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Functions and sources of event-related EEG alpha oscillations studied with the Wavelet Transform☆

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Abstract

Objectives: By using the Wavelet Transform, a time frequency representation with nearly optimal resolution, we studied responses to stimulation in the 'alpha' range (10 Hz).

Methods: Visual evoked responses of 10 healthy subjects were studied with 3 different stimulus types (no-task VEP, non-target and target stimulus).

Results: Upon all the stimulus types, event-related responses in the 10 Hz ('alpha') range were distributed in the whole scalp, best defined in the occipital locations, the responses on the anterior electrodes being less pronounced and delayed. In some subjects, these event-related responses were prolonged upon target stimulation in posterior locations.

Conclusions: These results point towards a distributed origin of event-related alpha oscillations with functional relation to sensory processing, and possibly to further processes. © 1999 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Evoked potential; Event-related potential; Wavelet; Alpha; EEG

1. Introduction

EEG alpha rhythm can be defined as an oscillation between 8 and 13 Hz, with an amplitude usually below 50 μV and localized over posterior regions of the head. Spontaneous alpha rhythms appear during wakefulness and they are best seen with eyes closed and under relaxation and mental inactivity conditions (Niedermeyer, 1993). Due to these properties, the alpha rhythm is mostly regarded as an 'idling rhythm.' However, this interpretation has recently been challenged. As Niedermeyer (1997) states: 'physiological alpha rhythms are likely to have closer relationships to 'events' than one might have thought earlier' (see Hari and Salmelin, 1997 for corresponding data obtained with magnetoencephalography). Additionally, it has been suggested to refer to several types of oscillations in the 10 Hz frequency range as alpha oscillations in a wider sense (Galambos, 1992; Başar et al., 1997). Among these signals, event-related alpha oscillations (a term we use as a shorthand for '8–15 Hz oscillations temporally related to a certain event,' e.g. a sensory stimulus; also denoted as alpha responses) have been suggested as functional correlates of certain stages of processing in the brain (Başar et al., 1997). As the analysis of such oscillations must take into account the temporal relation to the event processed by the brain, the usual methods of EEG frequency analysis are not satisfactory. By using a comparatively new method of time-frequency analysis, the Wavelet Transform, the present paper aims at characterizing event-related alpha oscillations with regard to their possible functional correlates and to their sources.

More precisely, the aim of this work is to confirm the hypothesis of a relation between alpha responses and sensory processing by analyzing the task-dependence of alpha responses. Furthermore, our data implies that alpha responses are likely to be generated by several generators distributed in the brain. These findings are supported in the optimal performance of the Wavelet Transform and in turn they show its usefulness in the analysis of event-related potentials (ERPs).

1.1. Alpha oscillations: earlier studies

Although alpha oscillations have been widely studied, their sources and functional correlates are still under discussion. Earlier pioneer studies date back to the work of Adrian

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(1941), who discovered that a single tactile stimulus elicited rhythmic 10/s 'after discharges' in the thalamus. Andersen and Andersson (1968), by using barbiturate alpha spindles that resemble spontaneous EEG alpha activity, go further by proposing a 'facultative pacemaker' in the thalamus after observing a high degree of synchrony between thalamic and cortical rhythms. Lopes da Silva et al., (1973a) criticized the use of barbiturate spindles as a model of alpha activity. In dogs, they found significant coherence between thalamic and cortical electrodes, but they also found greater cortico-cortical coherence, incompatible with the thalamic pacemaker theory of Andersen and Andersson (Lopes da Silva et al., 1973b). Furthermore, by computing phase differences between several deep electrodes in dogs, Lopes da Silva and Storm van Leeuwen (1977) demonstrated the existence of a dipole generator of alpha waves 1100 mm below the cortical surface. Alpha rhythms were also observed in in vitro experiments by Jansen and Llinas (Jahnsen and Llinás, 1984a; Jahnsen and Llinás, 1984b), demonstrating that isolated thalamic neurons have oscillatory behaviors of 6 or 10 Hz depending on the initial polarization levels of the membrane potentials. Nunez (Nunez, 1981; Nunez, 1989; Nunez, 1995) related alpha oscillations with standing waves, thus proposing a global theory for the generation of alpha activity (instead of local epicenters).

1.2. Event-related alpha oscillations

Alpha rhythms are present in a spontaneous way or can be generated as a response to external or internal events (e.g. sensory stimuli), as Galambos (1992) pointed out. In his definition, event-related rhythms are divided into induced rhythms (weak time-locking to the event), evoked rhythms (strong time-locking) and emitted rhythms (occurring in anticipation of expected stimuli). Our study refers mainly to the second class (phase-locked alpha responses as components of averaged ERPs. For theories and experimental results about the relationship between spontaneous and event-related alpha oscillations (which is beyond the scope of this article, see Başar, 1980; Başar et al., 1998).

As to the functional meaning of these event-related alpha-oscillations, a number of studies were undertaken (see e.g. Başar et al., 1997 for an overview). Alpha oscillations were found to be related to memory processes and movements (Pfurtscheller and Klimesch, 1992), as well as to several other brain functions, as the following examples demonstrate.

1. Cross-modality experiments: in scalp occipital locations (overlying the visual cortex), evoked alpha rhythms were elicited by visual (adequate) stimuli but not by auditory (inadequate) stimuli. Similar results were also obtained with deep electrode recordings in cats, supporting an interpretation of the evoked alpha rhythm as a correlate of sensory processes (Başar and Schürmann, 1996).
2. Omitted stimulation experiments: in this auditory evoked potential set-up, every fourth tone is omitted and the subject is requested to pay attention to the omission. With this internal stimulation, pre-stimulus EEG shows an alpha phase ordered reproducible pattern linked to a cognitive process, probably related with short-term memory (Başar et al., 1992).

These experiments, and many other works reviewed in Başar et al. (1997), show how alpha rhythms could be correlated even to sensory or cognitive processes depending on the task performed and generators involved.

1.3. Wavelet Transform

Conventional analysis of ERPs is based on amplitude and latency measurements of different frequency peaks. In order to study the behavior of different oscillations upon stimulation, a frequency representation such as the one accessed with the Fourier Transform is very useful due to the fact that oscillations are clearly visualized as peaks in the frequency domain. However, Fourier Transform is not adequate for non-stationary signals and the time evolution of the frequency patterns is lost (Mpitsos, 1989; Blanco et al., 1995a; Blanco et al., 1995b; Quian Quiroga et al., 1997).

Several suggestions have been made as to overcome these problems, including the Wavelet Transform. The Wavelet Transform is an alternative frequency representation that proved to have many advantages: with wavelets the time evolution of the frequency patterns can be followed with an excellent resolution (Appendix A), and furthermore, Wavelet Transform does not require stationarity. These advantages are crucial when analyzing signals as ERPs, where all the interesting activity takes place in fractions of a second.

