, Cz, P3, O1) recording sites according to the international 10-20 system against the reference of earlobes. All electrode impedances were maintained at less than 5 KOhms. The EOG was also registered to mark eye movement artifacts. A detailed description of the EEG amplification, digitization and artifact elimination steps are given in a companion paper (Başar-Eroğlu et al., 1992).

The auditory stimuli were 80 dB, 1500 Hz tones (0.5 ms rise-time and 800 ms duration) presented binaurally. The light stimulator was a 20 W fluorescent bulb which was electrically triggered with steps of 800 ms duration.

Experimental paradigms

A regular recording session in three steps, with short resting periods in between, was carried out on the same day. Firstly the spontaneous EEG was registered for a few minutes, which served to determine global characteristics of the subject's spontaneous EEG activity and arousal state at the beginning of the experiments. It also enabled the subject to become familiar with the experimental conditions. For one group of subjects the auditory evoked potential (AEP) paradigm and omitted stimulus paradigm with auditory stimulation were applied. The same paradigms with visual stimulation, visual evoked potential (VEP) paradigm and omitted stimulus paradigm with visual stimulation, were applied to the second group of subjects to avoid any learning effect due to the similarity of the cognitive task in both sensory modalities.
A schematic illustration of both paradigms is shown in Fig. 1. In standard EP recordings, the interstimulus interval varied randomly between 2.5–4 s with a mean value of 3 s whereas in the omitted stimulus paradigm, the stimuli were delivered with 3 s regular intervals. In the omitted stimulus paradigm, every 4th stimulus was omitted and the subject's task was to predict and to mark mentally the time of occurrence of omitted signals. The task had not been told to subjects beforehand to avoid their unwanted cooperative efforts during the previous stages (EEG, EP) of the experiments.

Data analysis was based on the Combined EEG-EPogram Analysis method described in several previous publications of Başar et al. (Başar, 1980; Başar and Özesmi, 1972; Başar et al., 1975a, b, c). For a detailed description of the Combined EEG-EPogram Analysis method and the statistical tests used see the companion paper (Başar-Eroğlu et al., 1992).

RESULTS

Although no strategy for fulfilling the time prediction task was imposed, all subjects reported at the end of the experiments that their expectancy was highest to the 3rd stimulus (the predecessor of the omitted stimulus) in the omitted stimulus paradigm. They told that they could attain the rhythm of the stimulations just after the 2nd stimulus by comparing the onset times of the 1st and 2nd stimuli, and that they attended to the 3rd stimulus to test their feeling of the rhythm. The 1st stimulus after the omission served also as a control of their performance in the prediction of the virtual onset of the omitted stimulus. The responses to 1st stimulation after the omission were incomparable with other responses, because, from a strictly physical point of view, they followed twofold longer ISIs. These responses can be compared in another study with EPs recorded with longer ISIs (for example a pseudo-
Fig. 2. Superimposed standard VEPs (VEP) and responses to the 3rd attended light stimuli in the visual omitted stimulus paradigm (3. ATT) of 10 subjects obtained from frontal (F3), parietal (P3) and occipital (O1) regions.

Fig. 3. Superimposed standard AEPs (AEP) and responses to 3rd attended tones in the auditory omitted stimulus paradigm (3. ATT) of 10 subjects obtained from frontal (F3), parietal (P3) and vertex (Cz) regions.
Visual Stimulation  \( n = 10 \)

---: 3. ATT.

---: VEP

Fig. 4. Time-domain grand averages of standard VEPs (VEP) and responses to the 3rd attended light stimuli in the visual omitted stimulus paradigm (3.ATT) obtained from F3, P3 and O1 leads (upper part) and corresponding AFCs (lower part) \( (n = 10) \).

Auditory Stimulation  \( n = 10 \)

---: 3. ATT.

---: AEP

Fig. 5. Time-domain grand averages of standard AEPs (AEP) and of responses to 3rd attended tones in the auditory omitted stimulus paradigm (3.ATT) obtained from F3, P3 and Cz leads (upper part) and corresponding AFCs (lower part) \( (n = 10) \).
random series of intervals with a mean value of 6 s). In the preliminary data analysis the responses to 2nd stimuli have been found to show slight differences compared with the standard EPs. Considering these points and the subjects' reports we focused our attention on the comparison of the responses to the 3rd attended stimuli with standard EPs.

