On the basis of a systems theoretical approach it was hypothesized that event-related potentials (ERPs) are superpositions of stimulus-evoked and time-locked EEG rhythms reflecting resonance properties of the brain (Başar, 1980). This approach led to frequency analysis of ERPs as a way of analyzing evoked rhythms. The present article outlines the basic features of ERP frequency analysis in comparison to ERP wavelet analysis, a recently introduced method of time-frequency analysis. Both methods were used in an investigation of the functional correlates of evoked rhythms where auditory and visual ERPs were recorded from the cat brain. Intracranial electrodes were located in the primary auditory cortex and in the primary visual cortex thus permitting “cross-modality” experiments. Responses to adequate stimulation (e.g., visual ERP recorded from the visual cortex) were characterized by high amplitude alpha (8–16 Hz) responses which were not observed for inadequate stimulation. This result is interpreted as a hint at a special role of alpha responses in primary sensory processing. The results of frequency analysis and of wavelet analysis were quite similar, with possible advantages of wavelet methods for single-trial analysis. The results of frequency analysis as performed earlier were thus confirmed by wavelet analysis. This supports the view that ERP frequency components correspond to evoked rhythms with a distinct biological significance.

Key Words: EEG; evoked potential; event-related potential; frequency analysis; wavelet analysis; evoked rhythm.
1. INTRODUCTION

According to our long-standing working hypothesis, event-related potentials\(^1\) (ERPs) are due to a superposition of stimulus-induced and time-locked EEG rhythms and thus reflect resonance properties of the EEG (Başar, 1972, 1980, 1998a, 1998b). Resonance is the response that may be expected of underdamped systems when a periodic signal of a characteristic frequency is applied to the system, with “surprisingly” large output amplitudes for relatively small input amplitudes. Since the EEG rhythms\(^2\) are natural frequencies of the brain (and not noise, see Başar, 1990), the analysis of brain resonance phenomena must be strongly taken into account to understand brain responses. These results and interpretations were reached by means of ERP analysis in the frequency domain as introduced by Başar (1972) two decades ago. Başar and co-workers, by leaning on experimental data from intracranial recordings of the cat brain, have further introduced the concept of synchronized resonances (or synchronized selectivities). Later the same research group introduced the concept of diffusely distributed oscillatory systems in the brain (in the delta, theta, alpha, and gamma frequency ranges). In recent years, the introduction of the wavelet transform to signal analysis has brought an important advance, and this method has also been successfully applied for the analysis of brain signals according to properties of brain waves (Heinrich, Gaus, & Dickhaus, 1991; Bartnik, Blinowska, & Durka, 1992; Samar, Swartz, & Raghuvir, 1995; Ademoglu, 1995; Demiralp, Ademoglu, & Başar, 1995). The goal of the present article is multifold:

1. The theoretical foundation, conceptual basis, and principal application of ERP frequency analysis will be didactically presented.
2. The physiological relevance of ERP frequency components will be explained. This task will be done by giving cross-modality experiments as an example.
3. The results of such cross-modality experiments—obtained by means of “conventional” ERP frequency analysis (digital filtering, etc.) and wavelet analysis—will be presented.
4. Results of wavelet analysis will be compared to results of conventional frequency analysis.
5. The concept of diffusely distributed oscillatory systems in the brain will be discussed in relation to problems of perceptual binding.

In the present report, we will first outline the theoretical basis and the principal methods of frequency domain analysis of ERPs in the framework of the “Brain Dynamics Research Program.” Furthermore, the background and

---

1 This term also comprises evoked potentials.
2 In the frequency ranges: delta, 0.5–3.5 Hz; theta, 4–7 Hz; alpha, 8–15 Hz; beta, 15–30 Hz; gamma, 30–80 Hz (also referred to as “40-Hz range”).
principles of ERP analysis by means of wavelet transformation will be intro-
duced. The methods and results of auditory and visual ERP measurements
in the auditory and visual cortices and hippocampus of the cat brain will be
presented. These results and the role of oscillatory responses for cognition
will be discussed in relation to the cross-modality concept and in the theoreti-
cal framework of systems analysis and brain dynamics.

1.1. Resonance Phenomena in the Brain and Methods of Investigation

Concerning resonance phenomena in general, *Galilei* (Discorsi a Due Nu-
ove Scienze, 1638) stated,

First of all one must observe that each pendulum has its own time of vibration, so
definite and determinate, that it is not possible to make it move with any other period
than that which nature has given it. On the other hand one can confer motion upon
a heavy pendulum which is at rest by simply blowing against it. By repeating these
blasts with a frequency which is the same as that of the pendulum one can impart
considerable motion.

During the period between 1970 and 1980 Başar and co-workers developed
a theory of general resonance phenomena in the brain. This theory took into
account pioneer experiments performed by van der Tweel (1961), Spekreijse
and van der Tweel (1972), Lopes da Silva, van Rotterdam, Storm van Leeu-
wen, and Tielen (1970a, 1970b), and Regan (1966). With respect to the brain,
resonance is defined as the ability of brain networks to facilitate (or activate)
electrical transmission within determined frequency bands, when an external
sensory stimulation signal is applied to the brain (Başar, 1972, 1980). Ac-
cording to this approach, different neural populations activated during the
information processing in the brain in a parallel and/or sequential manner
show resonant behavior in a frequency range depending on their innate oscil-
latory properties. The activation times and durations of various brain struc-
tures involved in the process might also show considerable differences (for
a review of oscillations at the cellular level, see Llinas, 1988). The result of
the superposition of these activation patterns or *evoked rhythms* builds up
the ERPs measured by using macroelectrodes in these brain structures or on
the surface of the scalp. (As an example of an evoked rhythm, we refer to
the *alpha response*, an oscillatory response in the alpha frequency range in
the first 200 to 300 ms after stimulus.) Similar concepts of ERPs as brain
resonance phenomena have been used by other research groups (Dettmar &
Volke, 1985; Klauck, Heinrich, & Dickhaus, 1990; Röschke & Aldenhoff,
1991; Röschke, Mann, Riemann, Frank, & Fell, 1995).

1.2. Experimental Approaches at Resonance Phenomena of the Brain

In the classical way of describing resonance phenomena the system to be
analysed is *stimulated with sinusoidal input functions*. Thus, the investigator
finds the system’s *frequency characteristics* (or transfer function) and, in
particular, its maximal responsiveness (or maximal transmission) in a given preferred frequency.

Usually, physiologists prefer the method of transient analysis. This method consists of the study of a system by application of either step or impulse functions at the input of the system. The method of transient responses has the following advantages: the observer immediately sees the responses of the system under study when sudden changes (jumps or steps) in the input function occur. The greatest disadvantage of the method stems from the fact that distinct components of the system studied are not visible in the transient response. When two, three, or more components exist in the system response, the observer cannot distinguish these different components without further mathematical analysis.

Başar and co-workers (Başar, 1972; Başar, Gönder, Özesmi, & Ungan, 1975a, 1975b; Başar, 1980), however, have used a different approach, which overcomes this disadvantage and is based on a procedure widely used in the analysis of dynamic systems. The frequency characteristics of a system can be computed by (1) "stimulating" the system with an impulse or step function, (2) recording the transient response, and (3) applying standard Fourier techniques to the transient response revealing the characteristic frequencies of the system ("transient response frequency characteristics," see Başar, 1980 for details). This has been the starting point for asking questions about the distinctiveness and functional significance of those characteristic frequencies.

1.2.1. Combined Analysis Procedure: Frequency Domain Analysis of ERPs

The general methodology for the frequency domain analysis of spontaneous EEG activity and ERPs can be outlined as follows (see Başar, 1980 for details; see under Methods for a concrete example including technical details; an overview is given in Fig. 1):

1. A sample of the spontaneous activity of the studied brain structure just prior to the stimulus is recorded and stored in the disk memory of the computer.