2. Methods

2.1. Subjects and experimental setup

Experiments were carried out on 10 voluntary healthy subjects without any neurological deficit or medication known to affect the EEG. In an acoustically isolated and dimly illuminated room two types of experiments were performed (note that these conditions were chosen to minimize spontaneous alpha oscillations, which is favorable for recording alpha responses to visual stimuli) (Başar, 1980).

1. Visual evoked potential (VEP): subjects were watching a checkerboard pattern (sidelength of the checks: 50'), the stimulus being a checker reversal ($N = 100$ stimuli).
2. Non-target/target stimuli: subjects were watching the same pattern as above. Two different stimuli were presented in a pseudo-random order. Non-target stimuli (75%) were pattern reversal, and target stimuli (25%) consisted of a pattern reversal with horizontal and vertical displacement of one-half of the square side length.

Subjects were instructed to pay attention to the appearance of the target stimuli (N = 200 stimuli).

The inter-stimulus interval varied pseudo-randomly between 2.5 and 3.5 s. After each pattern reversal, the reverted pattern was shown for 1 s, then the pattern was re-reverted. Recordings were made following the international 10/20 system in 7 different electrodes (F3, F4, Cz, P3, P4, O1, O2) referenced to linked earlobes. Data were amplified with a time constant of 1.5 s and a low-pass filter at 70 Hz by using a Schwarzer EEG machine. For each single sweep, 1 s pre- and post-stimulus EEG were digitized with a sampling rate of 500 Hz and stored in a hard disk by using a Brain Data EEG acquisition unit (note that the length of the post-stimulus EEG corresponds to the time during which the reverted pattern was visible).

2.2. Data analysis and processing

After visual inspection of the data, 30 sweeps free of artifacts were selected for each type of stimulus (VEP, non-target and target) for the analysis. The multi-resolution decomposition method was used for separating each single sweep into scale levels (wavelet software courtesy of Dr. A. Ademoglu and Professor T. Demiralp), by using a quadratic B-Spline as mother wavelet. After a 5 octave wavelet decomposition, the coefficients of the following bands were obtained (Fig. 3; band limit values are rounded): 63–125, 31–62 (gamma), 16–30 (beta), 8–15 (alpha), 4–7 (theta) and 0.5–4 Hz band (delta). Coefficients of the scale level corresponding to the alpha band were submitted to further analysis. For each subject, the alpha coefficients of the 30 single sweeps were averaged and then compared statistically. Finally, results for all subjects were averaged to obtain a grand average. The temporal resolution of the scale corresponding to the alpha band was 64 ms. However, we should remark that the real resolution will depend on the characteristics of the signal and the mother function (i.e. how the mother function matches the signal). In this respect, the optimal resolution of B-Splines was shown with numerical computations (Unser et al., 1992). It is also interesting to note that non-redundancy is important for increasing the computational speed.

2.3. Statistical analysis

For statistical analysis, wavelet coefficients were rectified for each subject. Then, the maximum coefficients and their time delay with respect to the stimulus occurrence were computed in the first 500 ms post-stimulation, due to the fact that upon inspection no maximum alpha responses were observed later than this value. Comparison between modalities and electrodes were done by using a multiple factor ANOVA test with two factors: stimulus type (VEP, non-target and target) and electrode location (F3, F4, Cz, P3, P4, O1, O2).

Since some subjects showed a slow decay of the alpha responses upon target stimulation in occipital and parietal electrodes, for these electrodes the mean value of the rectified coefficients were compared in a 'late' time window extending from 500 to 1000 ms by using a one-way ANOVA test (factor stimulus type: VEP, non-target and target).

2.4. Comparison between wavelets and conventional digital filtering

Fig. 1 gives some examples of single-trial evoked potentials, thus allowing us to compare results obtained with Wavelet Transform and with digital filtering. In addition, the figure shows the relation between the wavelet coefficients and the waveforms reconstructed from the wavelet coefficients for the scale corresponding to the alpha band (note that throughout this article the statistical tests refer to wavelet coefficients, while figures show the corresponding reconstructed waveforms). We would like to remark that the sweeps selected do not necessarily show a clear event-related response, but they are suitable for showing the better resolution achieved with the multi-resolution decomposition based on the Wavelet Transform in comparison with conventional digital filtering. The digital filter used was an 'ideal filter' (i.e. a digital filter based on band pass filtering in the Fourier domain used in several earlier papers) (Başar, 1980), with the filter limits set in agreement with the limits obtained with the multi-resolution decomposition for the alpha band.

As a general remark, we can state that with the wavelet coefficients a better resolution and localization of the features of the signal is achieved. In between the vertical dotted lines in sweep #1, 3 oscillations in the alpha range are shown, with the last oscillation having a larger amplitude as observed in the original sweep. This is well resolved with the wavelet coefficients as well as in the reconstructed form. However, the fine structure of this train of alpha oscillations is not resolved by digital filtering; i.e. reading a maximum from this curve is imprecise. In sweep #2, in between the dotted vertical lines, a transient is shown with a frequency clearly lower than the range of alpha band. The digital filtering does not resolve this transient and it spuriously 'interpolates' alpha oscillations in continuity with the ones that precede or follow the transient. However, the wavelet coefficients show a decrease in this time segment, this phenomenon being also visible in the reconstructed form. Something similar occurs in sweep #3 with the transient marked with an arrow. In fact in this last case, the transient is due to the cognitive P300 wave typically obtained upon target stimuli. With wavelets it is visible that, as in the original signal, there is no important contribution of alpha oscillations in this time range, the digital filter having not enough resolution for resolving this. The better time-frequency resolution of wavelets (in this case a better frequency localization for a certain time range) can be also seen in sweep #4. In the original signal, in between

