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Spectral dynamics of electroencephalographic activity during auditory information processing

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Abstract

Dynamics of electroencephalographic (EEG) activity during auditory information processing were evaluated in response to changes in stimulus complexity, stimulus discriminability and attention using the oddball paradigm. In comparison to pre-stimulus baseline conditions, auditory stimulation synchronized EEG activity in delta, theta and alpha frequency bands. Event-related synchronization (ERS) effects were greatest at approximately 3 Hz (theta frequency band), and their magnitude depended on stimulus and task demands. Event-related desynchronization (ERD) of EEG activity was observed in the beta frequency band. This effect was greatest at approximately 21 Hz but occurred only for easily discriminable stimuli in attention-related target conditions. Because active discrimination tasks also required a button-press response with the right hand, ERDs involved more complex responses that may be related to a combination of perceptual, motor and cognitive processes. These results demonstrate that oddball and attention-related EEG responses to auditory stimulation could be characterized in the frequency domain. The specific design and analysis features described herein may prove useful since they provide a simple index of the brain's response to stimulation while at the same time provide powerful information not contained in typical time domain analysis.
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Key words: Electroencephalography; Event-related synchronization; Event-related desynchronization; Event-related brain dynamics; Spectral analysis; Time domain analysis; Psychophysics

1. Introduction

Understanding the neural events, which subserve sensory, motor and cognitive processing, is of fundamental importance to neuroscience research. A common approach to studying information processing in neural systems is based on a time domain strategy whereby composite time-averaged waveforms are extracted from epochs of electroencephalographic (EEG) activity by stimulus-triggered events. By averaging over many individual trials, event-related potentials (ERPs) can be delineated from background noise when signal-to-noise ratio reaches a favorable state. This approach assumes that data contained within individual recording epochs are composed of a linear combination of time invariant phase-locked responses and background noise.

Stimulus-induced rhythmic EEG activity, which is not phase locked to an event, is also contained within individual trials, but this activity is *not* detected by the time domain ERP. Time domain processing techniques, such as linear averaging, remove non-phase-locked EEG activity by phase cancellation (Makeig, 1993; Pantev, 1995). This limitation can be significant because non-phase-locked EEG rhythmicities are also reactive to internal or external events and changes in their intrinsic resting or idling states can be detected by appro-

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Abbreviations: EEG, electroencephalographic; ERP, event-related potential; RMS, root mean square; ERS, event-related synchronization; ERD, event-related desynchronization; MMN, mismatch negativity; EOC, electro-ocular; SPL, sound pressure level; JND, just noticeable difference; ANOVA, analysis of variance; PM, phase modulation; AM, amplitude modulation

priate methodology and analysis. Indeed, sensory stimulation and/or motor tasks can modulate EEG in a dynamic manner by synchronizing or desynchronizing ongoing activity in various frequency bands (Pfurtscheller and Lopes da Silva, 1999; Pfurtscheller, 1999, 2001). However, detecting synchronized or desynchronized EEG activity requires special design considerations and analysis techniques. These methods include comparison of event trials to a comparable pre-stimulus baseline, use of frequency domain spectral analysis, as well as other analytical processing not typically applied in time domain ERP experiments.

Various methods are available for spectral analysis (e.g., Marple, 1987). However, similar results may also be obtained by selectively bandpass filtering EEG, computing signal power (i.e., root mean square (RMS) values or estimating intertrial variance) and averaging over individual trials (Kalcher and Pfurtscheller, 1995). With this methodology, increases in band power of rhythmic EEG activity in response to sensory or motor events have been termed event-related synchronizations (ERSs); decreases in band power of rhythmic EEG activity in response to sensory or motor events have been termed event-related desynchronizations (ERDs) (Pfurtscheller, 2001). ERS and ERD of rhythmic EEG activity have been correlated with various cognitive processes related to attention, memory and language (e.g., Krause et al., 1996; Basar et al., 1999; Klimesch et al., 2001).

To date, limited information is available on the behavior of rhythmic EEG in response to auditory stimulation under different experimental conditions (e.g., Makeig, 1993; Krause et al., 1994, 1995; Pantev, 1995; Fell et al., 1997; Sutoh et al., 2000; Crone et al., 2001; Gurtubay et al., 2001; Kolev et al., 2001; Kaiser et al., 2002). In the present study we used the *oddball paradigm*, since the relative simplicity of this approach has proven useful to study different degrees of information processing on ERPs. With this method, infrequent target/deviant stimuli (oddballs) are presented randomly within a stream of frequent standard stimuli. Depending on instructional set, individuals can either actively discriminate or passively listen to the oddballs, while at the same time ignoring the standards. Active listening requires the ability to discriminate between stimulus conditions, retain relevant stimulus features in memory, and direct attention to the task. When data are sorted by stimulus type and time averaged over individual trials, two separate ERPs are manifest; the ERP to the standard and the ERP to the target/deviant stimulus. The ERP to the standard is considered obligatory, in the sense that it occurs even when the experimental task does not require an active discrimination. When active discrimination to the target is required, either by silent counting or by button-press response

selection, a more complex waveform can be manifest. The additional positive wave or waveform complex detected in the latency range of approximately 300 ms (P300) has been interpreted as an index of attention and memory updating or inhibition of stimulus-related cortical excitation (e.g., Squires et al., 1975; Donchin and Coles, 1988; Birbaumer et al., 1990; Picton, 1992; Polich, 1999).

Similarly, if the same oddball paradigm is applied but active discrimination is not required, two response types are also evident. There is an obligatory response to the standard, and depending on stimulus and recording parameters, a differential response to the deviant[1] stimulus can also be delineated. Under these conditions, the response to the deviant is reportedly indexed as an enhanced negativity. This differential response in brain state is subsumed under the rubric of mismatch negativity (MMN) (Näätänen, 1992). Given that averaged time domain waveform analysis is the method typically used in this area of research, MMN is distinguished from P300 based on post-stimulus latency (100–200 ms range) and because MMN is thought to be independent of attention (i.e., active discrimination). Current dogma suggests that MMN is representative of a centrally located, involuntary change-detection mechanism, activated during sequential stimulus tasks where a deviant stimulus is perceptually different from an internally represented standard (Näätänen, 1992).

Several investigations have examined the frequency domain response of rhythmic EEG within the context of the oddball paradigm and the P300 time domain response. Many of these studies provide limited information because they focus on only a narrow spectral band of EEG activity. For example, Fell et al. (1997) examined RMS values of EEG bandpass filtered between 30 and 45 Hz (i.e., gamma band power). They found increased gamma power in trial averages for the target stimulus. However, single trial analysis showed a decrease in gamma power relative to baseline. In contrast, Gurtubay et al. (2001) applied wavelet analysis in the range of 30–60 Hz and obtained an increase in gamma activity. Sutoh et al. (2000) examined alpha band activity quantified as the band power of the signal passed through a Gabor filter centered at 10 Hz. They found reduced power for target but not for standard stimuli. Spencer and Polich (1999) performed spectral analysis with an unidentified method used to compute band power in classical delta, theta, and alpha frequency bands. They found increased power in delta and theta bands that covaried with manipulations that

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[1] We use the terminology *standard* and *target* to indicate those stimulus conditions in the oddball paradigm where active discrimination is required; in passive listening conditions, the terms *standard* and *deviant* are applied.

enhanced the P300 (i.e., counting targets, reduced probability of targets). Yordanova et al. (2001) examined EEG power in lower (7–10 Hz) and higher (10–14 Hz) alpha bands. They found that both lower and higher frequency alpha bands showed similar task and electrode effects for ERDs and P300.

The present study used the oddball paradigm to examine dynamics of event-related changes in scalp-recorded EEG activity during auditory information processing. Herein, we focus on changes in underlying EEG rhythmicities by experimentally controlling (1) stimulus complexity, (2) stimulus discriminability, and (3) attention to specific events. These initial experiments serve to illustrate the application of broadband spectral analysis, combined with specific design considerations and statistical analyses as a means of quantifying auditory event-related EEG activity. Broadband spectral analysis is a method for studying event-related changes in EEG that could be instrumental in gaining a more comprehensive understanding of perceptual and cognitive aspects of neural information processing in humans.

2. Materials and methods

2.1. Participants

Ten adults (four males; six females) ranging in age from 18 to 52 years, with no reported hearing deficits (pure tone thresholds < 20 dB hearing level (HL), 0.25–4.0 kHz, bilaterally), participated in this experiment. All individuals were briefed as to the nature of the experiment and provided signed informed consent. The Internal Review Board (IRB) of the Albany Medical College approved the study.