2. A stimulation signal is applied to the experimental animal (or human subject). This signal may be a light flash or an acoustical stimulation, for example, an auditory step function in the form of a tone burst of 2000 Hz and 80 dB.

3. The single evoked response following the stimulation is also stored in the disk memory. (The EEG just prior to the stimulation and the resulting

---

1 Based on a decomposition onto sinusoidal and cosinusoidal basis functions.

2 Although this method is applicable only to linear systems it is also useful for the analysis of nonlinear systems with regard to a primary global approach.
ERP are stored together as a combined record, the so-called, "EEG-ERPogram".

4. The operations explained in the three steps above are repeated about 100 times. (The number of trials depends on the nature of the experiment and the behavior of the subject or the experimental animal.)

5. The "raw" ERPs stored in the disk memory of the computer are averaged using offline selective averaging as described previously (Başar, 1980; Başar et al., 1975a), i.e., epochs showing movement artifacts, sleep spindles, or slow waves were eliminated.

6. The selectivity averaged ERP is transformed to the frequency domain with the Fourier transform in order to obtain the amplitude frequency characteristics $|G(j\omega)|$ of the studied brain structure. This results in a plot of the
individual frequencies that comprise the ERP against the log of the frequency over the entire range of available frequencies.

7. The frequency band limits of the amplitude maxima (component peaks) in $|G(j\omega)|$ are measured and used to define the ideal filter characteristics in order to isolate each component.

8. The stored and selected epochs of EEG-ERPograms are filtered with the properly chosen filters described in step 7. In other words, a time domain weighting function is obtained by means of an inverse Fourier transform and convoluted with the ERP in order to extract the band-limited time-domain component of interest (e.g., the theta component, 4–7 Hz, the alpha component, 8–15 Hz).

1.3. Wavelet Analysis

Recently, a new technique called the wavelet analysis has often been used by engineers, physicists, and mathematicians who are interested in performing signal analysis in the frequency domain (see Samar et al., 1995, for discussion).

The wavelet transform is a powerful tool for the time-frequency (or time-scale) representation of a time series. Especially, when dealing with transient and non-stationary signals such as ERPs, the identification of the onset point and duration of a certain frequency component or a functional component within a certain frequency band in the time series gains importance beyond the information on the frequency content of the whole epoch in general. Considering also the working hypothesis of resonance phenomena in the brain, the time-frequency representation of the brain signals gains extreme importance.

The conventional frequency domain analysis methods based on the Fourier transform assume the stationarity of the processed signal epoch and estimate the mean weight of different frequency components in the whole epoch. The basic model applied makes use of sinusoidal basis functions in the decomposition of the time-series into frequency components. However, when dealing with signal epochs containing transient components with varying frequency contents, durations, and on-set times, an approach is necessary which can detect time-dependent changes in the frequency content of the signal.

A first approach for the time-frequency representation of a time series is the short-time Fourier transform which divides the time domain into uniformly spaced epochs and applies Fourier transform to these intervals. The basic decomposition model applied in each of these intervals is again based on stationary sinusoids. However, the wavelet transform as a more general form of time-scale analysis methods can use basis functions having compact support (well-localized in time). Additionally, instead of using uniformly spaced time and frequency windows, the wavelet transform makes use of logarithmically ordered frequency bands which require shorter time intervals.
for higher frequencies and longer time intervals for lower frequencies (see Demiralp et al., 1999).

1.4. Cross-Modality Experiments—A Tool for Investigating Functional Roles of ERP Frequency Components

Once the frequency components are obtained in the way outlined above, the following question arises: Can we distinguish separate functional roles of frequency components? For the analysis of functional meanings of frequency components, a number of paradigms are established, most of them cognitive ERP paradigms, e.g., the well-known P300 paradigms (for a review, see, e.g., Başar-Eroğlu, Başar, Demiralp, & Schürmann, 1992). The recent results of our group further showed that the time-locking and enhancement of these frequency responses depend on the following (and possibly further) parameters:

1. task relevance (oddball, 3rd attended signal in the omitted stimulus paradigm, Demiralp & Başar, 1992; Başar-Eroğlu et al., 1992)
2. topography (Schürmann & Başar, 1994)
3. species (human subjects or animals, Schütt, Başar, & Bullock, 1992; Schütt & Başar, 1992)

For the present study, we measured plain sensory ERPs with additional topographical information (Schürmann & Başar, 1994; Başar & Schürmann, 1994): We performed cross-modality experiments by recording EEG-ERP epochs with intracranial electrodes in primary sensory cortical areas of the cat brain. When applying auditory stimuli, these stimuli were adequate for the auditory cortex and inadequate for the visual cortex. (‘‘Adequate stimulation’’ refers to sensory stimulation that directly excites the receptors and ascending pathways of a primary sensory system (e.g., visual stimuli directly excite the visual system). ‘‘Inadequate stimulation’’ refers to sensory stimuli that, via cross-modal interaction beyond the receptor level of the primary sensory system for those stimuli, may indirectly excite a different sensory system.)

As outlined above, the approach used in our earlier studies and in the present study is based on frequency domain analysis of ERPs consisting of two main steps:

1. Computation of the amplitude frequency characteristics (AFCs) by transforming the averaged ERP to the frequency domain.
2. Digital filtering with filter limits chosen adequately according to the amplitude frequency characteristics.
In the present study, additionally, we will apply the wavelet transform (WT)—as characterized above—to the same data in order to compare the results of both conventional and novel techniques. Wavelet analysis is, as yet, seldom applied in brain research, although it is now very popular in mathematical and engineering sciences.

2. METHODS

Intracranial EEG/ERP measurements were carried out in $N=6$ cats with implanted electrodes in the auditory cortex (Gyrus ectosylvianus anterior, GEA), occipital cortex (OC), and hippocampus (HI). For details concerning electrode positions and surgery, the reader is referred to Başar-Eroğlu, Başar, & Schmielau (1991a).

2.1. Data Acquisition and Experimental Design

EEG amplification. All data were amplified by means of a Schwarzer EEG machine with a time constant of 0.3 s. A low-pass filter with cut-off frequency at 70 Hz ($-24$ dB/octave) was applied to data to avoid aliasing in the following digitization step.

Digitization of the EEG. After the application of the above-mentioned anti-aliasing filters to the analog signal, 1 s pre- and 1 s post-stimulus EEG were digitized with a sampling rate of 500 points/s and stored on the hard-disk of the computer.

Data recording and stimulation were controlled by a HP 1000 F computer, which was also used for the off-line analysis of the data.

Artifact rejection. Two artifact rejection procedures were applied in addition to the manual off-line selective averaging: (1) Trials with high amplitudes (i.e., blocking the amplifier or exceeding the analog-to-digital converter’s range) were rejected. (2) The EEG was monitored and recorded continuously on paper during the experiments and the subjects were observed via closed circuit TV, so that the technician could mark the trials with artifacts during the recording. It is also possible to pause the recording procedure by a button press, if long-lasting artifacts occur in the EEG.

Stimulations. Auditory stimuli were tone bursts of 1000 ms duration, 2000 Hz frequency, and 80 dB sound pressure level. The rise time was 0.5 ms. Auditory stimuli were presented binaurally via loudspeakers. The light stimulator was a 20-W fluorescent bulb which was electrically triggered. The duration of the light step was also 1000 ms.

Cross-modality experiments. The above-mentioned stimuli permitted adequate and inadequate stimulation of both the auditory and visual cortices.