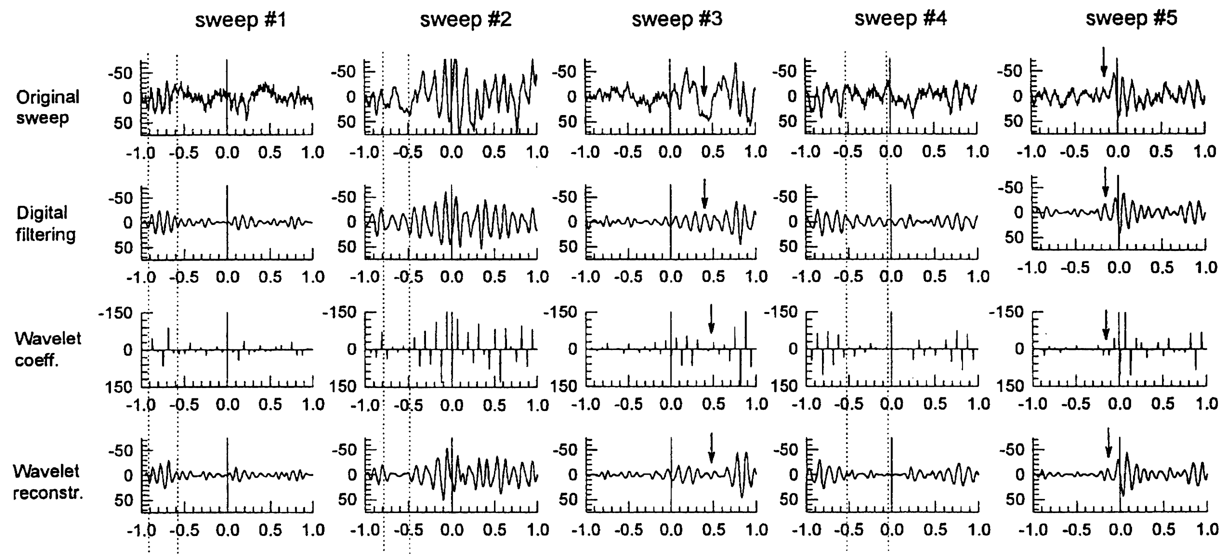

Fig. 1. Examples of the better performance obtained with the Wavelet Transform in comparison with digital filtering in 6 single sweeps. The first row shows the original signal, the second row the result after a digital filtering in the alpha range (8–15 Hz) and the last two rows show the wavelet coefficients in the alpha band and the reconstruction of the signal from the coefficients.

the vertical dotted lines there is a marked oscillation of about 4–6 Hz, corresponding to the theta band. The digital filtered signal shows an alpha oscillation not present in the original signal. However, due to its better resolution, the wavelet coefficients and the reconstructed signal show a clear decrease for this time range. Finally, sweep #5 shows a ringing effect (i.e. spurious oscillations appearing before the stimulation time point due to time resolution limitations). The oscillation before the stimulation time is marked with an arrow and appears in the digital filtered signal with more amplitude than in the original signal, this effect being overcome with wavelets.

3. Results

The grand average wideband filtered (0.5–70 Hz) evoked potentials are shown in Fig. 2. The left side corresponds to VEP, the center to non-target stimuli and the right side to target stimuli. The P100 response is clearly visible upon all stimuli types at about 100 ms, and is best defined in occipital locations where it reaches amplitudes of about 8 μV. In the case of target stimulation, a marked positive peak appears between 400 and 500 ms, according to the expected cognitive (P300) response.

As an example, Fig. 3 shows the multi-resolution decomposition and the reconstruction of the different scales from the left occipital event-related responses of the subject J.A. upon target stimulus. The left part of the figure shows the wavelet coefficients used for statistical calculations. The right part shows the corresponding reconstructed waveforms which are given in the following figures for better visualization of the responses. In this case, in the first 300 ms we can observe an increase in the alpha and theta band. Moreover, there is an increase in the delta band only upon target stimulus correlated with the P300 response. As this study deals with alpha responses in relation with earlier hypotheses (see Section 1), in the following we will only analyze the results of the scale level 4, corresponding to the alpha band (8–15 Hz).

Fig. 4 shows the wavelet components in the alpha band for the subject J.A. for all the electrodes. One second pre- and 1 s post-stimulation are plotted. Alpha components corresponding to the pre-stimulus EEG have about 5 μV and upon all our stimulus types, post-stimulus amplitude increases are clearly marked in posterior locations reaching values up to 20 μV. Furthermore, in posterior electrodes responses upon target stimulation are prolonged compared with the other two stimulus types.

One subject (A.F.) showed a different behavior, reaching pre-EEG activity values of up to 15 μV without post-stimulus amplitude increases. The lack of event-related responses should be attributed to the high spontaneous alpha activity that distorts the response to the stimuli.

Results for the grand average of the 10 subjects (Fig. 5) are qualitatively similar to the ones outlined for the first subject. Amplitude increases were distributed over the whole scalp for the 3 stimulus types, best defined in the occipital electrodes. The multiple factor ANOVA test showed no significant differences between stimulus types. However, the electrode differences were significant, confirming the predominant localization of the amplitude increases in the occipital locations with a lower response in the anterior electrodes ($P < 0.01$; Table 1).

The delay of the maximum response in occipital electrodes was about 180 ms after stimulation (Table 2). In parietal