2.2. Data acquisition

EEG activity was recorded from 24 electrodes, covering left, right and central scalp locations (F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T3, T4, T5, T6, FPz, Cz, Fz, Pz, A1, A2, M1, M2, PM1, PM2) based on the 10–20 system of the International Federation (Jasper, 1958). Non-standard sites over left and right mastoid (M1, M1) and posterior left and right mastoid locations (PM1, PM2) were included to obtain more comprehensive coverage over lateral scalp areas and to aid in spatial filtering (Laplacian) operations. Scalp electrodes were equally spaced at a distance of 6 cm (facilitated by use of a commercially available recording cap), all referenced to a non-cephalic sterno-vertebral site (Stephenson and Gibbs, 1951) and grounded to the left forearm. Two additional bipolar channels were used for monitoring vertical and horizontal electro-ocular (EOC) activity. These channels were included so that EEG contaminated with high level EOC activity could be removed from the data prior to analysis. The horizontal EOC channel, with electrodes placed over the outer canthus of each eye, was used to detect high amplitude low frequency lateral eye movements. The vertical EOC channel, with electrodes placed over superior and inferior orbicularis oculi muscles of the left eye, was used to detect eye blinks. EEG activity was collected and stored in digital form on a trial-by-trial basis using a commercially available hardware and software configuration (SCAN and STIM systems, NeuroScan, Inc., El Paso, TX, USA). Signal processing (i.e., spectral analysis, time domain averaging, spatial filtering, generation of scalp topographies) was performed off-line.

During EEG data collection, individuals were tested in a lighted, commercially constructed sound attenuating test booth (Tracoustics, RE 145) and were seated on a padded reclining chair with head, leg and arm support. Participants were instructed to remain awake, keeping eyes open and focused on a designated point on a wall looking straight ahead. They were also advised to minimize any unnecessary eye movements, body movements or muscle contractions during individual test conditions. EEG activity was collected over a 1200 ms time epoch (600 ms pre-stimulus silent interval; 600 ms post-stimulus interval), amplified ×20 000, filtered between 0.1 and 300 Hz (12 dB/octave slope; Grass Model 12 Neurodata Acquisition System) and digitized at a rate of 1000 Hz with 16-bit resolution (Fig. 1). Triggering for EEG data acquisition, A/D conversion and stimulus presentation were performed by the aforementioned STIM and SCAN systems. Individual trials of EEG activity exceeding +50 μV were rejected as artifacts and not included in data collection.

The experimental task followed an oddball paradigm and the design consisted of eight separate conditions that evaluated differences in stimulus complexity (pure tones vs. frequency-modulated tone glides), stimulus discriminability (easy vs. difficult discriminations) and attention (conditions requiring active discrimination to the target vs. passive listening to the deviant). Stimuli were presented binaurally at a level approximating 80 dB sound pressure level (SPL) through insert earphones (Etymotic-ER3A). Pseudo-random interstimulus intervals (3.0 s, ±0.5 s) were used and the eight experimental conditions were presented to each participant in a different random order. In the attend conditions, individuals were instructed to press a button on an instrument panel with their right index finger (STIM system response pad, P/N 1141) to indicate every time the target/oddball stimulus was discriminated from the stream of standard stimuli. The button-press response also allowed for reaction time measures to the target stimulus to be recorded. In the no attend conditions, individuals

Experimental Paradigm
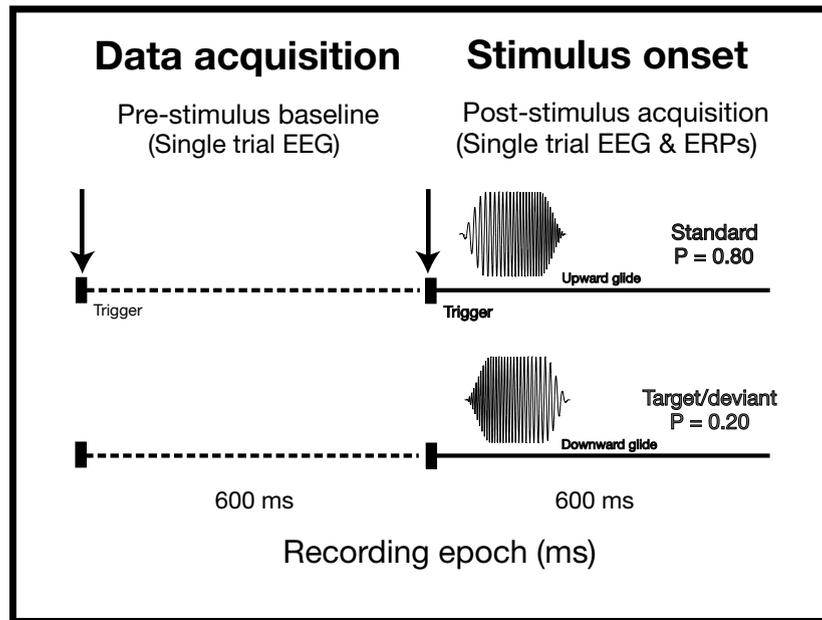
Fig. 1. Schematic diagram of the oddball paradigm used to evaluate ERPs, ERSs and ERDs. Data acquisition of rhythmic EEG is initiated by a trigger, which encompasses a total recording epoch of 1200 ms; a silent 600 ms pre-stimulus baseline interval, followed by a 600 ms post-stimulus interval. The post-stimulus interval is triggered by the onset of an auditory stimulus (tone burst or frequency-modulated tone glide). Standard and target/deviant stimuli have different probabilities of occurrence (standard, $P = 0.80$; target/deviant, $P = 0.20$) with a total of 240 trials. Target trials were presented randomly and a variable intertrial interval was used (3 ± 0.5 s).

were instructed to listen passively (no button press or silent counting was required).

2.3. Data analysis

To assess for changes in underlying EEG rhythmicities, each 600 ms segment of raw EEG (pre-stimulus baseline interval or post-stimulus interval) was detrended by removing the mean and linear component. Then, autoregressive spectral analysis (maximum entropy method, 40th order Berg model; Marple, 1987) was used to quantify the frequency composition of each pre- and post-stimulus epoch. Because spectral resolution of the autoregressive model is less dependent on length of the data segment than Fourier-based methods, the autoregressive model is considered superior to Fourier-based techniques when relatively short time epochs are analyzed (Florian and Pfurtscheller, 1995; McFarland et al., 2000). In our analysis procedure, autoregressive coefficients were computed on each data segment. Then, high resolution broadband EEG spectra were obtained by convolving these regression coefficients with sine waves spaced in 1 Hz steps over a bandwidth from 1.0 to 80 Hz. Next, the RMS values of the voltage signals were obtained. This allowed for the entire spectrum of each pre- and post-stimulus interval to be compared graphically and evaluated statistically. However, because the pre- and post-stimulus recording epochs were 600 ms long, this time restriction imposed a limit on the lowest frequency that could be resolved. Nevertheless, by comparing baseline vs. standard or baseline vs. target/deviant conditions, event-related changes in EEG spectra could be ascertained. ERSs or ERDs were determined by computing Pearson's product moment correlation (Pearson's r) on each spectral bin for all standard and target/deviant conditions. The correlation was computed between stimulus condition and the magnitude of the spectral band on each individual trial. In this computation, the stimulus condition was a dummy variable with 0 representing the baseline and 1 representing the stimulus interval. The Pearson's r statistic was selected because correlation coefficients derived from this analysis represent a normalized difference metric that is signed (i.e., this ratio analysis has coefficients with both positive and negative values). Positive correlation coefficients represent *synchronization* of EEG activity at different frequencies; negative correlation coefficients represent *desynchronization* of EEG activity at different frequencies. Given the properties of Pearson's r, the magnitudes of this measure range from 0 (no correlation) to ± 1.0 (where $+1.0$ represents greatest synchronization; -1.0 represents great-

est desynchronization). To allow for the spatial distributions of the correlation indices to be evaluated in a comprehensive manner, ERSs/ERDs were also plotted as topographic maps. To enhance the spatial distinctiveness of the topographic representations, data were converted to a reference-free format (Laplacian transformation) prior to all spectral analyses, using a set of nearest neighbor electrodes (Hjorth, 1975). For most regions on the head, each electrode was at the center of four symmetrically placed surrounding nearest neighbor electrodes forming the corners of a square. At the edges or boundaries of the recording montage, there were fewer neighboring electrodes and therefore the neighboring electrodes were not symmetrically placed. In both cases, this represents the Laplacian as computed by the finite difference method (Zhou, 1993).