2.2. Data Analysis: Amplitude Frequency Characteristics and Digital Filtering for the Investigation of Brain Resonance Phenomena

Amplitude frequency characteristics were obtained as described above. For the subsequent digital filtering, fixed filter limits were used rather than determining the bands adaptively in order to match the band limits, as closely as possible, to the band limits associated with the wavelet decomposition. The maximal peak-to-peak amplitudes of the filtered ERP components in a predefined time window were measured and statistically processed.

2.3. Time-Frequency Analysis of ERPs by Means of Wavelet Analysis

In the current study, quadratic B-spline wavelets are used for their good time frequency localization properties and their linear phase. For the computation of the wavelet transform
3. RESULTS

3.1. Averaged ERPs

The time series (wide-band filtered, 0.3–70 Hz) of ERPs recorded from the auditory cortex (gyrus ectosylvianus anterior, GEA), occipital cortex (OC), and hippocampus (HI) are given in Fig. 2. The figure shows results in a typical animal. In GEA and OC, marked modality-dependent differences are visible. With respect to GEA, the response to auditory stimulation has a maximal post-stimulus amplitude of approximately 40 µV. In contrast, the response to visual stimulation has an amplitude of approximately 20 µV. In OC, the amplitude of the auditory ERP is approximately 50 µV, whereas the amplitude of the visual ERP is nearly 150 µV (note the marked differences with respect to the overall waveshapes). Hippocampal (HI) response amplitudes are approximately 40 µV for auditory stimulation and approximately 60 µV for visual stimulation.
FIG. 3. Grand average ERPs (N = 6). Left column, auditory stimulation; right column, visual stimulation. Recordings from auditory cortex (GEA), visual cortex (OC), and hippocampus (HI). Along the x-axis, time in ms; along the y-axis, amplitude in μV (negativity upwards).

The respective grand average curves are given in Fig. 3. They are in accordance with the results for the typical animal. Distinct modality differences are observed for all locations, with an auditory ERP of approximately 15 μV maximal post-stimulus amplitude and a visual ERP of approximately 10 μV amplitude in GEA. With respect to OC, the auditory ERP has an amplitude of approximately 15 μV whereas the visual ERP amplitude is approximately 70 μV. In HI, response amplitudes are approximately 15 μV for the auditory ERP and approximately 25 μV for the visual ERP.
3.2. Amplitude Frequency Characteristics

Amplitude frequency characteristics were computed from averaged ERPs for the electrode locations mentioned above, i.e., GEA, OC, and HI.\(^5\)

3.2.1. Auditory Cortex—GEA

Figure 4-GEA shows amplitude frequency characteristics for the auditory cortex with auditory vs visual stimulation. For the grand average, the center frequency is around 9–10 Hz for auditory stimulation (‘‘adequate’’). This is in contrast with visual stimulation where a trough in the 8-Hz range is observed.

\(^5\) Note that averaging across individual cats was performed in the frequency domain.
3.2.2. Visual Cortex—OC

Figure 4-OC shows amplitude frequency characteristics for the visual cortex with auditory vs visual stimulation. For auditory stimulation (‘‘inadequate’’), no marked maxima in the alpha range are visible. However, responses to visual stimuli show a dominant peaking in the 10-Hz range, with a peak frequency of 12–13 Hz.

3.2.3. Hippocampus—HI

Figure 4-HI shows amplitude frequency characteristics for hippocampal recordings. For auditory stimulation a response in the 10-Hz range is visible; the grand average amplitude frequency characteristics reveal a frequency responsiveness in the 8–10 Hz range. Visual stimulation also elicits maxima in the alpha range. In the grand average, the maximum is centered at 12 Hz. This means that the response is shifted to higher frequencies in comparison to auditory stimuli.

3.3. Results of Digital Filtering

3.3.1. Typical Animal

The results obtained in the experimental animal ‘‘lara14/5’’ are shown in Fig. 5 (left, responses to auditory stimuli; right, responses to visual stimuli). For each type of stimulus, three electrode locations are shown. The uppermost row shows wide-band-filtered responses; the filter limits for the other curves are as given in the figure (gamma, beta, alpha, theta, delta). The figure permits a comparison of responses to ‘‘inadequate’’ stimuli (visual ERP in GEA and auditory ERP in OC) vs responses to ‘‘adequate’’ (auditory ERP in GEA and visual ERP in OC) stimuli: it can be seen that the alpha range shows the largest differences, with marked alpha responses to adequate stimuli whereas inadequate stimuli do not elicit alpha responses (no enhancement). Large inadequate vs adequate differences are also observed in the beta and delta components of the visual ERP. In all other recordings, this inadequate vs adequate difference is smaller. Note that although the visual ERP in GEA (‘‘inadequate’’ stimulation) is barely visible in wide-band filtered curves, there is still a theta response (residual response).

Interim Summary. It may be pointed out that high-amplitude alpha responses were characteristic of responses to adequate stimuli in primary sensory areas. Adequate vs inadequate differences were larger for alpha responses than for theta responses. This supports the hypothesis that alpha responses are predominantly associated with primary sensory processing.

3.3.2. Statistical Analysis

The effects of stimulus modality on the frequency content of the ERPs of primary sensory cortices and the hippocampus were subjected to statistical
Results of band-pass filtering in a typical animal (same as in Fig. 4). Left, auditory stimulation; right, visual stimulation. Each column refers to an electrode site (auditory cortex: GEA; visual cortex: OC; hippocampus: HI). The uppermost row shows the wide-band filtered curve. The further rows show the frequency components gamma (32–64 Hz), beta (16–32 Hz), alpha (8–16 Hz), theta (4–8 Hz), and delta (0.5–4 Hz).

Analysis which yielded several significant results as outlined below. The following preliminary remark has to be made: It is well known that the primary visual and auditory areas display strong ERPs to adequate stimuli but not to inadequate stimuli. An important question arising from this finding is whether this difference is reflected in the whole frequency content of the signals, or whether it is the result of a dominant change in certain frequency bands. In order to identify the relative contribution of the respective frequency ranges to the compound ERP, we used the following normalization procedure: to take into account inter-individual differences in ERP amplitude, we computed relative amplitudes (amplitude of the respective ERP component divided by amplitude of the wide-band filtered ERP). The results are shown in Fig. 6. A “modality” (auditory, visual) × “lead” (GEA, OC,
HI) repeated measures ANOVA was conducted on each of the frequency components separately. The results are given in Table 1.

For auditory vs visual stimuli, differences were largest in the alpha range, with higher alpha response amplitudes for adequate stimuli (auditory ERP in GEA, visual ERP in OC) than for inadequate stimuli (acoustical stimuli in OC, visual stimuli in GEA). This result corresponded to a significant **mo-

---

**TABLE 1**

Repeated Measures ANOVA Statistics of the Effects of the Stimulation Modality, Topography (Lead), and Modality × Topography (Lead) on the Relative Amplitudes of the Band-Pass Filtered Frequency Components

<table>
<thead>
<tr>
<th>Modality</th>
<th>Lead</th>
<th>Modality × lead</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delta</td>
<td>0.74</td>
<td>N.S.</td>
</tr>
<tr>
<td>Theta</td>
<td>5.80</td>
<td>0.04</td>
</tr>
<tr>
<td>Alpha</td>
<td>0.50</td>
<td>N.S.</td>
</tr>
<tr>
<td>Beta</td>
<td>5.98</td>
<td>0.037</td>
</tr>
<tr>
<td>Gamma</td>
<td>0.17</td>
<td>N.S.</td>
</tr>
</tbody>
</table>

*Note.* Relative amplitudes were computed by dividing the peak-to-peak amplitude of the frequency component in the post-stimulus period to the peak-to-peak amplitude of the unfiltered response (GEA, HI, OC).
FIG. 7. Results of wavelet decomposition in a typical animal (same as in Fig. 5). Left, auditory stimulation; right, visual stimulation. Each column refers to an electrode site (auditory cortex, GEA; visual cortex, OC; hippocampus, HI). The uppermost row shows the wide-band filtered curve. The further rows show the frequency components gamma (32–64 Hz), beta (16–32 Hz), alpha (8–16 Hz), theta (4–8 Hz), and delta (0.5–4 Hz).

duality × lead” effect ($p < .05$). Differences for all other frequency ranges were smaller (except beta in OC). It is noteworthy that theta responses showed an opposite behavior, with slight, yet significant (“modality × lead”; $p < .01$) increases in amplitude for inadequate stimuli in comparison to adequate stimuli.