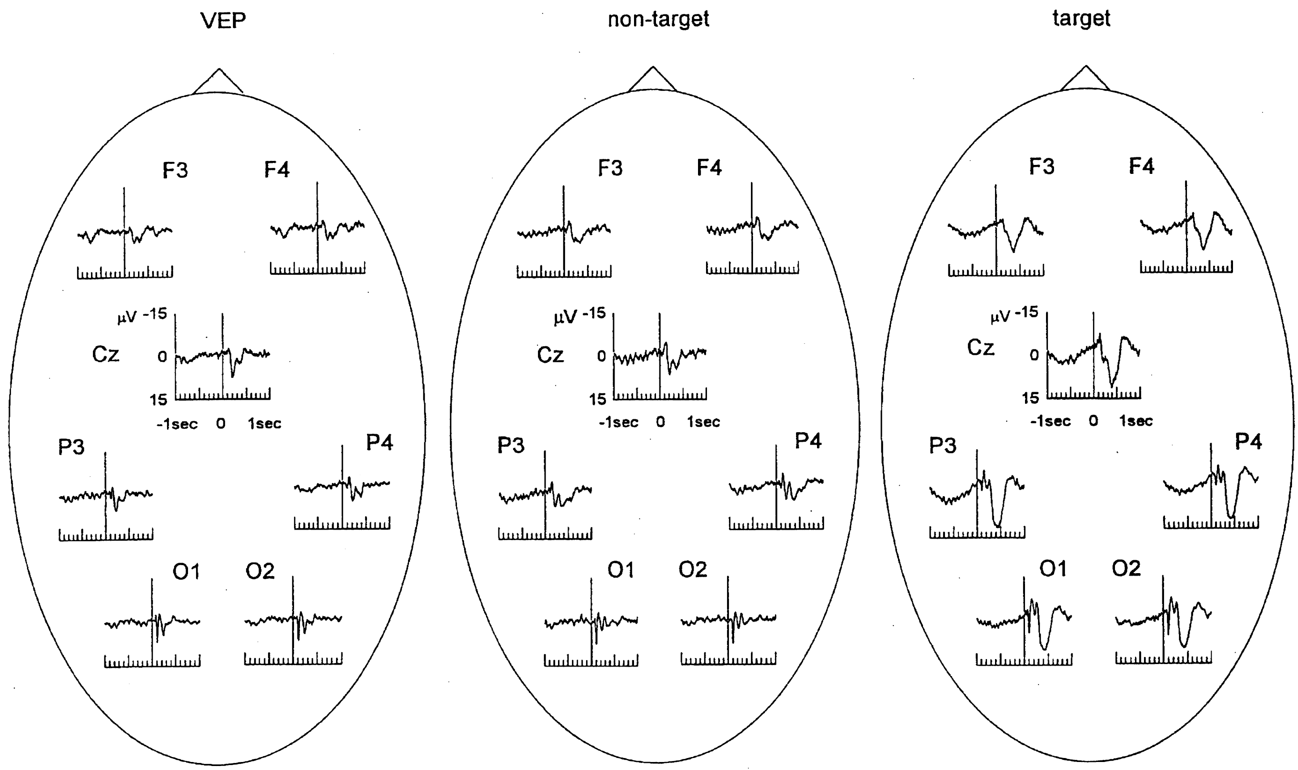

Fig. 2. Grand average of the event-related responses.

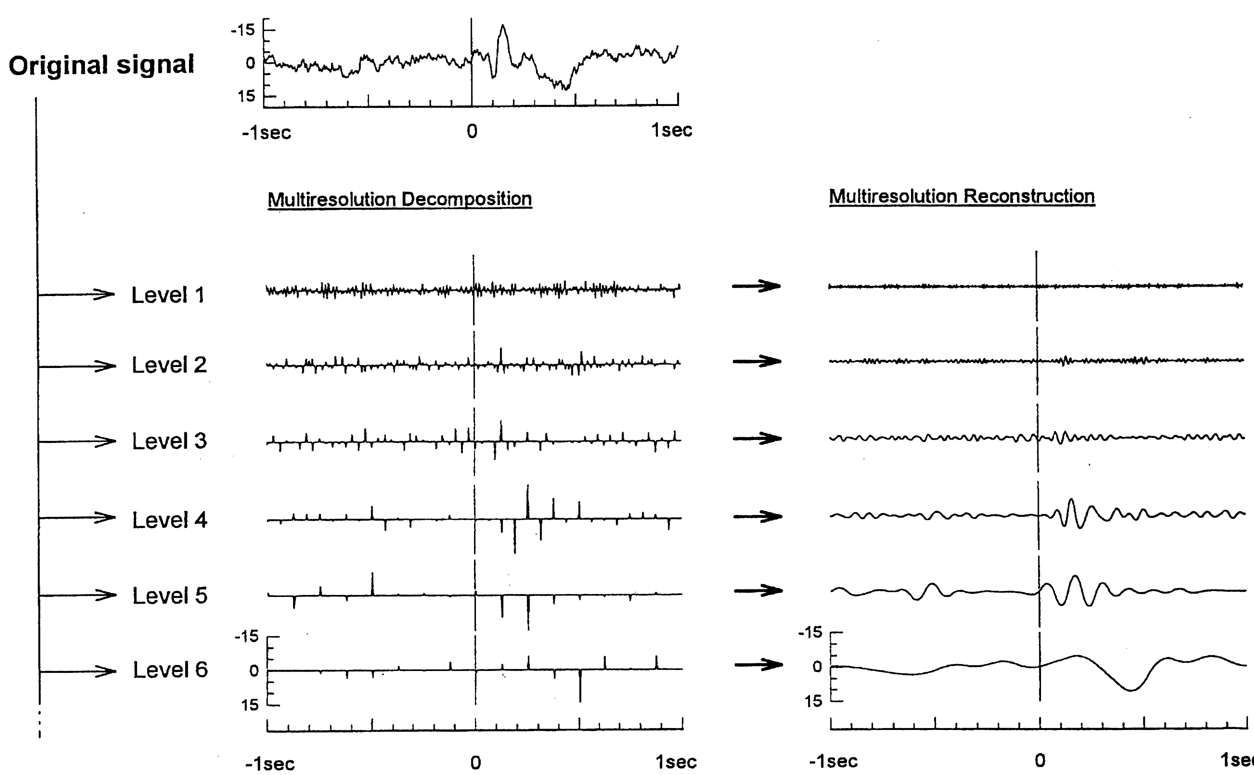

Fig. 3. Multi-resolution decomposition method for the event-related responses of the left occipital electrode of the subject J.A. upon TARGET stimulus. The signal is decomposed in scale levels, each one representing the activity in different frequency bands. The wavelet coefficients show how closely the signal matches locally the different dilated versions of the wavelet 'mother function' (in this case a quadratic B-Spline). Furthermore, by applying the inverse transform, the signal can be reconstructed from the wavelet coefficients for each scale level. Along the y-axis, values are in microvolts for the original signal and the reconstructed signals, and in arbitrary units for the wavelet coefficients.

electrodes the maximum appears about 30 ms later, and in central and frontal electrodes between 50 and 100 ms after the occipital one. After applying the multiple factor ANOVA test, we verified statistically that the frontal and central responses were significantly delayed in comparison with the occipital ones.

It is also interesting to note that responses at posterior electrodes upon target stimulation are prolonged in comparison with the non-target and VEP ones. This coherent alpha activity extended up to a second post-stimulation. With the other stimuli types, event-related responses have an abrupt decay after 200–300 ms post-stimulus. One-way ANOVA tests comparing stimulus type for the posterior electrodes (P3, P4, O1, O2) showed that this phenomenon was not statistically significant. However, it is interesting to remark that although this result was not consistent for the whole group it was clearly seen in some of the subjects, as in the case of the subject J.A. (Fig. 4).

4. Discussion

4.1. Functional correlates of alpha oscillations

Post-stimulus amplitude increases of alpha band were independent of the type of stimulus, and were thus not dependent on the cognitive process related with target stimuli. The ubiquity of the alpha responses we observed, may be interpreted in terms of a general responsiveness of several brain areas in this frequency range (Başar et al., 1997). However, taking into account the anatomy of the visual pathway (Shepherd, 1988; Mason and Kandel, 1991), the occipital maximum of these responses, as well as the short latency in occipital locations, points at a functional relevance of this alpha response in sensory processing.

Since the days of Adrian (1941), the evoked alpha response was interpreted as the reactiveness of the brain to sensory stimuli. Our work is a complementary approach extending earlier cross-modality experiments (without task, see Section 1), where sensory alpha responses were observed in several structures of the cat brain upon auditory and visual stimulation (for a review of these works see Başar et al., 1997). Although in some cases, as previously demonstrated by Başar (1980) and now observed in subject A.F., high spontaneous alpha activity could inhibit the event-related potentials, the sensory alpha response was clear and statistically significant (note that the experimental environment was chosen to minimize spontaneous alpha activity).