2.4. Stimuli and psychophysical testing

Auditory stimuli were constructed digitally and consisted of short duration (50 ms) pure tones or linearly ramped rising or falling frequency-modulated tone glides. All stimuli were shaped with a Blackman window having 5 ms rise/fall times. Tones were centered at 250 Hz and tone glides had a base frequency of 250 Hz. In order to control for discriminability, just noticeable differences (JNDs) were determined behaviorally for pure tone and tone glide stimuli prior to EEG data collection. Behavioral testing used a three-interval three-alternative forced choice (3-IFC) psychophysical procedure, embedded in an oddball paradigm. In each of three separate temporal intervals, two of the intervals contained the same stimulus and a third randomly selected interval, contained a stimulus that was different from the other two. The task was to select the interval that contained the odd stimulus. Participants were seated in front of a computer monitor and presentation of each auditory stimulus was synchronized with one of three spatially separated white squares on the computer screen. A mouse was used as a pointing device to select the box on the computer screen corresponding to the selection of the odd stimulus. For the task involving tonal stimuli, individuals were required to detect a higher frequency tone from two 250 Hz tones (greatest frequency difference between stimuli was 64 Hz). For the tone glide task, individuals were required to detect a falling glide from two rising glides (greatest bandwidth difference between stimuli was also 64 Hz). Stimuli were presented binaurally at approximately 80 dB SPL. A block-randomized presentation, from preselected frequency differences of 2, 4, 8, 16, 32, and 64 Hz (10 presentations per stimulus condition), was used to construct psychometric functions for the two different classes of stimuli. Performances were based on percent correct identification of the odd stimulus. Bisecting in-

dividual psychometric functions at the 70% level of performance produced tone and tone glide JNDs. Stimuli for the EEG component of the experiment were constructed off-line for each individual participant after differential thresholds were obtained for each stimulus type.

Pure tones and frequency-modulated tone glides were constructed to be either *easy* or *difficult* to discriminate. Targets/deviants for the tonal stimuli in the *easy* listening conditions consisted of frequency differences associated with +6.0 JNDs above the base frequency; targets/deviants for the tonal stimuli in the *difficult* listening conditions consisted of +1.0 JND above the base frequency (250 Hz tone bursts +1.0 JND; 250 Hz at +6.0 JNDs, re: individual discrimination thresholds). Rising and falling tone glide stimuli were constructed in the same manner for each individual. During data collection, the 250 Hz tone or the falling frequency tone glide always served as the target/deviant stimulus, whereas the higher frequency tones or the rising frequency tone glides always served as the frequent/standard stimulus (probability of occurrence; $P = 0.80$ standards, $P = 0.20$ targets/deviants; total stimulus presentations, 240 trials).
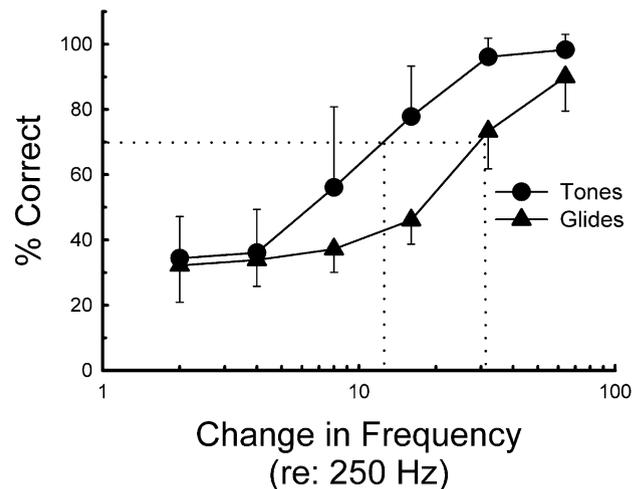
Fig. 2. Psychometric functions, averaged across individuals are shown for tone and frequency-modulated tone glide stimuli. The *y* axis represents percent correct identification of the oddball; the *x* axis represents the change in log frequency ranging from 2 to 64 Hz of the base frequency. The parameter of the graph is the different stimulus types. The filled circles and upward brackets represent mean values +1 standard deviation (S.D.) for tonal stimuli; the filled triangles with downward brackets represent mean values +1 S.D. for tone glide stimuli. JNDs were determined by bisecting individual psychometric functions at the 70% level of performance (dotted lines). This represents a point between chance (33.3% correct) and certainty (100% correct).

3. Results

3.1. Behavioral measures of psychophysical performance: frequency discrimination for tone and tone glide stimuli

Fig. 2 shows psychometric functions for tones and tone glide stimuli, averaged across all individuals. The average functions were representative of those obtained from individual performances. It could be seen that tone glides were more difficult to discriminate than simple tones. This resulted in higher JNDs for tone glides than for pure tone stimuli (average JND for tone glides, 33.6 Hz, S.D., 8.4 Hz; average JND for pure tones, 13.5 Hz, S.D., 5.8 Hz). The difference in performances between the two classes of stimuli is attributed to the complexity of dynamic frequency-modulated stimuli and potentially different discrimination skills needed in making these perceptual judgments.

Additional measurements were performed on button-press responses to target stimuli during EEG data collection. These included response accuracy and reaction time. We applied a repeated measure analysis of variance (ANOVA) with stimulus and discriminability as within subject's factors, to both percent correct responses (hits+misses divided by total responses) and reaction time in ms (hit trials only). The main effects of discriminability were significant for both percent correct ($F = 20.40$, $P < 0.002$) and reaction time measures ($F = 21.67$, $P < 0.002$). There were no significant main effects of stimulus type or interactions of this variable with discriminability. These results are shown in Table 1, where it can be seen that the discriminability manipulation was effective and equivalent across stimulus conditions.