3.4. Results of Wavelet Analysis of ERPs

3.4.1. Typical Animal

The analysis of auditory and visual ERPs in all three structures (GEA, HI, OC) by means of the wavelet method shows distinct response components in delta, theta, alpha, beta, and gamma frequency ranges, which are differently weighted according to the investigated brain structure and the stimulus modality. Figure 7 shows the results of the 5 octave wavelet analysis of the auditory ERP and visual ERP recorded from the GEA, HI, and OC leads of
FIG. 8. Amplitudes (mean values) of ERP components obtained by means of wavelet analysis, normalized in the following way: the absolute amplitude of each frequency component was divided by the amplitude of the wide-band filtered response (see text for details).

3.4.2. Statistical Analysis Concerning Cross-Modality Experiments

Amplitudes (measured as peak amplitudes of detail functions and normalized for the same reasons and in the same way as stated for digital filtering) are given in Fig. 8.

1. The dominant frequency components of the visual ERPs recorded in the OC area were in delta and alpha ranges with comparable weights, whereas the auditory ERPs of the auditory cortex (GEA) had a dominant component in the alpha range. There were significant effects of the topography (factor “lead”) on the delta and alpha components (Table 2).
2. Gamma responses were obtained in all three structures in both stimulus modalities. There were no significant differences between the gamma responses obtained in different structures, which is in accordance with our hypothesis of a distributed gamma response system (see below).

3. Alpha response components were most pronounced in the responses of the OC and GEA to adequate stimuli and in hippocampus in visual modality, whereas their amplitudes decreased extremely in responses of both GEA and OC to inadequate stimuli. The only significant effect of the factor “modality × lead,” which corresponds to the cross-modality effect, was on the alpha response component. It means that a significant topographical difference due to the application of stimuli of different sensory modalities was only obtained in the alpha frequency band (Table 2). The finer analysis of this result shows that there are significant increases in the contribution of the alpha components to the evoked responses of the GEA and OC, if the stimulation is the adequate one.

4. Hippocampus responded with a significantly higher alpha component to visual stimuli and with a significantly higher theta amplitude to auditory stimuli. At this point, it should be mentioned that the limits of the theta and alpha frequency ranges showed some changes in auditory and visual modalities. Therefore, the effect we obtained in the theta range (defined as 4–8 Hz in wavelet analysis), might be partly due to the low alpha components. For a precise judgment of this possibility wavelet decomposition could be applied in suboctaves of the theta range.

3.5. Statistical Comparison of Results of Wavelet and Frequency Analysis

The analysis of the frequency components of auditory and visual evoked responses recorded from the auditory cortex (GEA), hippocampus (HI), and

---

**TABLE 2**

Repeated Measures ANOVA Statistics on the Effects of Stimulation Modality, Topography (Lead), and Modality × Topography (Lead) on the Relative Amplitudes of the Wavelet Components

<table>
<thead>
<tr>
<th>Modality</th>
<th>Lead</th>
<th>Modality × lead</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>Delta</td>
<td>0.65</td>
<td>N.S.</td>
</tr>
<tr>
<td>Theta</td>
<td>14.5</td>
<td>0.004</td>
</tr>
<tr>
<td>Alpha</td>
<td>2.48</td>
<td>N.S.</td>
</tr>
<tr>
<td>Beta</td>
<td>17.9</td>
<td>0.002</td>
</tr>
<tr>
<td>Gamma</td>
<td>0.43</td>
<td>N.S.</td>
</tr>
</tbody>
</table>

*Note.* Relative amplitudes were computed by dividing the peak-to-peak amplitude of the frequency component in the post-stimulus period to the peak-to-peak amplitude of the unfiltered response (GEA, HI, OC).
TABLE 3
Amplitudes of the Delta, Theta, Alpha, Beta, and Gamma Response Components Measured in GEA, HI, and OC Electrodes of the Cats During Both AEP and VEP by Using the Band-Pass Filtering and Wavelet Decomposition Methods

<table>
<thead>
<tr>
<th>Frequency band</th>
<th>Band-pass filtering</th>
<th>Wavelet decomposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delta</td>
<td>47.47 ± 55.20</td>
<td>45.01 ± 45.44</td>
</tr>
<tr>
<td>Theta</td>
<td>28.18 ± 19.20</td>
<td>35.14 ± 30.48</td>
</tr>
<tr>
<td>Alpha</td>
<td>46.42 ± 50.04</td>
<td>51.72 ± 55.18</td>
</tr>
<tr>
<td>Beta</td>
<td>28.90 ± 27.05</td>
<td>29.12 ± 27.11</td>
</tr>
<tr>
<td>Gamma</td>
<td>12.91 ± 9.64</td>
<td>15.75 ± 14.56</td>
</tr>
</tbody>
</table>

Our further aim was to analyze statistically whether there are any differences in the quantification of the amplitudes of the evoked rhythms by both methods, which probably did not effect the current analyses but which, however, could be of interest for other neurophysiological questions. For this purpose, we applied a two factorial ANOVA analysis to the amplitudes of the frequency components of ERPs obtained by both methods. All the data obtained from GEA, HI, and OC leads and under two different conditions of ERPs (auditory ERP, visual ERP) were pooled and the effects of the frequency bands and the decomposition techniques were analyzed (Tables 3–5).

The results show that the wavelet transform leads to significantly different quantification of the amplitudes in the alpha frequency range. This might be the result of a higher time resolution due to the compact support of the used quadratic spline basis functions and due to the waveform characteristics of

TABLE 4
The Results of a Two Factorial ANOVA Analysis for Repeated Measures with Factors Filtering Method (Band-Pass, Wavelet) and Frequency Band (Delta, Theta, Alpha, Beta, Gamma)

<table>
<thead>
<tr>
<th>Factors</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Method</td>
<td>N.S.</td>
</tr>
<tr>
<td>Frequency band</td>
<td>$p &lt; .001$</td>
</tr>
<tr>
<td>Method $\times$ frequency band</td>
<td>$p &lt; .05$</td>
</tr>
</tbody>
</table>
this base function which fit well to the short-lasting (sharp) alpha responses occurring in the primary cortex after an adequate stimulus. The selection of basis functions resembling the basic waveform properties of different decaying oscillatory patterns in different frequency ranges could increase the effectiveness of the wavelet transform in the time-frequency analysis of specific neurophysiological signals (Samar et al., 1996).