However, we do not consider this process as the only one related with the alpha band. For example, in some subjects (Fig. 4) the alpha responses were prolonged upon target stimuli at posterior locations, possibly reflecting a relationship between alpha prolongation and cognitive processes. Low amplitude and low phase-locking of this late activity could be responsible for the lack of statistical significance when considering the whole group of subjects. For experimental results supporting cognitive functions of certain alpha oscillations, see several previous works (Stampfer and Başar, 1985; Başar et al., 1992; Kolev and Schürmann,

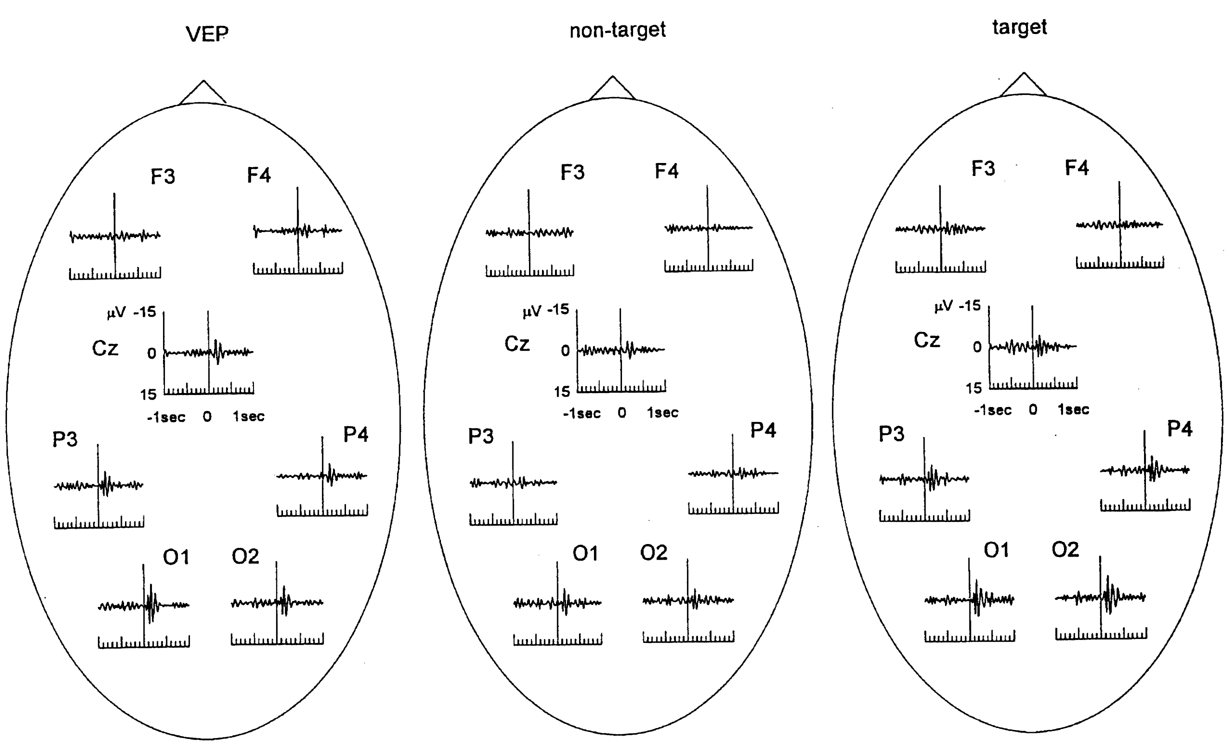

Fig. 4. Alpha band response of one typical subject (reconstructed from the wavelet coefficients corresponding to the alpha band).

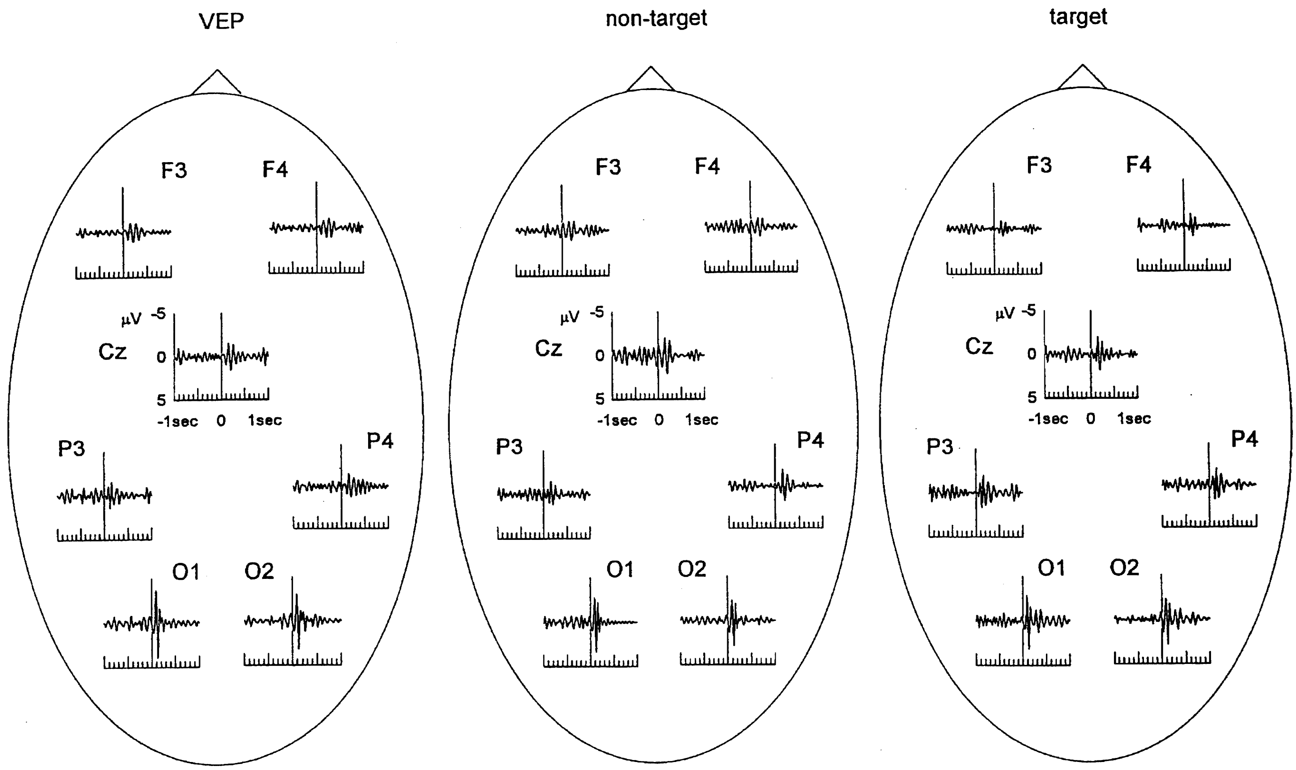

Fig. 5. Grand average of the alpha band responses (reconstructed from the wavelet coefficients corresponding to the alpha band).