3.2. ERP analysis

Fig. 3 (left column) shows examples of time-averaged long latency ERPs obtained within the oddball paradigm. Under these conditions, ERPs were elicited by tonal stimuli and participants were required to ignore
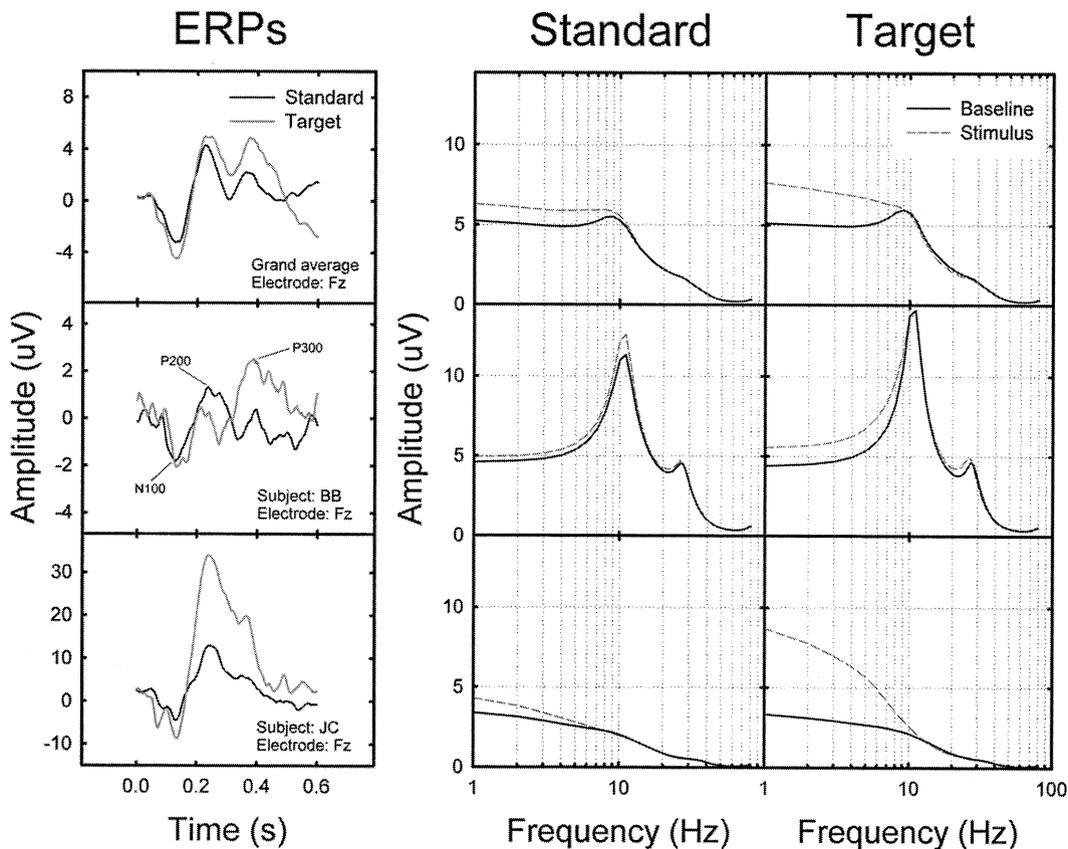
Fig. 3. Waveform plots (left column) showing long latency auditory ERPs to standard (solid black line) and oddball stimuli (solid gray line) at a single electrode site (Fz). Data shown are for tonal stimuli in the easy discrimination condition, which required active discrimination (i.e., tone easy attend condition). The top left plot (ERP column) is the grand average of 10 individuals. The lower two plots are for individual participants (BB and JC). The N100, P200 and P300 peaks are labeled in the middle plot. The next two columns show frequency spectra of EEG activity, which compare silent baseline and stimulus intervals for standard and target conditions. In column 2 (standard), the response to the stimulus only modulates energy in the frequency range ≤ 10 Hz. The response to the target (column 3) shows a much greater energy enhancement in the same frequency range.
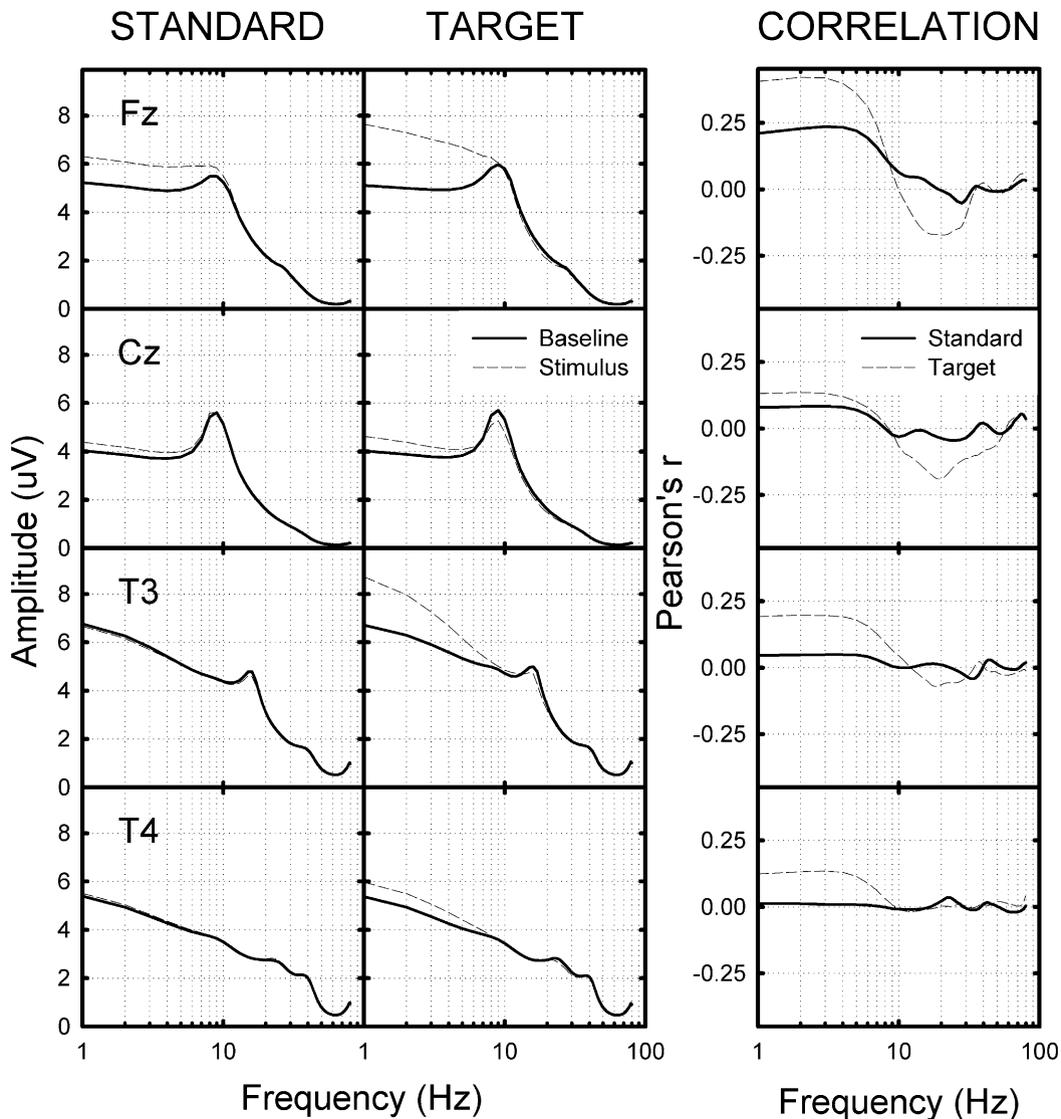
Fig. 4. Columns 1 and 2 show averaged EEG spectra for standard and target conditions, where spectra of the pre-stimulus baseline (solid lines) and post-stimulus response intervals (dashed lines) are superimposed on the same plot. The top two spectral plots are examples from central and fronto-central electrode sites (Cz, Fz); the bottom two plots show examples for left and right temporal electrode sites (T3, T4). The *y* axis represents EEG amplitude (μV); the *x* axis represents frequency (Hz). Column 3 shows pairwise correlation coefficients between pre-stimulus baseline and post-stimulus response intervals on a point-by-point basis for standard (solid line) and target conditions (dotted lines). The *y* axis represents Pearson's *r* correlation coefficients; the *x* axis represents frequency. ERSs are represented by positive values; ERDs are represented by negative values. Correlation data for standards and target conditions are superimposed in each graph. These data are for the tone easy attend condition.

Table 1
Percent correct and reaction time during the attend conditions

Stimulus	Discriminability	Percent correct (hits+rejections)/total	Reaction time (ms)
Tone	easy	98.2	573.8
Tone	difficult	93.8	750.6
Glide	easy	98.1	588.8
Glide	difficult	92.0	744.1

Percent correct represents the sum of hits and correct rejections divided by the total number of trials ×100. Reaction time (ms) is for hit trials only.

the standard and actively discriminate the target by pressing a button on a response box (i.e., tone easy attend condition). Separate time domain responses from a single electrode site were superimposed to help delineate differences between standard (solid black line) and target conditions (solid gray lines). The ERP to the standard showed negative and positive polarity peaks at various post-stimulus latencies (e.g., N100 and P200), representative of well-known long latency auditory ERPs, in addition to other peaks ranging up to 600 ms. In contrast, the response to the target generally showed enhanced N100 and P200 amplitudes, in addition to a prominent positivity in the latency range approximating 300 ms (P300). Also evident are marked individual differences in waveform morphology between participants BB and JC. These differences illustrate the range of responses that can be obtained from individu-

als. In columns 2 and 3, separate frequency domain spectra are shown for standard and target stimulus conditions, where spectra of the post-stimulus response interval (dashed lines) are superimposed on spectra of the silent pre-stimulus baseline interval (solid line). These data are the averages of spectra computed from each 600 ms epoch from individual trials. When comparisons were made between pre-stimulus baseline and post-stimulus response intervals, several distinct features are evident: (1) the spectra of the post-stimulus interval to the standard stimulus showed increased amplitude for frequencies ≤ 10 Hz, and (2) the spectra of the post-stimulus interval to the target stimulus showed a much greater amplitude enhancement in this same frequency range. Enhancement of response amplitude to the targets reflects the fact that other intervening factors such as active discrimination and attention were required
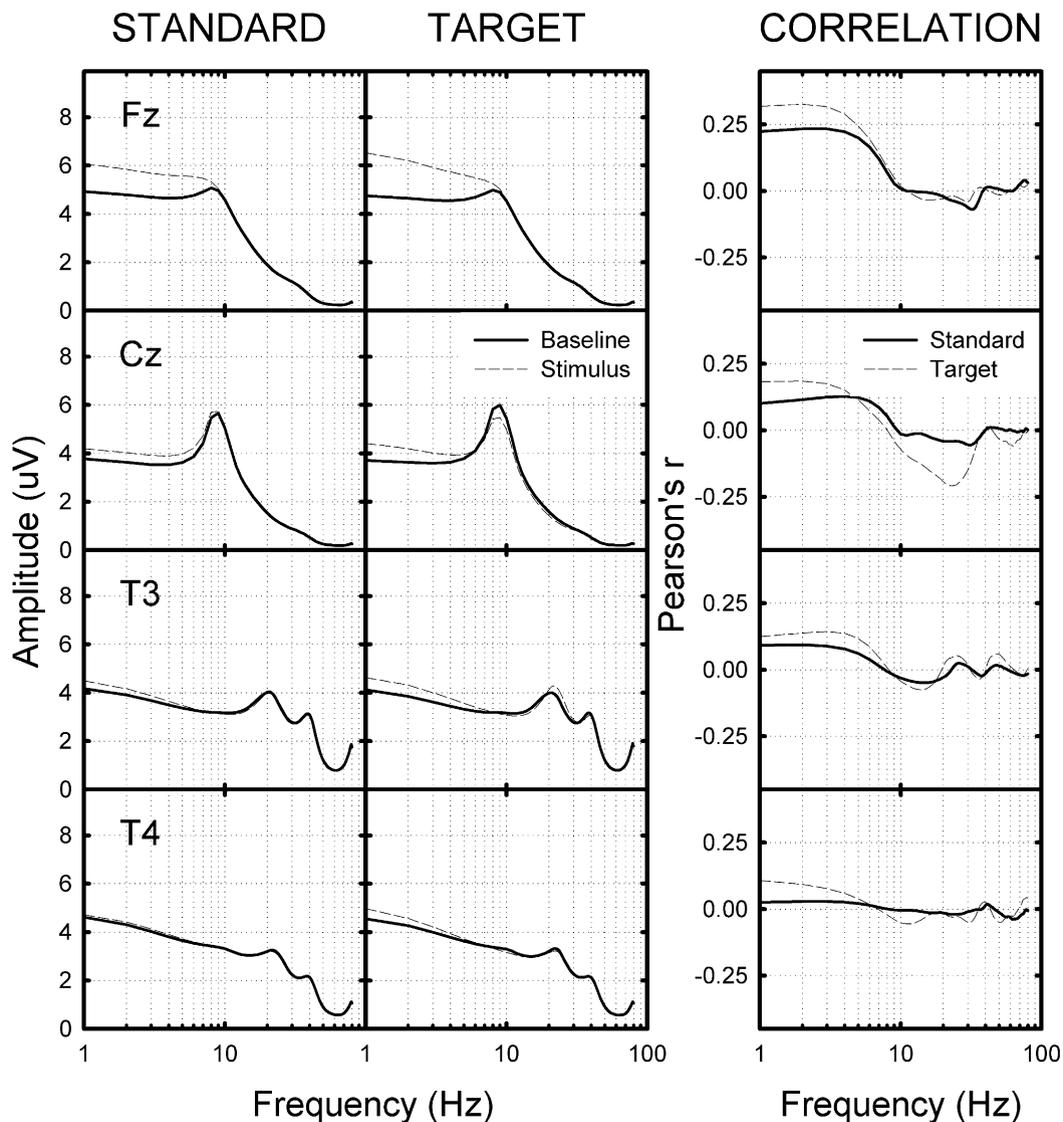
Fig. 5. Plots are organized identical to those described in Fig. 4. These data are for the tone difficult attend conditions.