3.6. Single-Trial Analysis of ERPs

3.6.1. Example of Single Trial Analysis

Figure 9A shows examples of single sweeps recorded in the primary visual cortex of the cat. Single sweeps recorded with auditory stimulation are in the left column; those with visual stimulation are in the right column. The filter limits are 8–15 Hz. Visual stimulation elicits distinct alpha responses, i.e., amplitude enhancement and phase-locking of the EEG. In contrast, these phenomena do not occur with auditory stimulation. It is only in the case of visual stimulation that a large number of sweeps show a high degree of similarity to the filtered averaged ERP (Fig. 9B). For visual stimulation, the unfiltered averaged ERP (Fig. 9C) shows a waveform which is in good accordance with the filtered averaged ERP of Fig. 9B. Amplitude frequency characteristics are displayed in Fig. 9D. For visual stimulation, they show a resonance maximum in the alpha range—in accordance with the distinct responses seen in single trial ERPs filtered in the alpha range (8–15 Hz).

3.6.2. Wavelet Analysis of Single Trials

In Fig. 10, a further improvement in the analysis of ERPs by using the wavelet transform is shown. In this example, the alpha component of the ERP was used to classify different types of single sweeps. Because the wavelet transform represents the time course of different frequency components of the signal by distinct coefficients with a relevant time resolution for that frequency range, it yields a significant data reduction, which allows a simpler analysis of the frequency components of the response. In this example, we classified the sweeps, showing (i) early alpha enhancement and (ii) prolonged or late alpha enhancement. The averages of these subgroups showed signifi-
FIG. 9. Example of ERP single trials in a typical animal (responses to visual stimulation). Left column, auditory cortex recordings ("inadequate" stimulation); right column, visual cortex recordings ("adequate" stimulation, see text). (A) Single trials, filtered with limits 8–15 Hz. (B) Averaged ERP, filtered with limits 8–15 Hz. (C) Averaged ERP, wide-band filtered. (D) Amplitude frequency characteristics.
FIG. 10. *Selective averaging* according to results of wavelet decomposition (see text for details). The left column refers to single trials with early alpha (8–15 Hz) wave packet, the middle column to single trials with prolonged alpha wave packet, and the right column to all single trials. The rows show the wide-band filtered averaged ERP, the averaged ERP filtered in the alpha (8–15 Hz) range, and the single trials filtered in the alpha (8–15 Hz) range.
cantly different shapes. Additionally, even by superimposing the broad-band filtered single sweeps of each group, the early and late or “prolonged alpha phase locking” can be clearly observed. In the early-alpha-response sweeps, a phase locking effect can only be obtained in the first cycle of the post-stimulus alpha activity whereas in the other subgroup phase locking is visible during two alpha cycles.

4. DISCUSSION

The main goal of this study is to show the relevance of the frequency domain and time-scale plane analysis methods for the analysis of evoked rhythms and/or resonance phenomena in the brain. On the basis of auditory and visual evoked potential measurements in cats we will first discuss the physiological interpretation of the results of the frequency domain analysis. Second, the question of whether or not the frequency components obtained by frequency domain analysis are “real components” will be addressed. Third, we will discuss whether wavelet analysis offers further advantages over established methods of frequency domain analysis.

In particular, this last question is closely connected with the physiological basis of the signals. Considering different specific resonant frequencies and activation time courses of various brain structures involved with the investigated brain process, a time-frequency approach is important in the analysis of the compound response to be able to identify functionally significant signal components and activation patterns in the subsystems of the brain.

A variety of experimental paradigms has been used to investigate possible psychophysiological correlates of these evoked EEG rhythms. Converging results support the view that evoked EEG rhythms are correlated with—at least partly—separable processes of information processing in the brain. Some examples are:

1. The importance of theta resonance phenomena in relation to cognitive behavior has been pointed out in a number of recent reports (Buzsáki, 1992; Miller, 1991; Lopes da Silva, 1992; Demiralp & Başar, 1992; Başar-Eroğlu et al., 1992).

2. The role of 8–12 Hz (alpha) oscillations in information processing in the cat visual cortex has been pointed out by Başar and colleagues (Başar, 1972; Başar et al., 1975a, 1975b, 1980; Başar & Schürmann, 1996) at the systems level and by Dinse, Krüger, and Best (1990) and Kopecz, Schöner, Spengler, and Dinse, (1993), and by Schreiner (1991) at the cellular level.

3. EP analysis based on systems theory rules and application of digital filters also showed that a marked 40-Hz component follows stimulation (Başar, Rosen, Başar-Eroğlu, & Greitschus, 1987). For further studies of evoked electric and magnetic 40-Hz activity see, e.g., Galambos, Makeig, & Talmachoff (1981), Pantev et al. (1991), and Ribary et al. (1992). A large number of studies at the single-cell level complement these results (Llinás, 1988;
Gray & Singer, 1987; Gray, König, Engel, & Singer, 1989; Eckhorn et al., 1988).

The concept of evoked and induced rhythms (Başar & Bullock 1992; Bullock, 1992) is a further approach parallel to frequency analysis and resonance phenomena. Results of several investigators working now with the concept of evoked rhythmicities and induced rhythmicities have recently been reviewed by Başar and colleagues (Başar, 1992; Başar, Schürmann, & Başar-Eroglu, in press) who emphasized that the complex dynamics of compound potentials and the resonance phenomena might play one of the most important roles in brain organization.

4.1. ERP Frequency Components as Correlates of “Induced Rhythms” and “Resonance Phenomena” in the Brain

Approximately 20 years ago our research group started publishing several reports concerning a working hypothesis on the brain’s EEG and ERPs. This hypothesis had several issues which were interrelated. In our view, the conventional averaged ERP—which is widely used and very popular—was considered only as a rough estimate of the brain’s EEG response, and it was claimed that the averaged ERP does not take into account dynamical changes in the brain’s intrinsic activity. On the contrary, single ERPs were considered as correlates of the brain’s quasi-invariant resonant modes containing important brain frequency codes related to central nervous system function (for details, see Başar, 1980, 1983; Başar et al., 1992).

In the scope of resonance phenomena in the brain (Başar & Bullock, 1992) it has been hypothesized that topographic differences of EEG responses might partly reflect the activity of distinct cortical areas for which the stimulation applied is either adequate or inadequate (Başar, Başar-Eroglu, Rahn, & Schürmann; 1991). The experimental bases of this hypothesis were combined measurements of EEG and ERP in the cat brain by means of intracranial electrodes: Responses to auditory and visual stimulation were recorded from the auditory cortex and from the visual cortex (“cross-modality” experiments, cf. Hartline, 1987).

The present study is mainly based on intracranial recordings in cats. We demonstrated high amplitude responses recorded from primary sensory areas responding to adequate stimuli. The lack of such responses to inadequate stimuli is another fact refuting the objection that alpha response-like waveforms are a mere result of digital filtering. The good spatial resolution of such recordings may compensate for the lack of spatial resolution in human scalp measurements.

What are the physiological implications of these differences? As to different functional roles of ERP frequency components, the hypothesis underlying this approach was as follows: alpha responses appear to be related to primary sensory processing whereas theta and/or slower responses appear to be involved mainly in associative and cognitive processes.
4.1.1. Physiological Implications of ‘‘Cross-Modality’’ Experiments: Possible Functional Roles of the Evoked Alpha

Our results in cross-modality experiments demonstrate that the differences between responses to adequate stimulation and responses to inadequate stimulation (‘‘adequate/inadequate differences’’) were marked in the alpha frequency range and less marked in the theta range. This hints at a possible special role of the alpha response in primary sensory processing.

In contrast, ERP theta components appear to be less dependent on whether the stimulus is adequate or not, which is compatible with a predominantly associative-cognitive role of the theta response—as hypothesized above and as published earlier (Başar et al., 1991; Demiralp & Başar, 1992; Başar-Eroglu et al., 1992).