1992; Klimesch, 1997; Maltseva and Masloboev, 1997; Petsche et al., 1997). Further experiments applying different types of tasks should be performed in order to learn more about possible relations between event-related alpha oscillations and cognitive processing.

4.2. Sources of the alpha oscillations

Another interesting question about event-related alpha oscillations deals with its sources of generation. We found that alpha responses were best localized in occipital electrodes, but these responses were also present in other locations with some time delay. Owing to the high differences in the time of appearance of the alpha responses between occipital and anterior electrodes, the hypothesis of a single generator and the presence of distributed responses due to volume conduction must be ruled out. A more plausible idea is to think about several generators activated at different times and with different strength, depending on the stimuli and paradigm used. Several previous findings support this view. Alpha rhythms were described mainly in the thalamus and cortex (Adrian, 1941; Andersen and Andersson, 1968; Lopes da Silva and Storm van Leeuwen, 1977), but alpha activity was also found in other structures like the brainstem, cerebellum and limbic system (for a review see Başar et al., 1997). Further evidence showing that alpha rhythms cannot be explained through generators only in the thalamus or cortex, are the experiments performed on the cerebral ganglion of aplysia and with the isolated ganglia of Helix

Table 1
MANOVA comparison of the maximum alpha band wavelet components for the factor electrode[a]

Electrode Mean ± SEM	F3 6.27 ± 0.56	F4 6.72 ± 0.64	Cz 9.80 ± 0.99	P3 8.96 ± 0.85	P4 8.85 ± 0.85	O1 12.65 ± 1.36	O2 11.63 ± 1.22
F3	XXX	–	< 0.05	–	–	< 0.01	< 0.01
F4		XXX	< 0.05	–	–	< 0.01	< 0.01
Cz			XXX	–	–	< 0.05	–
P3				XXX	–	< 0.01	–
P4					XXX	< 0.01	< 0.05
O1						XXX	–
O2							XXX

[a] SEM, standard error of the mean; –, no significance.

Table 2
MANOVA comparison of the time delays of the maximum alpha band wavelet components for the factor electrode[a]

Electrode Delay (ms) ± SEM	F3 246.03 ± 21.09	F4 290.86 ± 23.35	Cz 248.20 ± 22.76	P3 209.20 ± 20.51	P4 209.27 ± 22.10	O1 172.37 ± 18.42	O2 181.03 ± 17.45
F3	XXX	–	–	–	–	< 0.05	< 0.05
F4		XXX	–	< 0.01	< 0.01	< 0.01	< 0.01
Cz			XXX	–	–	< 0.05	< 0.05
P3				XXX	–	–	–
P4					XXX	–	–
O1						XXX	–
O2							XXX

[a] SEM, standard error of the mean; –, no significance.

pomata (Schütt and Başar, 1992; Schütt et al., 1992). These studies provided evidence that 10 Hz activity can be recorded in vitro in these small neural populations, each consisting only of approximately 2000 neurons.

Due to the high differences in the amplitudes and delays between the responses in different locations, we do not consider a possible explanation of our results in terms of a global wave phenomenon (Nunez, 1981; Nunez, 1989; Nunez, 1995).

Our results imply that several structures in the brain generate event-related 10 Hz oscillations. Referring to such oscillations as alpha oscillations, this is consistent with Başar's view of distributed alpha systems in the brain (Başar et al., 1997).

4.3. Utility of the Wavelet Transform in the analysis of EEGs and ERPs

Wavelet decomposition turned out to be a very useful tool for analyzing event-related potentials. Advantages of Wavelet Transform and the multi-resolution decomposition were presented in Section 2 and with more mathematical detail in

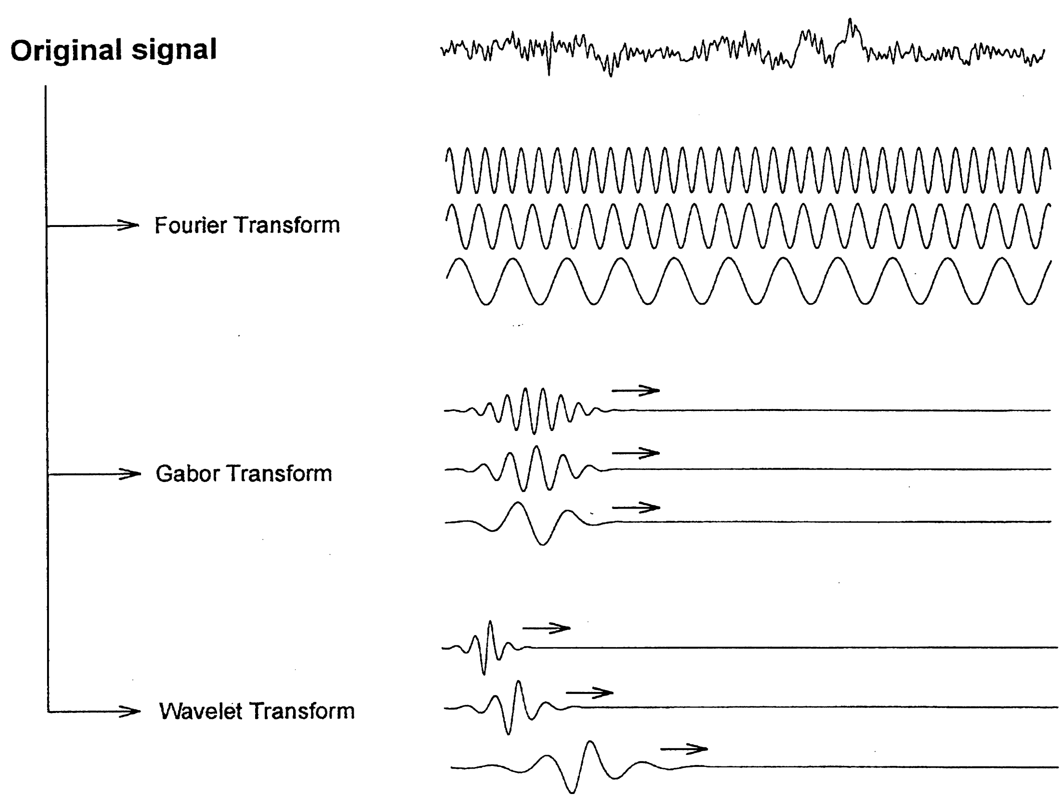

Fig. 6. Frequency and time-frequency methods. The Fourier Transform is obtained by correlating the original signal with complex sinusoids of different frequencies (upper part). In the Gabor Transform, the signal is correlated with modulated sinusoidal functions that slides upon the time axis, thus giving a time-frequency representation (middle part). Wavelets give an alternative time-frequency representation but due to their varying window size, a better time-frequency resolution for each scale is achieved (bottom part). Furthermore, the function to be correlated with the original signal can be chosen depending on the application (e.g. in the graph quadratic B-Splines are shown).