In both sensory modalities the responses obtained from four recording sites (F3, Cz, P3 and O1) have been analyzed. For limitations of space in the following figures data obtained from F3, P3 and O1 in visual modality and from F3, P3 and Cz in auditory modality are shown. Thus, data from two recording sites close to association areas (frontal-F3 and parietal-P3) and for each modality data from the location most commonly used to record the responses (occipital-O1 for visual and vertex-Cz for auditory modality) are given. However, the tables contain the results obtained in all four recording sites.

Averaged responses

The bottom row of Fig. 2 shows the averaged responses, superimposed, of 10 subjects recorded from F3, P3 and O1 leads upon application of the standard VEP paradigm. The upper row of the same figure illustrates the responses of the same subjects to the 3rd attended visual stimuli (3.ATT) in the visual omitted stimulus paradigm.

Fig. 3 shows analogous results derived from F3, P3 and Cz leads in similar paradigms but with acoustic instead of visual stimulation (AEP and 3.ATT). In both sensory modalities amplitudes of the responses increased when the subjects had to perform the time prediction task.

Amplitude frequency characteristics (AFCs)

In Figs. 4 and 5 the grand averages in the time domain and the AFCs obtained from the corresponding grand averages are shown.

Differences in frequency contents of responses obtained from various brain areas

In both sensory modalities the AFCs showed differences in frequency contents of evoked responses obtained from various recording areas. In VEPs elicited in occipital and parietal areas the alpha band activity was most prominent whereas in frontal VEP the difference between theta band amplitude and alpha band amplitude was smaller. On the other hand the low theta peaks with center frequencies around 3.5 Hz showed further differences in frontal, parietal and occipital regions. In the parietal area the theta band activity showed a homogeneous single peak, whereas in occipital recording a shoulder in 4 Hz and in frontal recording a similar side peak at 5 Hz were identified (Fig. 4, solid lines).

The AEPs showed at vertex a peak at 7 Hz with a shoulder in the alpha range (10 Hz) whereas in the parietal region 7 Hz as well as 10 Hz activities were at the same level with another side peak occurring at 4 Hz. The frontal area showed a concave shape in the 3–6 Hz band (Fig. 5, solid lines). Differences in the frequency contents of the EPs obtained from primary sensory areas and nonprimary areas of the brain in these sensory modalities have been studied in a recent paper of Başar et al. (1991). Therefore, we will not go further into the description of these differences.

Differences between the grand averages and AFCs of evoked and the 3rd attended responses

Comparison of the grand averages indicated increases in the amplitudes of the N100-P200 complex and the N140-P200 complex in responses to the 3rd attended stimuli compared with the standard EPs in auditory and visual modalities respectively. However, the wave shapes were quite similar and any components which differed temporally from the peaks and valleys of the standard EPs were not detected. In AFCs an increase in the theta frequency band between 3–6 Hz was observed. However, alpha response amplitude (6–13 Hz to acoustical stimulation and 8-15 Hz to visual stimulation) kept the same magnitude or decreased in all recording locations (Figs. 4 and 5, dashed lines).

The previous results of Başar et al. (1991) showed that the responses of nonprimary areas to visual or acoustical stimulation consisted mainly of theta rhythmicities while those of primary sensory areas were of the alpha frequency range. Accordingly, we have focused our attention on
changes in theta and alpha components of EPs and ERPs.

Adaptive filtering of evoked responses

The averaged responses were filtered in various frequency bands by means of digital filters with zero phase-shift. The filter band limits were selected according to the maxima in AFCs. Fig. 6 shows the VEPs and the responses to the 3rd attended light stimuli (3.ATT) in the omitted stimulus paradigm (superimposed) and the grandaverages obtained in both conditions filtered in the theta frequency band (3-6 Hz). Fig. 7 shows the analogous results in the auditory modality. In the case of the experiments with the time prediction task (3.ATT) an evidently consistent increase in the amplitude of theta oscillation was observed especially in the frontal (F3) and parietal (P3) areas. Alpha and beta band responses showed no consistent change. Therefore, these waveforms are not illustrated, but these frequency components are included in the following histograms and tables (Figs. 8 and 9, Tables I and II).