On the basis of cross-modality experiments, ‘‘it may become possible to describe in the brain global interacting areas or structures which would be defined as a diffuse ‘alpha response system’ and a ‘diffuse theta response system.’ Exact locations and exact functions cannot as yet be properly defined,’’ as stated in a previous study (Başar et al., 1991, p. 32). It is hypothesized that the alpha response system is more related to sensory differentiation whereas the diffuse theta response system—which is similarly a parallel responding system—is involved more in associative and cognitive behavior of the brain.

Similar results were obtained in human occipital ERPs (Başar & Schürmann, 1994). The ‘‘adequate/inadequate’’ differences, however, were particularly marked for the alpha (8–15 Hz) component of the ERP, i.e., acoustical stimulation elicits no alpha enhancement in left occipital recordings. The occipital electrode being adjacent to the visual cortex, we refer to these measurements as ‘‘cross-modality’’ experiments (‘‘inadequate,’’ auditory stimulus/visual cortex; ‘‘adequate,’’ visual stimulus/visual cortex).

Hartline (1987, p. 708) deals with multisensory representation of space in the central nervous system and states, ‘‘The visual cortex is thought to participate in processes subserving the recognition of objects or patterns. Though this part of the brain is considered to be involved exclusively with vision, in cats about one-third of the neurons in area 17 (striate cortex), 18, and 19 are reported to be responsive to sound as well as to visual input.’’

Furthermore, ‘‘a large number of neurophysiological studies showed that primary sensory stimuli elicit impulses or volleys converging over thalamic centers to primary sensory areas. On the other hand, the ‘sensory stimulation of second order’ usually reaches the cortex over association areas (see, for example, Shepherd, 1988). Due to this consideration it is conceivable that the responses in the lower frequency ranges (theta, delta) might reflect the responsiveness of various brain areas in cases of association processes involved in global associative cognitive performance’’ (Başar et al., 1991, pp. 31–32).
On the basis of cognitive ERP measurements, Başar-Eroğlu et al. (1992) assumed that the brain’s alpha, theta, and delta responsiveness is functionally related to cognitive processes such as selective attention, learning, and decision making. The cross-modality responses of this study support this hypothesis. In other words, we assume—according to Hartline (1987)—that the occipital response is a cross-modality response which is probably not elicited directly by visual stimulation; it is evoked or induced through cognitive mechanisms acting mostly in association areas of the brain including the forebrain, parietal areas, and the limbic system. This last aspect further justifies regarding the theta response as a predominantly cognitive component.

This interpretation is also supported by results obtained with a different paradigm: it is mainly slow frequencies that contribute to differences between ERPs obtained in an omitted stimulus paradigm and ERPs recorded in a session without cognitive load: In a time prediction task, selective averaging of responses to the last stimulus before omission showed increased delta-theta amplitudes (Demiralp & Başar, 1992). This is noteworthy because the increase was most prominent in frontal and parietal electrodes which are closely related to association areas of the brain (for a comparable study on cats, see Demiralp et al., 1994).

Furthermore, the interpretation is supported by ERP measurements in a group of multiple sclerosis (MS) patients (Başar-Eroğlu et al., 1993; Schürmann, Warecka, Başar-Eroğlu, & Başar, 1993). We regard this demyelinating disease as a model of impaired sensory input with consequences for primary sensory processing rather than associative-cognitive processing in the brain. We recorded visual and auditory ERPs in a MS group in comparison with a control group. It was found that alpha responses were markedly reduced in the MS group whereas theta responses were unaltered. This is in agreement with the above-mentioned hypothesis that alpha responses mainly reflect primary sensory processing and theta responses mainly associative-cognitive processing.

4.1.2. Brain Resonance Phenomena, Induced Rhythmicities, and Their Manifestation in ERPs and Other Measures

According to the working hypothesis underlying our study, ERPs can be considered as resonance phenomena of the EEG. Examples of resonance phenomena have been found both in cat intracranial recordings and in human scalp recordings. Results obtained with methods from nonlinear dynamics indicating that the ‘‘spontaneous’’ EEG is not merely ‘‘noise’’ also support the hypothesis outlined above (Babloyantz, Nicolis, & Salazar, 1985; Röschke & Başar, 1985, 1988; Röschke & Aldenhoff 1991; for an overview see, e.g., Başar, 1990).

As to the cellular level, Llinás (1988) pointed out that oscillations in the 6-Hz, 10-Hz, and 40-Hz ranges might allow single neurons to be woven into
functional states representing external reference frames. Recent findings by Gray and colleagues (Gray & Singer, 1987; Gray et al., 1989)—confirmed and extended by Eckhorn et al. (1988)—deal with 35–85 Hz oscillatory responses. The responses occur in synchrony for cells located within a functional column, thus possibly establishing relations between features in different parts of the visual field. The responses are tightly correlated with local oscillatory field potentials.

4.2. ERP Frequency Components—“Real Components” Related to Psychophysiological Functions

The ERP frequency components (obtained by adaptive digital filtering) and also the amplitude frequency characteristics reflect a global and general frequency behavior (or frequency contents) of the compound potentials, which we call ERPs. As outlined by Başar (1980, chapters on the neural correlates of EEG and ERPs), the compound potentials and the filtered responses give only a general idea about the frequency distribution of the real neuronal activity. As indicated by Başar (1980) in his chapter on resonance phenomena in physics, we have here an analogy with quantum mechanics in which the position, exact location, or exact energy of a given elementary particle can be described only with the probability wave. In other words, “wave packets” in modern physics have been used in order to give a cloudy description and not a very exact physical entity of the observed particles. By the analysis of frequency responses of the compound potentials we aim also to obtain a cloudy information about the frequency amplitude: The results have to be interpreted only globally. Accordingly minor changes of filtered responses or minor peakings in the amplitude frequency characteristics should not strongly be taken into account. Only major and dominant changes in the filtered ERPs or drastic changes in the amplitude frequency characteristics can be analyzed when trying to find psychophysiological correlates of ERPs.

In our analysis we have indicated only such major changes in the ERPs. They were usually due to anatomical differences of the structures studied or dependent on the type of experiments performed. Pathological changes also gave rise to such results. In the following we will give some important examples demonstrating that we are not performing an arbitrary analysis of frequency components. The dissection of the ERP into frequency components can give us a very good idea as to the real psychophysiological contents of the potential, when the concept is carefully applied.

4.2.1. Example from Experiments with Behavioral Paradigm: P300

An important result of the frequency analysis of the P300 response (obtained by using an oddball paradigm) is the observation that a major change occurs in the amplitude frequency characteristics and in filtered responses.
The response contains a relevant increase in the delta frequency range in comparison with the sensory ERP recorded without task (for an illustration, see, e.g., Başar-Eroğlu et al., 1992; Demiralp et al., 1999).

If the experimenter changes the paradigm and increases the expectancy for the target signal we are dealing with a different task. In this case, a series of three stimuli and a target signal are repetitively applied. When the subjects pay attention to the third signal, an important increase in the theta frequency channel can be observed, which is also accompanied with a 40 Hz response increase (Demiralp & Başar 1992). The general observation was that increases in the theta components are accompanied by increased focused attention. But most relevant increases of the theta components are located in frontal and parietal recordings.

In the experiments with the oddball paradigm, we have also another observation related to the 10-Hz frequency component. The 10-Hz response is not increased in this type of experiment, but the 10-Hz oscillation is prolonged (Kolev & Schüttmann, 1992). This shows that alpha responses recorded under certain conditions may not be exclusively related to primary sensory processing but may have a wider range of functions (as outlined by the participants of the congress “Alpha Processes in the Brain” in 1994; cf. Başar et al., in press-a).