during these conditions. These broadband spectral representations showed that stimulus- and attention-related changes in the post-stimulus interval were reactive in specific frequency bands and that event-related frequency domain representation of EEG spectra provided a relatively simple way of distinguishing stimulus- and attention-related responses from baseline activity. We now focus on frequency domain representations of event-related EEG activity and other analyses performed on this data set.

Samples of grand averaged EEG spectra at central (Fz, Cz) and temporal (T3, T4) scalp locations are shown for easy and difficult tonal stimulus conditions that required active discrimination of the target (Figs. 4 and 5). For comparison, a similar tonal stimulus condition is also shown where active discrimination was not required (Fig. 6). As a means for comparing various experimental conditions, EEG spectra in response to standard stimuli (columns 1, dashed lines) and target/deviant stimuli (column 2, dashed lines) were superimposed on EEG spectra for silent pre-stimulus baseline intervals (solid lines). Based on broadband spectral analysis, there are several observations that can be made from these comparisons: (1) Most of the energy within the pre-stimulus baseline and post-stimulus interval was contained in the frequency range ≤ 10 Hz. (2) In both pre-stimulus baseline and post-stimulus response intervals, peaks in energy concentrations differed. At central scalp locations, the dominant energy peak was contained within a frequency band between 8 and 10 Hz (alpha/mu); at temporal sites, two peaks of energy concentrations were evident; one centered at
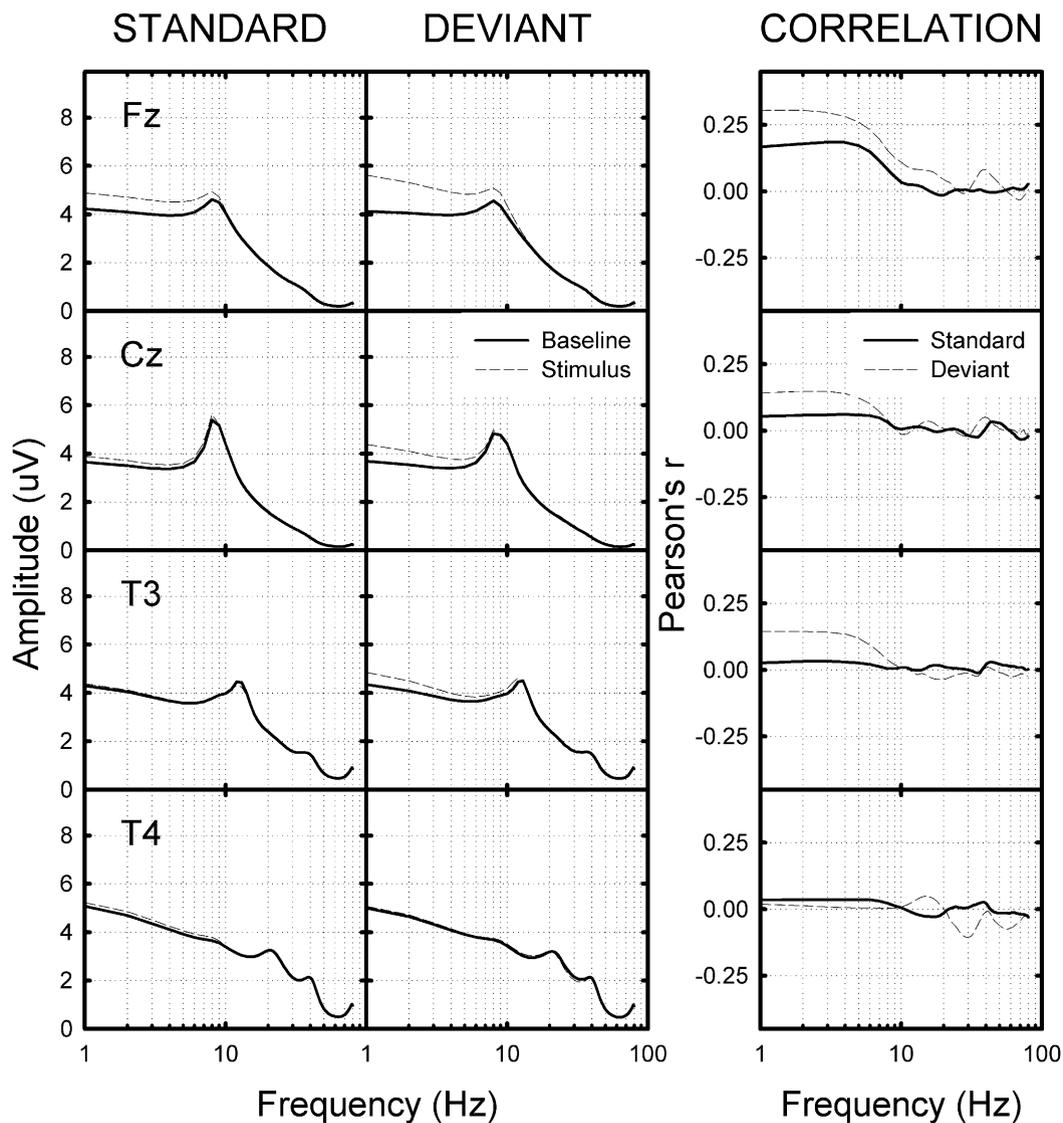
Fig. 6. Plots are organized identical to those found in Figs. 4 and 5. In these correlation plots, it can be seen that the ERDs are absent. These data are for the tone easy no-attend conditions.
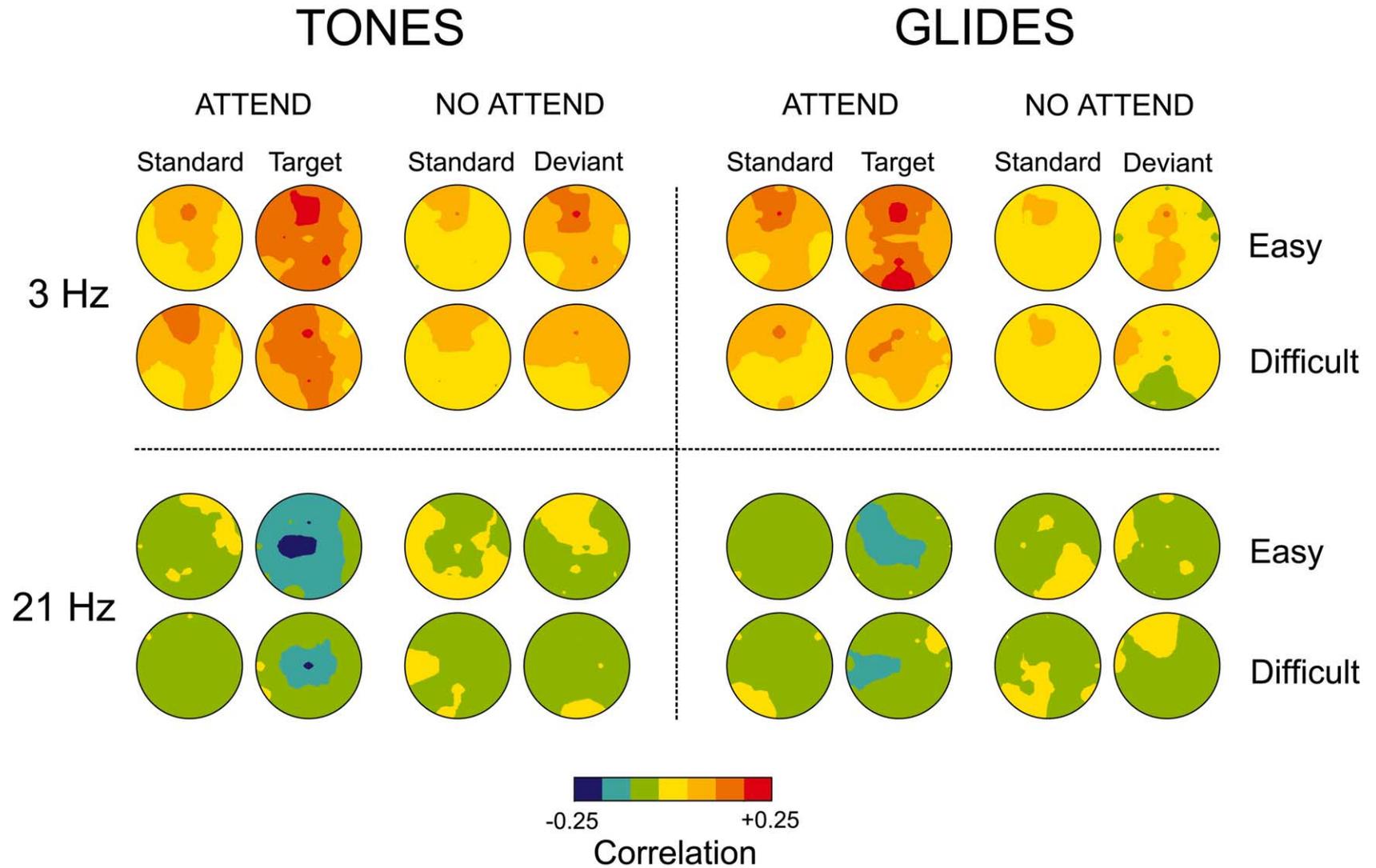
Fig. 7. Grand average Laplacian transformed correlation topographies for the different experimental conditions. In these graphs, the correlation of the Laplacian is plotted. Data shown are for two frequencies, 3 and 21 Hz. Positive and negative correlation values are differentiated by color.