For statistical evaluation of these results, the maximum amplitudes of the oscillations of a certain frequency band in the first 250 ms of the evoked responses were measured, and the differences between the values obtained in standard EPs and responses to the 3rd attended stimuli were tested via the Wilcoxon-test for paired differences. The median values and 95% confidence intervals of amplitudes of theta, alpha and beta components of EPs and the responses to the 3rd attended stimuli obtained in all four recording sites are displayed in histograms in Figs. 8 and 9. The medians of the amplitudes of these frequency components, the percent change between both conditions (percent of the standard EP amplitude) and corresponding significance levels are given in Tables I and II in visual and auditory modalities respectively. The percent values are based on the median values.

![Visual Stimulation](https://example.com/visual_stimulation)

Filter: 3 - 6 Hz

\[5 \mu V\]
\[2.5 \mu V\]
\[0\] 250 500 ms

3.ATT

\[5 \mu V\]
\[2.5 \mu V\]
\[0\] 250 500 ms

VEP

\[5 \mu V\]
\[2.5 \mu V\]
\[0\] 250 500 ms

F3

\[n = 10\]

\[5 \mu V\]
\[2.5 \mu V\]
\[0\] 250 500 ms

P3

\[n = 10\]

\[5 \mu V\]
\[2.5 \mu V\]
\[0\] 250 500 ms

O1

Fig. 6. Superimposed standard VEPs (VEP) and responses to the 3rd attended light stimuli in the visual omitted stimulus paradigm (3.ATT) of 10 subjects and their grand averages filtered in theta frequency band (3-6 Hz).
The amplitudes of theta oscillations in responses to the 3rd attended stimuli in visual modality showed an increase of 48% of the standard VEP in the frontal region ($P < 0.01$) and 45% of the standard VEP in the parietal region ($P < 0.05$). In vertex and occipital areas there were also significant increases of theta components but they were less ample in comparison to frontal and parietal responses (Cz: 26%, $P < 0.05$ and O1: 11%, $P < 0.05$). Alpha and beta band amplitudes showed statistically insignificant decreases in all recording sites.

In the auditory modality there were also significant increases of theta components in frontal and parietal regions (F3: 44%, $P < 0.01$ and P3: 10%, $P < 0.05$). The parietal theta increase was, however, less in comparison to responses in the visual modality. In vertex and occipital regions no significant changes in theta components were observed between AEPs and responses to the 3rd attended tones. Alpha and beta components showed no significant changes in any of the recording sites.

**DISCUSSION**

*Topographical differences in the frequency contents of EPs*

Differences in frequency contents of EPs obtained from different brain locations suggest that responses recorded in different areas of the brain might originate from different neuron populations with possible different functional meanings.

Başar et al. (1991) assumed the impossibility of designing a pure sensory or pure cognitive paradigm in EP research. Even under minimal conditions necessary for sensation, the higher cognitive functions of the brain are not totally rejected. On the other hand, a well defined cognitive performance needs to be controlled by certain physical events as an interface between

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**Fig. 7.** Superimposed standard AEPs (AEP) and responses to the 3rd attended tones in the auditory omitted stimulus paradigm (3.ATT) of 10 subjects and their grand averages filtered in the theta frequency band (3-6 Hz).
the internally running events in the subject’s brain and the experimenter. Therefore, with the standard EP procedures, besides sensory processing, various cognitive processes come into play. Recent studies of Posner and Petersen (1990) have emphasized the topographical characteristics of cognitive processing. Goldman-Rakic (1988) showed in a neuroanatomical study parallel distributed networks in the primate association cortex. The assumption of Başar et al. (1991) together with the results of the psychological and neuroanatomical studies mentioned above (Posner and Petersen, 1990; Goldman-Rakic, 1988) suggest a distributed sensory-cognitive parallel processing system in the brain. In such a system the primary sensory processes and various associative or cognitive functions might be coactivating in different brain structures during the perception of a physical stimulus. This type of distributed parallel processing could be responsible for differences in frequency contents of responses obtained in different locations.