Appendix A (see also Chui, 1992; Strang and Nguyen, 1996). We would like to comment on two issues. First, Wavelet Transform lacks the requirement of stationarity, which is crucial for avoiding spurious results when analyzing brain signals, already known to be highly non-stationary. Second, owing to the varying window size of the Wavelet Transform, a better time-frequency resolution can be achieved. In the case of evoked potentials, only the first 100 ms of the response are relevant and then a good time resolution is essential, in order to make any physiological interpretation of the evoked response.

Several works applied the Wavelet Transform to the study of EEGs and ERP (see a review in Unser and Aldroubi, 1996; or in Samar et al., 1995). One first line of application is for pattern recognition in the EEG. This is achieved by correlating different transients of the EEG with wavelet coefficients of different scales. Schiff et al. (1994a) used a multi-resolution decomposition implemented with B-Spline mother functions for feature extracture in subdurally recorded EEG epileptic seizures. They showed a better performance in comparison with the Gabor Transform, and a similar resolution compared with the continuous Wavelet Transform but with a marked decrease in the computational time. Other works also used this approach for automatic detection of spike complexes characteristic of epilepsy, thus helping in the analysis of EEG recordings from epileptic patients (Schiff et al., 1994b; Clark et al., 1995; Senhadji et al., 1995).

Demiralp et al. (1999) used coefficients in the delta frequency band for detecting P300 waves in single trials of an auditory oddball paradigm. Furthermore, they used this approach for making a selective average of the single trials, thus obtaining a better definition of the P300. Başar et al. (1999) reported the utility of Wavelet Transform for classifying different type of single sweep responses to cross-modality stimulation (see Section 1).

A digital filtering of ERPs based on the Wavelet Transform was proposed by Bertrand et al. (1994). They used the method as a noise reduction technique, reporting better results than the ones obtained with Fourier based methods, especially in the application to non-stationary signals. The main goal of this type of filtering is to extract the event-related responses from the single sweeps by eliminating the contribution of the ongoing EEG, thus avoiding the necessity of averaging the single sweeps. In this context, Bartnik et al. (1992) characterized the event-related responses from the wavelet coefficients, then using selected coefficients for isolating the event-related responses from the background EEG in the single trials; a similar approach also being later proposed by Zhang and Zheng (1997).

A further decomposition of the scale levels obtained from the multi-resolution decomposition (i.e. a subdivision of the frequency bands) can be achieved by using wavelet packets. Blanco et al., (1998) used 'trigonometric wavelet packets' and described the temporal evolution of frequency peaks during a Grand Mal seizure, confirming with a better resolution the previous results obtained by using Gabor Transform (Quian Quiroga et al., 1997). Furthermore, they defined an information entropy from the wavelet coefficients for quantifying the distribution of EEG activity (related with order and disorder) in different frequency bands. Furthermore, this entropy defined from the wavelet coefficients turned out to be very useful in characterizing event-related responses (Quian Quiroga et al., 1999; Rosso et al., 1998).

Akay et al. (1994) used the Wavelet Transform for characterizing electrocortical activity of fetal lambs, reporting much better results than the ones obtained with the Gabor Transform. Thakor et al. (1993) analyzed somatosensory EPs of anesthetized cats with cerebral hypoxia, by using the multi-resolution decomposition. They report that selected coefficients are sensitive to neurological changes, with comparable results obtained with Fourier-based methods. Ademoglu et al. (1997) used wavelet analysis for discriminating between normal and demented subjects by studying the N70-P100-N130 complex response to pattern reversal visual evoked potentials. Kolev et al., (1997) used the multi-resolution decomposition for studying the presence of different functional components in the P300 latency range in an auditory oddball paradigm. Başar et al. (1999) used the wavelet decomposition for studying the alpha responses to cross-modality stimulation, reporting similar results than the ones obtained with digital filtering.

In this work, we showed with some selected sweeps how the multi-resolution decomposition implemented with B-Splines functions leads to a better resolution of the event-related alpha oscillations, in comparison with a conventional ideal filter used in several previous works. Moreover, due to the fact that the multi-resolution decomposition method is implemented as a filtering scheme, it can be seen as a way to construct filters with an optimal time-frequency resolution. This exemplifies and complements the theoretical description of the advantages of wavelets introduced in the methods section. In this work, the access to an optimal time-frequency resolution was very important for investigating functional properties of event-related alpha oscillations and for demonstrating their distributed nature. Furthermore, the multi-resolution decomposition is a way of data reduction, thus providing relevant (i.e. non-redundant) coefficients that allow a straightforward implementation of statistical tests.

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Appendix A. Wavelet Transform and multi-resolution decomposition

In this section, we will present in a very intuitive way the concept of Wavelet Transform and multi-resolution decomposition, especially focussing on their advantages over previous methods for representing the signals in the frequency domain.

A.1. From Fourier to wavelets

Until now, the most widely used frequency representation has been the Fourier Transform. It quantifies the amount of activity in different frequency bands by calculating the correlation (i.e. the 'matching') between the original signal *x(t)* and sines and cosines of different frequencies (represented by the complex functions $e^{-i\omega t}$; see upper part of Fig. 6; Dumermuth and Molinari, 1987; Lopes da Silva, 1993).

$$X(\omega) = \int_{-\infty}^{+\infty} x(t)\cdot e^{-i\omega t}\cdot dt \equiv \langle x(t) \mid \mathrm{e}^{-i\omega t}\rangle \tag{A.1}$$

In the following, we will keep the bracket notation for denoting correlation. The Fourier Transform gives a useful representation but it has two main disadvantages. Firstly, it requires stationarity of the signal, while EEGs are known to be highly non-stationary (Mpitsos, 1989; Lopes da Silva, 1993; Blanco et al., 1995a), and secondly, the Fourier Transform gives no information about the time at which the frequency patterns occur.