approximately 20 Hz (beta frequency band) and another centered at approximately 40 Hz (gamma frequency band). These dominant peaks over temporal scalp locations (associated with beta and gamma activity) were generally not reactive to auditory stimulation. (3) There were increases in energy in response to the various stimulus conditions.

Further characterization of dynamic changes in EEG activity is provided in column 3 (correlation), representing synchronization and desynchronization indices for standard (solid line) and target/deviant conditions (dashed line). For each experimental condition, Pearson's r was computed between the stimulus condition (pre-stimulus baseline vs. the post-stimulus response interval) and the spectral amplitude for each trial on a point-by-point basis. For example in column 3 (Fig. 4), a stimulus effect can be seen at the Fz electrode in response to the standard (solid line). This plot showed

a prominent ERS (positive correlation, $r > 0.2$) for EEG activity below 10 Hz; above 10 Hz, little or no differential effects between standard and baseline conditions were evident (i.e., $r \sim = 0$). In comparison to the standard, the response to the target (dashed line) was more complex. There was an enhanced ERS (positive correlation, $r > 0.40$) below 10 Hz. In addition, there was a prominent ERD (negative correlation, $r \sim -0.2$) peaking between 20 and 21 Hz. In this example, there were simultaneous synchronization and desynchronization effects at different frequencies. Synchronization and/or desynchronization indices (column 3) provide information about event-related EEG activity that cannot be ascertained from commonly used time domain ERP analysis.

Also provided are Laplacian transformed correlation topographies. These color-coded topographic representations allow for more spatial detail to be delineated at
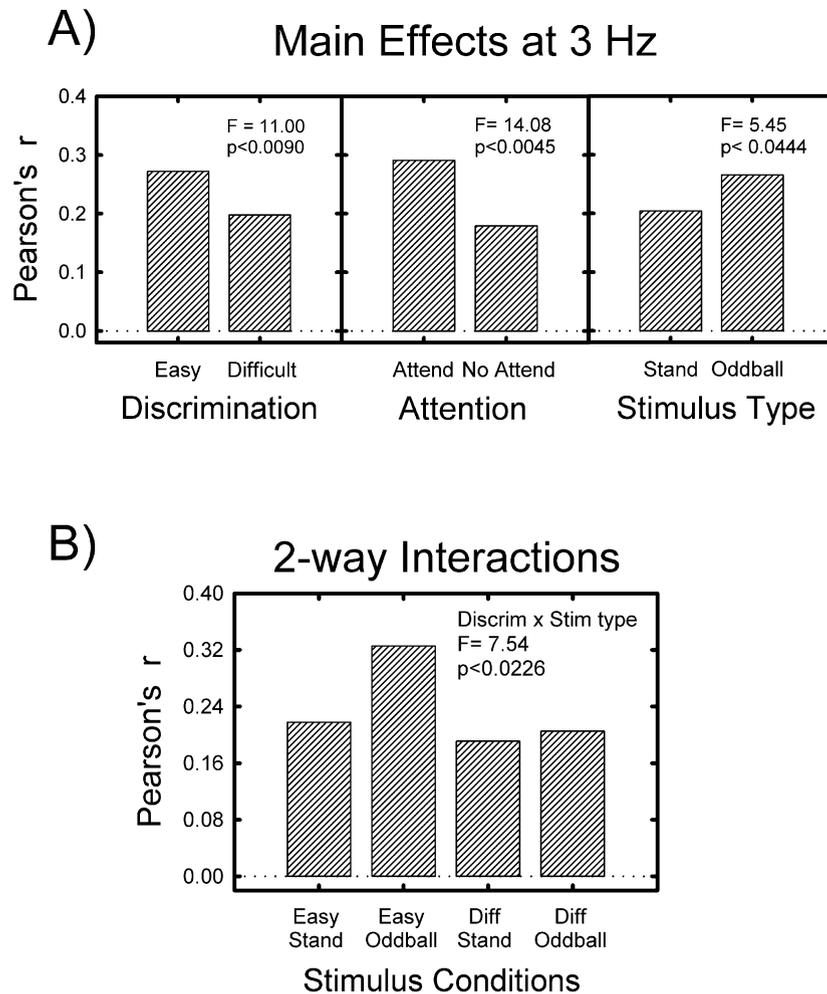
Fig. 8. (A) Bar plots showing statistical main effects of discriminability, attention and stimulus type for ERS effects assessed at 3 Hz and for the Fz electrode. The y axis represents Pearson's r and the x axis presents different experimental conditions. Larger ERSs occurred during easy discrimination conditions, when attention was required for oddball stimuli. (B) Bar plots showing two-way discrimination-by-stimulustype statistical interaction. Largest ERS effects occurred in the easy listening condition and for target type stimuli.

selected frequencies across scalp locations then was available from the spectral plots for individual channels. Fig. 7 shows grand averaged topographic maps at 3 and 21 Hz for the various experimental conditions. By visual inspection of the spectral plots and correlation topographies, specific electrode sites were selected as a way to quantify changes in ERSs/ERDs by statistical analysis. Separate five-way repeated measures ANOVA was computed on spectral bands and locations showing synchronization (3 Hz at Fz) and desynchronization (21 Hz at C3) effects. In these analyses, effects of stimulus complexity (tones vs. tone glides), stimulus discriminability (easy vs. difficult), attention (attend vs. no attend), stimulus type (standard vs. oddball) and interval (baseline vs. stimulus) were evaluated.