**Increases in N1-P2 amplitudes**

Our results about the increases in the N100-P200 amplitudes in responses to the 3rd attended stimuli compared with the standard EPs in the auditory modality support the findings of Picton and Hillyard (1974). Picton and Hillyard reported a substantial increase in N100 and P200 components of the auditory evoked potential if attention was directed toward auditory stimuli in order to detect an occasional fainter 'signal' stimulus, and interpreted this finding as an enhancement of exogenous, obligatory N100 generator activity. However, Näätänen (1988) suggested that this increase in N100-P200 amplitude could be caused by a superimposition of the processing negativity, an endogenous component generated by a different mechanism than the exogenous, obligatory N100 generator mechanism. Desmedt et al. (1983) reported P100 enhancement and appearance of new components, P40 and N60 in responses to 'infrequent target' signals by somatosensory stimulation. Hillyard and Picton (1979) showed P1 and N1 enhancement in VEPs during spatial visual attention tasks.

In the present study, attention was not directed to qualitative changes but to the onset of the stimuli. In our paradigm where every 4th stimulus was omitted and the virtual onset of the omitted stimulus was to be marked mentally, the subjects attended especially to the onset of the 3rd stimulus with a high expectancy. According to the subjects' reports, which they offered at the end of each experiment, they had developed the expectancy by marking the distance between the 2nd and the 1st stimuli. In this type of cognitive task, where the attention of the subjects was directed by their own initiative to the onset of the 3rd stimulus, we also registered an increase of the N100-P200 complex in auditory and N140-P200 complex in visual responses to the 3rd stimuli. These changes are, probably, not due to the pro-

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*Fig. 8. Medians and 95% confidence intervals of the amplitudes of theta (3–6 Hz), alpha (8–15 Hz) and beta (15–30 Hz) components of standard VEPs (VEP) and responses elicited by the 3rd attended light stimuli in the visual omitted stimulus paradigm (3.ATT).*

*: p < 0.05
**: p < 0.01

□️: VEP
####: 3. ATT.
cessing of the stimulus characteristics and/or decision making but due to expectancy and attention directed to the stimulus onset.

*Increase of the theta-response*

In further analysis in the frequency domain we found that the increase in the amplitudes of responses was mainly affected by the selective enhancement of the theta components. The same theta increase is seen in both auditory and visual modalities. This change in the low frequency components of the ERP is modality independent.

Başar and coworkers (Başar, 1980, 1988; Başar and Özsesi, 1972; Başar et al., 1975a, b, c) have shown that sensory EPs might be considered as a superimposition of wave packets in various frequencies with varying degrees of frequency stabilization, enhancement and time locking within conventional frequency bands of the ongoing EEG activity. Furthermore, the authors showed that these phenomena can occur interindependently in various frequency bands in separate applications of the stimulus (sweeps) along an ERP recording. “These variations support the hypothesis that different neural or psychophysiological mechanisms come into operation following stimulation” (Stampfer and Başar, 1985).

In a recent study Başar et al. (1991) emphasized that the response of a primary sensory area consisted mainly of an enhancement in the alpha (8–13 Hz) frequency band to adequate stimuli whereas its response to inadequate stimulation was dominated by theta activity. The authors found a parallelism between these findings and

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![Bar chart](image.png)

*Fig. 9. Medians and 95% confidence intervals of the amplitudes of theta (3–6 Hz), alpha (6–13 Hz) and beta (15–30 Hz) components of standard AEPs (AEP) and responses elicited by the 3rd attended tones in the auditory omitted stimulus paradigm (3.ATT).*
TABLE I

Medians of the amplitudes of theta (3–6 Hz), alpha (8–15 Hz) and beta (15–30 Hz) frequency components of standard VEPs (VEP) and responses elicited by the 3rd attended light stimuli in the visual omitted stimulus paradigm (3.ATT)

Percent changes of amplitudes between two conditions (as the percent of the standard VEP amplitude) are given in the parentheses and significant differences are marked by symbols (* P < 0.05, ** P < 0.01).