In other words, the global changes in ERP frequency components do not occur equally in all frequency windows or electrode locations. It was shown that the P300 during focused attention in the cat brain causes a drastic increase in the hippocampal theta response (Başar-Eroğlu et al., 1991a, 1991b), but the same increase reaching the range of 40% was not observed in the auditory cortex, and the most relevant increase was seen within the CA3 layer of the hippocampus. In all these types of experiments, such results are considered to be “relevant changes” if our comparison shows increases of more than 30% of the amplitude of the frequency response component.

4.2.2. Application of Pharmacological Agents

By the application of pharmacological agents we have seen also important changes in ERPs, as for example:

1. When applying ceruletide to cats we have observed a major change in the amplitude frequency characteristics, especially in the hippocampus of the cat—mainly in the slow frequency range around 4 Hz. The entire ERP recorded in hippocampus turns out to be a “theta oscillation” also visible without application of filters (Başar-Eroğlu, Başar, & Zetler, 1996).

2. According to the analysis of ERP recorded from isolated ganglia of helix pomatia application of dopamine elicits a major increase in the 40-Hz response at more than 100%. Various other components did not show such pronounced changes (Schütt et al., 1992; Schütt & Başar, 1992).
4.2.3. Cross-Modality Experiments

One of the most important demonstrations concerning the physiological correlates of frequency components is obtained by the application of cross-modality experiments. This being the core topic of the current study, we only add that the results measurements with scalp electrodes in human subjects (Başar & Schürmann, 1994) are consistent with the data obtained in cats: 10-Hz enhancements, in the filtered ERPs, or the dominant frequency peaks in the alpha frequency range in amplitude frequency characteristics can be obtained if the physiological sensory stimulation is an adequate one. In the visual cortex only visual stimulation can give rise to highly significant increases in the alpha frequency range, whereas the theta response is not affected so much by inadequate stimulation.

If the recorded frequency response of all components by frequency analysis would be obligatory then we would see all these changes together. Here again a component is dominating if the sensory stimulation is adequate for the analyzed structure. This is an excellent example that the dissection of frequency components in frequency bands reveals functional relations.

4.2.4. Experiments with Multiple Sclerosis Patients

The finding that the alpha response in the occipital cortex of multiple sclerosis patients is highly attenuated or sometimes completely absent supports the above-mentioned consideration (Başar-Eroglu et al., 1993; Schürmann et al., 1993). The alpha response in the occipital location is related to sensory perception induced with light if the sensory nerve (in this case the optic nerve) is injured. According to expectations (on the basis of cross-modality experiments as mentioned above), the alpha response is the response component with the most marked amplitude attenuation. Here we have again an important explanation to correlate the frequency components with function and pathological influence on change of the function. The difference between alpha responses in healthy subjects vs MS patients is illustrated in Fig. 11.

4.2.5. The Hippocampus Is a Supramodal Center

The hippocampus is a polysensory and supramodal center (for an overview and references, see Başar, 1980). In this structure all types of sensory stimuli give rise to high 10-Hz enhancements. On the contrary, the ERPs in the thalamic or cortical ERPs can react with large alpha enhancements, only to adequate stimuli. This is not the case in the hippocampus, in which all modalities can give rise to enhancements also in the alpha frequency range. Again, we can see here that the 10-Hz response component of the ERPs is not obligatory and it is completely different depending on stimulus modality and structure studied.
FIG. 11. Comparison of alpha responses, control group vs multiple sclerosis (MS). Left column, recordings in a subject from the control group; right column, recordings in an MS patient. (A) Single EEG-ERP trials filtered in the 8–15 Hz (alpha) range. (B) Averaged ERP, filtered in the 8–15 Hz range. (C) Averaged ERP, wide-band filtered. (D) Amplitude frequency characteristics computed from the averaged ERPs shown in (C).
4.2.6. Defined Brain States Show Oscillatory Behavior without Filtering

A general statement must be emphasized here: In some experiments we were able to show that, in some particular states of the brain, ERPs turn out to be oscillatory responses with a homogenous frequency. Experiments with stimuli at the sensory threshold provided a good example. During these experiments the 10-Hz frequency response and higher frequency responses vanish. Moreover, the ERP is a type of slow delta oscillation, which can be seen without using any filter. During experiments with the 40-Hz activity one can often see a superimposed 40-Hz oscillation already in the compound ERP, again without any filtering (Schürmann, Başar-Eroğlu, & Başar, in press). It is particularly in MEG recordings that such homogeneous oscillatory frequency responses can be recorded. Sometimes two different recordings at a small distance can show only theta oscillations or pure 10-Hz oscillations (Saermark, Mikkelsen, & Başar, 1992).

A further possibility to obtain such responses consists of selective averaging: when inspecting the set of single trial ERPs, examples with almost homogeneous theta oscillations or almost homogeneous alpha response oscillations can be found. If we group these examples into different subsets and compute averages for each of the subsets we obtain oscillatory response waves with a unique frequency (Başar, 1988). In other words, although the only goal of ERP filtering is to give a global idea of the frequency contents of the response, the ERP components obtained by digital filtering are related to a real process: this is because the compound potentials contain superimposed activities originating from several neural populations. Consequently, we can only be certain about the functional correlates if changes in the ERP frequency components are great.

These examples are stated here in order to respond to answer a frequent question: “Are theta or alpha components or 40-Hz components somewhat not harmonics of a strong response?” For example, if Fourier analysis or digital band-pass filtering is applied to an impulse function, then we would find several components on account of the nature of the applied mathematical methodology. Minor peakings in response can be certainly due to harmonic components, but a three- to fivefold increase in the delta frequency range without any change in the alpha frequency domain, as observed in a study of the P300 response (Başar-Eroğlu et al., 1992), can never be explained with such harmonic changes.

Changes in the harmonic components do occur in a parallel manner: if the largest component increases or disappears then the harmonics increase or disappear in a parallel manner. We emphasize, however, that changes in the frequency response amplitudes are not harmonic but relevant components as long as major peakings—and not small deviations—are evaluated. On the other hand, in our search for global sensory and cognitive components the expression “cloudy information” is appropriate. Every scientist has to
find strategies in order to correlate the frequency components with psycho-
physiological correlates. This is not just the application of a mathematical
method, but an ensemble of strategies with biological knowledge, behavior
knowledge, and computer application.

4.3. Role of Wavelet Transform Methods in the Analysis of Functional
ERP Components

The TRFC method based on the Fourier transform and wavelet analysis are
complementary methods to investigate brain oscillatory waveforms. Fourier
analysis gives a general knowledge about the center frequencies of the oscil-
latory components of EEG or ERPs for the whole observation window. To
obtain more detailed information on the time-frequency properties of the
signal, the application of wavelet analysis is necessary. The information ob-
tained by the TRFC method on the main frequency components of the signal
is important in designing the wavelet analysis. By using this information,
the frequency ranges of interest can be defined which is helpful in the deci-
sion for the number of octaves of the wavelet decomposition and if a suboc-
tave analysis is needed.

1. As an example, we mention the analysis of P300 experiments indicat-
ing a dominant delta response of subjects following target signals. By using
this global information, the number of octaves in the wavelet decomposition
was selected in such a way that the delta frequency range could be analyzed
separately (see Demiralp et al., 1999).

2. Another example is the analysis of the alpha response in the cross-
modality experiments. By means of the Fourier analysis we have been able
to show that the brain responses to adequate sensory stimuli contain large
alpha components. Then, the wavelet analysis was applied to follow the time
course of the alpha component in detail.

The advantages of using the wavelet analysis in the decomposition of ERPs
into frequency components are threefold:

1. Due to the possibility of using functions with compact support, the
time-localization of the frequency components can be obtained with a higher
precision.

2. As the wavelet analysis does not require the use of a fixed time win-
dow, it is especially advantageous when dealing with signals such as ERPs
which contain wave packets that differ significantly in duration and fre-
quency content.