3.3. ERSs

ERS effects were limited to frequencies at and below 10 Hz. Largest effects occurred in the theta frequency band (greatest at approximately 3 Hz) and had a topographic focus at fronto-central scalp locations (Fig. 7). Therefore, we used the 3 Hz point at the fronto-central electrode (Fz) for statistical analysis. In terms of overall energy, the pre-stimulus interval had a mean voltage of 4.99 μV while the post-stimulus interval had a mean voltage of 5.99 μV in the 3 Hz band ($F = 17.88$, $P < 0.002$). This indicates an increase in energy in response to stimulus conditions and is also reflected in the fact that all values of Pearson's r were positive in this band. We next used the Pearson's r statistic to quantify
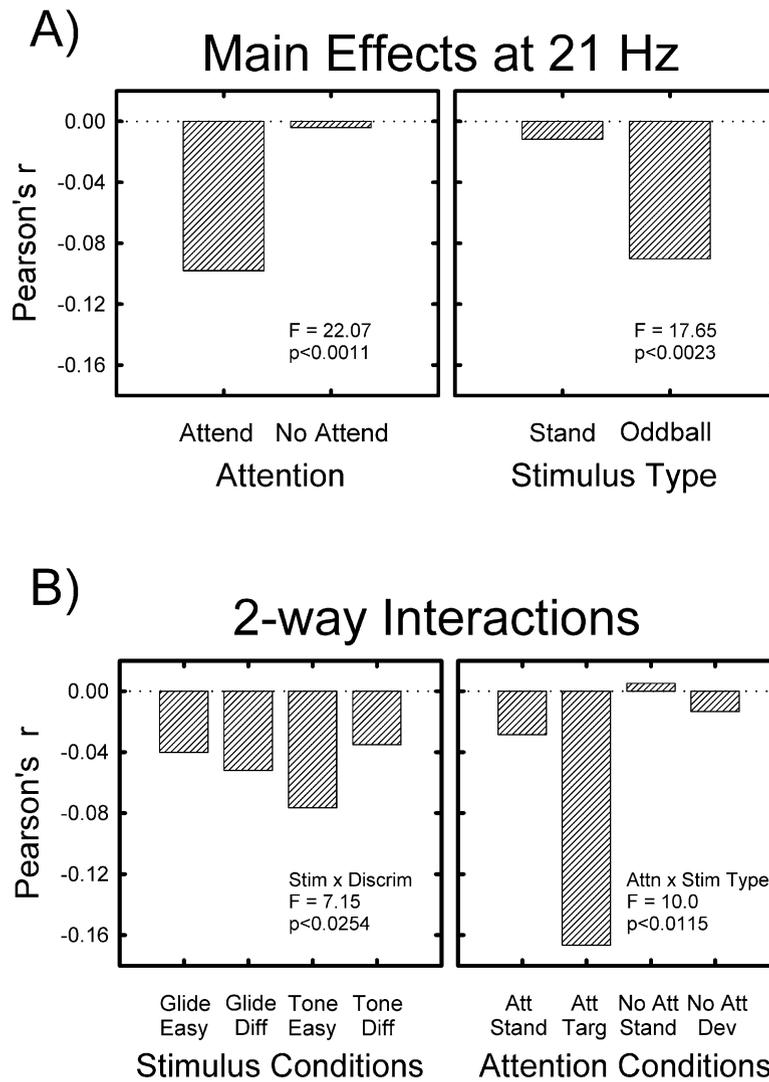
Fig. 9. (A) Bar plots showing statistical main effects of attention and stimulus type for ERD effects assessed at 21 Hz for the C3 electrode. The y axis represents the magnitude of the Pearson's r, the x axis represents different experimental conditions. Largest ERD effects occurred during attend conditions and for oddball stimuli. (B) Bar plots showing significant two-way stimulus-by-difficulty (left) and attention-by-target interactions (right). The stimulus-by-difficulty interaction (left) shows largest ERDs that occurred for tonal stimuli in the easy discriminable condition; attention-by-target interaction (right) shows largest ERDs that occurred in the attend conditions for target type stimuli.

response magnitude under the various conditions. Results showed significant main effects of stimulus discriminability ($F = 11.00$, $P < 0.009$), attention ($F = 14.08$, $P < 0.005$), and stimulus type ($F = 5.45$, $P < 0.044$) (Fig. 8A). Significantly greater synchronization effects occurred for more easily discriminable stimuli during oddball conditions, which required attention/active discrimination. However, there was also a significant two-way, discriminability-by-stimulus type interaction ($F = 7.54$, $P < 0.023$). This interaction reflects the fact that the effects of oddball presentation were mainly observed with easily discriminable stimuli (Fig. 8B). The topography of this interaction can be seen for either tones or frequency-modulated tone glide target stimuli (Fig. 7). Whereas ERS effects were greatest over fronto-central locations, ERSs were also evident over temporal scalp locations (left > right). Indeed, it is notable that the effects of stimulus type did not interact with attention ($F = 1.06$, $P < 0.330$). This result indicates that the oddball effect was similar regardless of task requirements. In addition, the lack of any interactions with attention indicates that attention enhances the 3 Hz ERS uniformly across conditions.

3.4. ERDs

ERDs were clearly evident in the beta frequency range (~ 21 Hz) with a focus over the left lateral central scalp location (C3). Therefore, the C3 electrode was used for ANOVA. There were significant main effects of attention ($F = 22.07$, $P < 0.001$) and stimulus type ($F = 17.65$, $P < 0.002$) (Fig. 9A). ERD effects were greatest in the attend condition and for the oddball stimuli. There were several significant two-way interactions: stimulus-by-discriminability ($F = 7.15$, $P < 0.025$) and attention-by-stimulus type ($F = 10.0$, $P < 0.012$) (Fig. 9B). The stimulus-by-discriminability interaction was characterized by larger desynchronization effects for tonal stimuli in the easy discrimination condition. The attention-by-stimulus type interaction was characterized by larger desynchronization effects for target stimuli in the attend condition. Lastly, there was also a borderline three-way discriminability-by-attention-by-target interaction ($F = 4.82$, $P < 0.056$; plot not shown). This three-way interaction indicates that regardless of stimulus complexity, the ERD effect was most prominent for easily discriminable targets in the attend condition. The foci of these interactions are clearly evident in the topographic representations (Fig. 7).

4. Discussion

We used both simple tones and more complex frequency-modulated tone glides to study event-related

changes in EEG rhythmicities within the oddball paradigm. Tones and tone glide stimuli were chosen for their ability to robustly activate auditory cortical areas (Kaas et al., 1999; Pardo and Sams, 1993). From a historical perspective, the dominant neurophysiological method for studying human information processing in the auditory modality has been the time domain analysis of averaged waveforms from scalp electrodes. While useful, it is becoming evident that this method does not extract maximum information from underlying brain activity nor does it provide the type of data necessary to understand the neural basis of dynamic events. In fact, when using time domain averaging, most EEG data are typically discarded, in favor of assessing averaged phase-locked responses; a practice that has obvious shortcomings. In contrast, there is a growing body of evidence linking perceptual, motor and cognitive processing (both real and imagined) to dynamic alterations in ongoing EEG activity. One approach to this problem is the analysis of band power changes (ERSs and ERDs) (Pfurtscheller, 2001). Other strategies provide alternative means to study brain dynamics under various conditions (e.g., Makeig et al., 2002). From a theoretical and practical standpoint, application of broadband spectral analysis of EEG rhythmicities, combined with specific design and analysis considerations, allows for a more comprehensive evaluation of event-related changes in brain dynamics, including the quantification of resting or idling background rhythms. At the same time, broadband spectral analysis is advantageous because it helps to guard against potential artifacts or interpretive problems associated with EEG rhythmicities, which can occur if only narrow-band frequency spectra are evaluated in isolation.

Issues regarding stimulus-induced phase modulation (PM) on EEG activity were initially described by Sayers and Beagley (1974) and Sayers et al. (1974) to account for the long latency AEP and this conceptual framework has been recapitulated with more contemporary analyses. Makeig et al. (2002) suggest that partial phase resetting or PM of EEG rhythms accounts for the negative peak of the visual ERP (N100), i.e., that the phase of an ongoing rhythm is shifted toward a particular value in relation to the stimulus. The alternative view, i.e., that the ERP is generated by fixed latency, fixed polarity brain events, is referred to as amplitude modulation (AM). Both processes (AM and PM) may contribute to the ERP. Penny et al. (2002) note 'looking at the ERP alone cannot necessarily reveal whether the underlying modulation is mediated by phase or amplitude. To decide whether an AM or PM mechanism underlies the ERP, one needs to look at the spectral characteristics of single-trial EEG. If there is no stimulus-induced increase in the power band of interest

(e.g., 10 Hz), then PM is the more likely mechanism'. Clearly, data from this experiment differ from Makeig et al. (2002) since increases in band power were observed in response to the stimulus. Our data provide support for the AM hypothesis, but do not rule out PM as a contributing factor. Thus, increases in band power could represent either phase-locked activity, activity that is not phase locked, or a combination of both.