<table>
<thead>
<tr>
<th></th>
<th>Theta (3–6 Hz)</th>
<th>Alpha (8–15 Hz)</th>
<th>Beta (15–30 Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>F3</td>
<td>VEP</td>
<td>4.6</td>
<td>3.5</td>
</tr>
<tr>
<td></td>
<td>3.ATT</td>
<td>6.8</td>
<td>3.0</td>
</tr>
<tr>
<td></td>
<td>(48%) **</td>
<td>(−13%)</td>
<td>(−7%)</td>
</tr>
<tr>
<td>Cz</td>
<td>VEP</td>
<td>6.7</td>
<td>4.8</td>
</tr>
<tr>
<td></td>
<td>3.ATT</td>
<td>8.4</td>
<td>3.8</td>
</tr>
<tr>
<td></td>
<td>(26%) *</td>
<td>(−19%)</td>
<td>(−12%)</td>
</tr>
<tr>
<td>P3</td>
<td>VEP</td>
<td>3.1</td>
<td>4.4</td>
</tr>
<tr>
<td></td>
<td>3.ATT</td>
<td>4.5</td>
<td>4.2</td>
</tr>
<tr>
<td></td>
<td>(45%) *</td>
<td>(−3%)</td>
<td>(−25%)</td>
</tr>
<tr>
<td>O1</td>
<td>VEP</td>
<td>4.5</td>
<td>5.2</td>
</tr>
<tr>
<td></td>
<td>3.ATT</td>
<td>4.9</td>
<td>4.2</td>
</tr>
<tr>
<td></td>
<td>(11%) *</td>
<td>(−20%)</td>
<td>(0%)</td>
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TABLE II

Medians of the amplitudes of theta (3–6 Hz), alpha (6–13 Hz) and beta (15–30 Hz) frequency band components of standard AEPs (AEP) and responses elicited by the 3rd attended tones in the auditory omitted stimulus paradigm (3.ATT)

Percent changes of amplitudes between two conditions (as the percent of the standard AEP amplitude) are given in the parentheses and significant differences are marked by symbols (* P < 0.05, ** P < 0.01).

<table>
<thead>
<tr>
<th></th>
<th>Theta (3–6 Hz)</th>
<th>Alpha (6–13 Hz)</th>
<th>Beta (15–30 Hz)</th>
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<tr>
<td>F3</td>
<td>AEP</td>
<td>4.7</td>
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<tr>
<td></td>
<td>3.ATT</td>
<td>6.7</td>
<td>6.1</td>
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<tr>
<td></td>
<td>(44%) **</td>
<td>(26%)</td>
<td>(−17%)</td>
</tr>
<tr>
<td>Cz</td>
<td>AEP</td>
<td>8.2</td>
<td>7.9</td>
</tr>
<tr>
<td></td>
<td>3.ATT</td>
<td>9.5</td>
<td>7.9</td>
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<tr>
<td></td>
<td>(16%)</td>
<td>(0%)</td>
<td>(−3%)</td>
</tr>
<tr>
<td>P3</td>
<td>AEP</td>
<td>4.0</td>
<td>3.9</td>
</tr>
<tr>
<td></td>
<td>3.ATT</td>
<td>4.4</td>
<td>4.9</td>
</tr>
<tr>
<td></td>
<td>(10%) *</td>
<td>(26%)</td>
<td>(−5%)</td>
</tr>
<tr>
<td>O1</td>
<td>AEP</td>
<td>2.3</td>
<td>2.8</td>
</tr>
<tr>
<td></td>
<td>3.ATT</td>
<td>2.3</td>
<td>3.5</td>
</tr>
<tr>
<td></td>
<td>(0%)</td>
<td>(26%)</td>
<td>(5%)</td>
</tr>
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</table>

studies which showed that primary sensory stimuli elicit impulses or volleys converging over thalamic centers to primary sensory areas, whereas the 'sensory stimulation of second order' usually reaches the cortex over association areas (Shepherd, 1988). In this framework the theta dominance during inadequate stimulation of a primary sensory area was interpreted as a possible manifestation of responsiveness of various brain areas in cases of association processes involved in global associative cognitive performance. Mizuki et al. (1980) showed that the midline prefrontal region of the cortex generated regular theta rhythms during the performance of simple repetitive mental arithmetic tasks.

The increases in the theta components of the ERPs in comparison to standard EPs is in agreement with the results of Başar et al. (1991) and Mizuki et al. (1983) mentioned above. Our findings supplement these results in terms of a probable functional assignment to theta band activity. Considering theta dominance in responses of primary sensory areas to inadequate stimulation and the appearance of theta rhythms in EEG recorded in association areas during mental tasks together with our results, we incline to explain that neural circuits which perform associative functions share a common information channel which operates in the theta frequency range.

Furthermore, topographical differences in weights of increases of theta components in ERPs suggest an association between the investigated cognitive function, the frequency content of the ERP and the topography of the frequency components.