3. By using time windows with relevant duration for each frequency
range, the wavelet transform yields a significant data reduction or data com-
pression. This feature is extremely helpful in identifying and isolating ERP
features in single ERP sweeps, where the information content is significantly
higher and more complex to analyze compared with the averaged response.
As we have shown in the example, where we can identify the different response subgroups by using the wavelet coefficients in different frequency bands of the single responses, this property opens an important window to a finer analysis of ERPs and extends the conventional averaging technique in terms of obtaining homogeneous subaverages with significantly lower variance.

The results given above demonstrate that wavelet analysis confirms all results obtained by application of the TRFC analysis and adaptive digital filtering:

1. The above-mentioned properties of the alpha response in the cat brain were demonstrated by wavelet analysis as well as by digital filtering.
2. The alpha response in the human brain with wavelet analysis confirms results of single-trial ERP analysis by means of digital filtering. There is a large alpha response to visual stimulation at a position close to the occipital cortex, where an auditory stimulation does not create a 10-Hz response.

The advantage of the wavelet analysis is especially in the field of single-trial analysis: the improvement over digital filtering is that searching for phase locked responses of a certain frequency in single trials is feasible. This is due to the significant data reduction especially in the lower frequency ranges resulting from the multiresolution properties of the wavelet transform. The advantages with respect to single-trial analysis apply both to the 10-Hz frequency range (see above) and to the delta frequency range (Demiralp et al., 1999). The results obtained so far by wavelet analysis underline and extend the view that alpha, theta, delta, and gamma responses are related to psychophysiological functions. In summary, the wavelet analysis confirms once more the expression ‘‘real signals’’ which we attribute to EEG frequency responses of the brain.

4.4. Diffuse Oscillatory Systems in the Brain

By means of the application of combined analysis procedure of EEG and ERPs we recently emphasized the functional importance of oscillatory responses (in the framework of brain dynamics) related to association and (‘‘long distance’’) communication in the brain. We assumed that alpha networks, theta networks, and gamma networks (or systems) are diffusely distributed in the brain (for the delta, theta, and alpha ranges, see Başar et al., 1991; Başar-Eroğlu et al., 1992; Schürmann & Başar, 1994; Başar & Schürmann, 1994, 1996; Parnefjord & Başar, 1995; Schürmann, Başar-Eroğlu, Kolev, & Başar, 1995; for the gamma range, see Başar & Schürmann, 1994; Başar-Eroğlu & Schürmann, 1994; Başar & Demiralp, 1995; Başar, Başar-Eroğlu, Demiralp, & Schürmann, 1995; Başar-Eroğlu, Strüber, Kruse, Başar, Stadler, 1996; Başar-Eroğlu, Strüber, Schürmann, Stadler, & Başar, 1996; Schürmann et al., 1997). We also have tentatively assigned functional prop-
erties, namely sensory-cognitive functions, to alpha and gamma resonant responses. According to this theory a sensory stimulation evokes 10-Hz enhancements in several structures of the brain, both cortical (primary auditory cortex, primary visual cortex) and subcortical (hippocampus).

The synchronous occurrence of such responses in multiple brain areas hints at the existence of distributed oscillatory systems in the brain. Such diffuse networks would facilitate the information transfer in the brain according to the general theory of resonance phenomena. Although alpha responses are observable in multiple brain areas, they are markedly dependent on the site of recording. The dependence of the alpha response on whether or not the stimulus is adequate for the brain area under study thus hints at a special functional role of alpha responses in primary sensory processing.

The distributed occurrence of alpha responses may also be discussed in relation to the problem of perceptual binding: Parallel distributed networks in the brain propagate any event into separately processed stimulus attributes, storing the memory of the corresponding information in different regions. Retrieval of this information from memory is mediated by multiple brain substructures. Recovery and cognitive evaluation of the event when it reoccurs engages anatomical areas dispersed throughout the brain. This statement is strongly based on cognitive experiments by means of single and multiple unit activity and field potentials in animals, event related potentials and EEG in humans, and a great variety of clinical studies by use of modern imaging techniques. The distributed alpha responses as reported here may add a further aspect to this problem which has so far been dominated by the widely discussed role of gamma responses for this process of perceptual binding (Gray & Singer, 1987; Gray et al., 1989; Eckhorn et al., 1988; for an overview including results at the EEG level, see, e.g., Başar-Eroglu et al., 1996).

The reader might wonder whether or not such synchronous alpha responses are due to activity at the reference electrode or due to volume conduction from other structures of the brain. Activity at the reference electrode is an improbable cause of the observed waveforms because the reference consists of the average of three electrodes at different points of the skull. Recordings from closely spaced hippocampal multielectrodes (i.e., from brain structures only about 1 mm apart) were markedly different from each other thus making volume conduction as the cause of the observed waveforms improbable (Başar, 1980).

Both aspects of alpha responses in the brain (presence in multiple brain areas and dependence on modality) have now been confirmed by means of wavelet analysis (only with minor deviation from previous results). The consistent results of both methods are a further hint at the existence of diffusely distributed oscillatory systems in the brain.

The term diffuse is used in order to describe the distributed nature of the alpha and gamma response in the brain. At this level of investigation, it is not possible to define the connections between the elements of these systems
by means of neuron-by-neuron tracking, or to define the directions of signal flow and exact boundaries of neuronal populations involved. However, this description is necessary to emphasize that rhythmic phenomena in these frequency ranges are not unique features of the observed single subsystem of the brain, and that their simultaneous existence in distant brain structures may be a relevant and important point in understanding the cooperative activities of distinct brain structures.

4.5. Proposals for Future Research

Wavelet analysis may prove to be useful for the analysis of cognitive ERPs, e.g., for the identification of P300 variants at single trial level, i.e., variations occurring during one experimental session and possibly related to differences in the subject’s evaluation of the stimulus (see Demiralp et al., 1999). Furthermore, a more detailed analysis of topographic aspects by means of wavelet analysis may be of interest (see, e.g., Lehmann, 1989; Skrandies, 1989, for a topographic study of cognitive ERP components). In addition to ERPs with cognitive paradigms, ERP measurements in pathological conditions are also promising for the future use of wavelet analysis (Samar et al., 1995).

4.6. Conclusion

In our presentation of the concept of ERP frequency analysis we demonstrated that certain experimental approaches allow the identification of psychophysiological correlates of the frequency components. Our tentative interpretation consists of the hypothesis—supported by the data shown—that alpha responses as recorded in these experiments might mainly reflect primary sensory processing. Additional support for this hypothesis can be derived from the observation of reduced alpha responses in multiple sclerosis patients with impaired sensory input. Furthermore, the data also support a cognitive role of theta responses—as previously derived from cognitive ERP measurements.

Based on a concept of ERPs as manifestations of brain resonance phenomena (Basar, 1980) we suggest the interpretation that neural structures with different resonance properties may be involved in the processing of the auditory and visual stimuli applied.

Furthermore, as these data were evaluated by means of Fourier analysis and adaptive digital filtering on the one hand and by wavelet analysis on the other hand, a methodological comparison is possible: the essential results obtained by both methods are similar, with some promising advantages of the wavelet transform for single-trial analysis.6

---

6 We are grateful to Dipl.-Ing. F. Greitschus and Dipl.-Ing. M. Gehrmann for hardware maintenance and software development, and to K. Leffler, R. Garnath, and G. Fletschinger for technical assistance and figure preparation.
REFERENCES


Ribary, U., Ioannides, A. A., Singh, K. D., Hasson, R., Bolten, J. P. R., Lado, F., Mogilner,