As we have emphasized, there is increased interest in event-related changes in rhythmic EEG activity because of its potential relationship to perception, cognition and consciousness (Engel and Singer, 2001). In the context of sensory events, dynamic modulations of EEG activity are often discussed in relation to the topic of perceptual binding (Von der Malsburg, 1995) and in particular to frequencies in the gamma range. In our spectral plots, distinct energy peaks in beta and gamma frequencies were localized over temporal scalp locations of each hemisphere and were dissociated from alpha/mu rhythms, which had a more central focus. These data are particularly noteworthy because beta and gamma peaks were observed in both the silent pre-stimulus baseline intervals as well as in post-stimulus response intervals. From a functional standpoint, gamma band activity was generally not as reactive to experimental conditions as other frequency bands. Indeed, experimental conditions which modulated (synchronized and/or desynchronized) EEG activity occurred in much lower frequency regions; ERSs occurred in the frequency range ≤ 10 Hz; ERDs occurred in a band centered around 21 Hz. Therefore, our discussion focuses on these frequency domains.

4.1. ERSs

ERSs were notable during standard and oddball (target/deviant) stimulus conditions. These effects occurred over a restricted bandwidth but were greatest in frequency bands commonly categorized as delta (0.5–3.5 Hz), theta (3.5–7.0 Hz), and to a lesser extent, alpha/mu (8.0–12.0 Hz). Whereas ERSs to standards and oddballs were greatest at frontal and fronto-central scalp locations and broadly distributed over large areas of cortex, prominent synchronizations also occurred over left and right temporal regions (T3 > T4). Additionally, by controlling for discriminability of frequency changes in the different classes of stimuli and by using experimental conditions that required active and passive listening, the dynamic modulations of EEG activity observed have functional significance. Indeed, regardless of stimulus complexity, greater synchronization effects occurred during easy discrimination conditions and for target/deviant stimuli. Thus, the salience of stimulus features appears to be an important factor governing

these effects. It has been suggested that increases in theta synchronization may reflect processes associated with encoding new information into working memory, the cognitive load of a specific paradigm, and/or as a generalized index of attention related to the demands of the task (Klimesch, 1999). Whereas the magnitude of theta synchronization was greater under conditions requiring active listening, it is noteworthy that synchronization in the theta frequency band can occur during passive processing as well. Indeed, theta band synchronization has been observed during passive listening in response to tonal stimuli (Kolev et al., 2001). Consistent with the conceptual framework discussed by Klimesch (1999), the topographic distribution of theta synchronization at temporal and frontal areas might reflect engagement of specific processing streams involved during auditory discrimination.

Phenomenologically, two distinct classes of ERPs are associated with the oddball paradigm. When subjects listen passively to stimuli, the difference between standard and deviant conditions is labeled MMN (Näätänen, 1990). Alternatively, researchers have focused on the P300 component elicited by the oddball when subjects actively process target type stimuli (Donchin and Coles, 1988). The present frequency domain analysis suggests that EEG in the 3 Hz band is enhanced during the oddball condition regardless of whether or not subjects actively attend to the target/deviant stimulus. Therefore, stimulus-related energy at 3 Hz may reflect an enhancement of the entire averaged waveform rather than just energy associated with a single peak. When viewed in this manner, one can then ask whether or not there are fundamental differences between MMN and P300. In this respect, it is interesting to note that the differential waveforms presented by Näätänen (1990), fig. 4, to illustrate MMN are clearly biphasic; showing a negative peak followed by a positive peak or in some instances, a relative positivity. Likewise, Fig. 3 shows a clear amplitude enhancement at N100, P200 and P300 for the oddball in the grand average of the tone easy attend condition. Thus, the averaged ERP to tonal stimuli is a series of alternating negative and positive polarity peaks, each of which is enhanced in the oddball condition. As illustrated in the examples of the two individual subjects (Fig. 3), characterization of the response to the oddball in the time domain can be difficult on an individual basis. In contrast, the frequency domain analysis shows a simple enhancement of low frequency energy.

4.2. ERDs

ERD was dissociated from ERS effects by it frequency content and because it occurred only for target stimuli requiring attention/active discrimination. In

those attention-related target conditions, a button-press response with the index finger of the right hand was used as a means to indicate a successful discrimination. As a result of this sensory/motor event, the topographic distribution of the ERD was greatest over the left central scalp location C3 (i.e., over the hemisphere contralateral to the finger used during active response selection). This focus corresponds to activation of the sensorimotor areas in the brain. Indeed, ERDs in upper alpha and lower beta frequency bands have been previously described secondary to voluntary finger movement tasks and active response selection paradigms (Pfurtscheller and Aranibar, 1979; Derambure et al., 1993; Toro et al., 1994; Stancak and Pfurtscheller, 1996; Kaiser et al., 2001). In addition, Kaiser et al. (2002) reported that beta band desynchronization occurs in sensorimotor areas when individuals were presented with lateralized changes in natural or artificial sounds. These effects suggest that lateralization tasks may activate motor networks in preparation for orientating.

4.3. Issues related to data interpretation and analysis

In four individuals with intractable partial complex seizures, Crone et al. (2001) evaluated the influence of auditory stimulation on ERS and ERD of EEG recorded from subdural electrodes placed in and around the superior temporal gyrus of the left hemisphere. Stimuli were tone or phoneme contrasts embedded within a two-interval forced choice paradigm, whereby participants performed a same/different discrimination task. The authors report that auditory discrimination produced ERD of alpha activity and ERS of gamma activity. These effects were greater for speech than for tonal stimuli. However, it is noteworthy that prior to data analysis, phase-locked components were removed from individual trials of EEG by a method described by Kalcher and Pfurtscheller (1995). This method consists of subtracting the ERP (i.e., averaged phase-locked activity) from individual trials of rhythmic EEG. The rationale for applying this technique was based on the premise that phase-locked activity might obscure reactive changes in the non-phase-locked EEG component. However, it is possible that a more complex model of the ERP is necessary in order for this type of analysis to be valid. For example, Lang et al. (1997) discuss modeling the ERP by assuming amplitude and latency modulation of the components. If AM of the ERP occurs, then on some trials removing the mean value (i.e., the time-averaged ERP) could result in overcompensation occur and production of a *ghost image* in the *corrected* data (i.e., subtracting out too much signal would produce a negative image of the evoked potential). Likewise, on other trials, undercompensation would occur.

Similar effects could result from PM of the ERP. Accordingly, the method of subtracting the mean proposed by Kalcher and Pfurtscheller (1995) needs to be evaluated more thoroughly before assuming that it effectively removes the phase-locked component contained within individual trials/epochs of EEG.

Presently, there are several methodological issues that need to be resolved before relevant comparisons can be made across studies and interpretations can be validated in a meaningful way. These include developing methods for differentially evaluating phase-locked versus non-phase-locked EEG, developing and improving methods of evaluating functional connectivity (coupling) of ERSs/ERDs across spatially distinct brain areas, and having a more concentrated effort towards ascertaining which approach, time domain or frequency domain analysis, is optimum for extracting event-related information from EEG.

The electrical response of the brain to auditory stimulation can be examined in the time domain using averaged ERPs or in the frequency domain, by considering reactive changes in ongoing EEG rhythmicities. Most research within the auditory modality has focused on averaged time domain waveform analysis, although recently there has been interest in frequency domain techniques (e.g., Makeig, 1993; Krause et al., 1994, 1995; Pantev, 1995; Fell et al., 1997; Sutoh et al., 2000; Crone et al., 2001; Gurtubay et al., 2001; Kolev et al., 2001; Kaiser et al., 2002). The present study documents that with appropriate methodology and design considerations, frequency domain analysis of rhythmic EEG activity is sensitive to the effects of stimulus discriminability (perceptual abilities) and attention. Time and frequency domain approaches are complementary, but it remains to be determined whether one approach is more convenient and useful for research and for clinical applications than the other. For example, time domain waveforms obtained in individuals can be idiosyncratic and as such, subjective analysis of components is often required. In contrast, frequency domain techniques may provide simpler metrics of the brain's response to stimulation and this may facilitate clinical or research investigations. On the other hand, frequency domain techniques do not provide precise localization in the time domain. As a result, there is a time/frequency tradeoff. However, the utility of both time and frequency domain approaches and answers to the questions we have raised herein will require further study to determine the optimum approach or combination of approaches for particular circumstances.

5. Conclusion

Auditory information processing can alter the dy-

namics of ongoing EEG by synchronizing and/or de-synchronizing EEG rhythms in various frequency bands. Our analysis showed that stimulus and task demands differentially affected ERSs or ERDs. We also showed that event-related beta band desynchronization, which occurred for easily discriminable auditory stimuli in attention-related target conditions, represented a component of the oddball paradigm that has *not* been previously described. The beta band ERD is associated with as yet an unidentified stage of neural information processing, which may be related to perception, cognition, response selection or a combination of processes. Further study will be necessary to delineate between these and other alternative explanations.

Acknowledgements

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