**Topography of theta increases in ERPs**

*Increase of theta components is highest in frontal recordings.* The highest, statistically significant, theta increases during cognitive performance were obtained in frontal and parietal recording sites. In the auditory modality, the theta increase was absolutely dominant in the frontal area (44% increase) whereas in the visual modality the theta increase in the frontal recording site was slightly higher than that in the parietal recording site (48% versus 45%). This selectivity has a parallelism with the results of Fuster (1991). Studies of
Fuster are based on single unit recordings in prefrontal cortex of monkeys, which showed a high anticipatory activation level of frontal neurons in time delay tasks. Since the cognitive task in our study was also mainly based on anticipation to an expected stimulus, it is not surprising that the greatest changes are in frontal regions.

Our findings showing the strong participation of the frontal cortex in fulfilling a cognitive task are also in accordance with the results of Knight et al. (1981) on patients with frontal cortex lesions. Results of these studies indicated that the frontal lobes exhibited a modulating influence upon the endogenous negativity of ERPs produced in selective attention tasks.

In the visual modality the secondary dominant theta increase occurs in parietal recordings. The parietal area was the secondary dominant theta center in the visual modality with a percent theta increase slightly below that obtained in the frontal area (45%) whereas in the auditory modality the increase of parietal theta activity was not so prominent (10%). This property of the visual ERP is in accordance with the specific functions of parietal cortex in visual information processing, as shown by means of cellular measurements on macaque monkeys (Mountcastle et al., 1975; Lynch et al., 1977). According to Mountcastle, 50% of the investigated neurons in the parietal association area 7 of the inferior parietal lobe are visual fixation cells which are active as the animal looks at visual targets that are linked by a strong motivational drive; the rest of the neuronal elements are light-sensitive with large and bilateral receptive fields (Yin and Mountcastle, 1977; Robinson et al., 1978). Lynch et al. (1977) suggest that the neurons in posterior parietal cortex are involved in selective visual attention processes. Mountcastle et al. (1981, 1984) showed that the enhanced responsiveness of light-sensitive neurons in the inferior parietal lobe does not merely occur with changes in general arousal but is more specifically related to the visual attention directed to the target light. Petersen et al. (1988) showed by means of positron emission tomography similar effects in the parietal cortex of normal humans.

The specific parietal theta increase we observed during visual perception in an attentive state with high expectation supports the view of Başar and Stampfer (1985) that the activity of neuronal populations involved in specific stages or parts of perceptual processes use different frequency channels, and hence these specific activities can be differentiated by means of the frequency analysis applied to the surface recorded evoked responses.

**Cognitive theta components of ERPs as a sign of hippocampo–cortical interaction**

Neuroanatomical studies show that the main thalamic input to the frontal cortex stems from the limbic system (Creutzfeldt, 1983). Hippocampus, which has been shown to play a key role in memory storage and learning (Zola-Morgan and Squire, 1990), is an important part of the limbic system.

The hippocampal theta rhythm is a well-established phenomenon (Elazar and Adey, 1967a, b). In studies of the authors on cats with intracranially implanted electrodes, it was shown that after application of a learning paradigm the coherences between hippocampus, subcortical and cortical structures (i.e., visual cortex) followed consistent patterns in the theta range upon sensory stimulation. Başar-Eroğlu et al. (1991a, b) showed using intracranial recordings carried out on awake freely moving cats that in various layers of the hippocampus theta responses occurred, which were temporally correlated with the P300 wave of the surface recorded ERP.

In the light of these results, our finding of an increased theta response in the surface recorded ERPs of frontal recording sites during the time prediction task might be a manifestation of a cooperative, associative activity of frontotemporal structures. These results will be discussed more in detail in a companion paper (Başar-Eroğlu et al., 1992).

**CONCLUSION**

Our results indicate the importance of the frequency analysis approach in identifying various psychophysiological components of ERPs. Similar
waves with similar latencies and amplitudes in the time-domain analysis can show differences and very simply be identified in frequency-domain presentation of the signal. Furthermore, such an analysis of surface recorded potentials in well designed human psychological experiments can be put together with those of subcortical recordings on animals showing characteristic rhythmic activity of deeper structures. This approach can lead to a better neurophysiological understanding of the surface recorded potentials obtained during various cognitive performances. To prove the method's abilities, it should be tested on a variety of well established time domain phenomena occurring in various ERP paradigms.

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