These disadvantages are partially resolved by using the Gabor Transform (also called the short-time Fourier Transform). With this approach, the Fourier Transform is applied to time-evolving windows of a few seconds of data smoothed with an appropriate function (Blanco et al., 1995b; Cohen, 1995; Quian Quiroga et al., 1997). Gabor Transform can be seen as a correlation between the signal and sines and cosines 'windowed' with an appropriate function (e.g. a Gaussian function as showed in the middle part of Fig. 6).

$$G_D(\omega, t) = \langle x(t) \mid g_D(t)\cdot \mathrm{e}^{-i\omega t}\rangle \tag{A.2}$$

Note that G_D (w,t) is the same as a Fourier Transform but with the introduction of the sliding window $g_D(t)$ of wide D and center in t. Then, the evolution of the frequencies can be followed and the stationarity requirement is partially satisfied by considering the signals to be stationary in the order of a few seconds (the window length). However, when windowing the data, one critical limitation appears due to the uncertainty principle (Chui, 1992; Cohen, 1995; Strang and Nguyen, 1996). If the window is too narrow, the frequency resolution will be poor (i.e. there will be 'not enough oscillations' for defining a frequency), and if the window is too wide, the time localization will be not so precise. If we denote by σ_t the time uncertainty (time duration) and by σ_ω the uncertainty in the frequencies (frequency bandwidth), the uncertainty principle can be expressed as follows:

$$\sigma_t\cdot\sigma_\omega \geq \frac{1}{2} \tag{A.3}$$

In other words, sharp localizations in time and frequency are mutually exclusive and they have a limit called the optimal time-frequency resolution. Data involving slow processes will require wide windows and, for data with fast transients (high frequency components) a narrow window will be more suitable. Then, due to its fixed window size (i.e. the same size for all frequencies), the Gabor Transform is not optimal for analyzing signals involving different ranges of frequencies.

In recent years, Grossmann and Morlet (1984) introduced the Wavelet Transform in order to overcome this problem. The main idea is to take narrow windows for high frequencies and wide windows for the lower ones, in order to have a sufficient number of oscillations at every scale (see bottom part of Fig. 6). This varying window size leads to a time and frequency resolution adapted to each scale (Mallat, 1989; Chui, 1992; Strang and Nguyen, 1996). Moreover, since each window contains only a few oscillations, wavelet decomposition lacks the requirement of stationarity.

Another characteristic of the Wavelet Transform is that the 'mother function' to be correlated with the original signal is not necessarily a sinusoidal one. On the contrary, there are several different wavelet functions that can be used as mother functions, each one having different characteristics that can be more or less suitable depending on the type of signals to be analyzed. All these advantages are particularly important when analyzing non-stationary signals of short duration such as ERPs.

A.2. Continuous and dyadic wavelets

As to the Wavelet Transform, the functions to be compared with the original signal are a set of elemental functions generated by dilatations and translations of a unique mother wavelet $\psi(t)$.

$$\psi_{a,b} = |a|^{-1/2}\psi\left(\frac{t-b}{a}\right) \tag{A.4}$$

where a and b are the scale and translation parameters, respectively. As a increases, the wavelet function becomes more narrow, and by varying b it is displaced in time. The continuous Wavelet Transform of a signal *x(t)* is defined as the correlation between the signal and the wavelet functions $\psi_{a,b}$ i.e:

$$W_\psi X(a,b) = \langle x(t) \mid \psi_{a,b}\rangle \tag{A.5}$$

The continuous Wavelet Transform maps a signal of one independent variable t onto a function of two independent variables *a,b*. This procedure is redundant and not efficient for algorithm implementations. In consequence, it is more practical to define the Wavelet Transform only at discrete scales a and times b. One way to achieve this is by choosing the discrete set of parameters $\left\{a_j = 2^j; b_{j,k} = 2^j k\right\}$. Then, replacing in Eq. (4), the wavelet functions to be compared with the original signal, called dyadic wavelets, will be:

$$\psi_{j,k} = |2|^{-j/2}\psi\left(2^{-j}t - k\right) \tag{A.6}$$

A.3. Multi-resolution decomposition

Contracted versions of the wavelet function will match the high- frequency components of the original signal and the dilated versions will match low-frequency oscillations. Then, by correlating the original signal with wavelet functions of different sizes we can obtain the details of the signal for different scale levels. These correlations with the different dyadic wavelet functions can be arranged in a hierarchical scheme called multi-resolution decomposition (Mallat, 1989). This method starts by correlating the signal with shifted versions (i.e. thus giving the time evolution) of a contracted wavelet function; the coefficients obtained therefore provide the 'detail' of the high-frequency components. The remaining part will be a coarser version of the original signal that can be obtained by correlating the signal with a 'scaling function', which is orthogonal to the wavelet function. Finally, the wavelet function is dilated and from the coarser signal the procedure is repeated, thus giving a decomposition of the signal in different scale levels, or what it is analog, in different frequency bands (Fig. 3). This method can be implemented with very efficient and fast algorithms, and gives an optimal time-scale representation of the signal. Furthermore, signals corresponding to the different scales can be reconstructed by applying an inverse transform (Fig. 3). Further details of the multi-resolution scheme and its implementation can be found in previous works (Mallat, 1989; Schiff et al., 1994a; Bartnik et al., 1992; Blanco et al., 1996; Strang and Nguyen, 1996; Demiralp et al. 1999; Blanco et al., 1998).

A.4. B-Spline wavelets

A final point, is how to choose the mother functions to be compared with the signal. In principle, the wavelet function should have a certain shape that we would like to localize in the original signal. However, due to mathematical restrictions, not every function can be used as a wavelet. Then, one criterion for choosing the wavelet function is that it looks similar to the patterns of the original signal. In this respect, B-Spline functions seem suitable for decomposing ERPs (see bottom part of Fig. 6). B-Splines are piecewise polynomial functions of a certain degree. The following properties make them very suitable for the analysis of ERPs (Chui, 1992; Unser et al., 1992; Strang and Nguyen, 1996; Unser, 1997):

1. Smoothness: the smooth behavior of B-Splines is very important in order to avoid border effects when making the correlation between the original signal and a wavelet function with abrupt patterns.
2. Time-frequency resolution: it was demonstrated that B-Spline functions have nearly optimal time-frequency resolution (i.e. nearly the maximum allowed by the uncertainty principle; Unser et al., 1992).
3. Compact support: this means that the wavelet function does not extend to infinity. This fact is important, in order not to include in a certain wavelet coefficient correlations with points far in the past or in the future.
4. Semi-orthogonality: the use of B-Splines as mother functions when applying the multi-resolution decomposition guarantees orthogonality between the different scales.

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