

DECREASE OF FUNCTIONAL COUPLING BETWEEN LEFT AND RIGHT AUDITORY CORTICES DURING DICHOTIC LISTENING: AN ELECTROENCEPHALOGRAPHY STUDY

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Abstract—The present study focused on functional coupling between human bilateral auditory cortices and on possible influence of right over left auditory cortex during dichotic listening of complex non-verbal tones having near (competing) compared with distant non-competing fundamental frequencies. It was hypothesized that dichotic stimulation with competing tones would induce a decline of functional coupling between the two auditory cortices, as revealed by a decrease of electroencephalography coherence and an increase of directed transfer function from right (specialized for the present stimulus material) to left auditory cortex. Electroencephalograph was recorded from T3 and T4 scalp sites, overlying respectively left and right auditory cortices, and from Cz scalp site (vertex) for control purposes. Event-related coherence between T3 and T4 scalp sites was significantly lower for all electroencephalography bands of interest during dichotic listening of competing than non-competing tone pairs. This was a specific effect, since event-related coherence did not differ in a monotic control condition. Furthermore, event-related coherence between T3 and Cz and between T4 and Cz scalp sites showed no significant effects. Conversely, the directed transfer function results showed negligible influence at group level of right over left auditory cortex during dichotic listening. These results suggest a decrease of functional coupling between bilateral auditory cortices during competing dichotic stimuli as a possible neural substrate for the lateralization of auditory stimuli during dichotic listening. © 2005 Published by Elsevier Ltd on behalf of IBRO.

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Abbreviations: ANOVA, analysis of variance; dBA, audio decibel; DL, dichotic listening; DTF, directed transfer function; EEG, electroencephalography; ErCoh, event-related electroencephalographic coherence.

0306-4522/05/\$30.00+0.00 © 2005 Published by Elsevier Ltd on behalf of IBRO.
doi:10.1016/j.neuroscience.2005.06.046

Key words: dichotic listening, complex tones, electroencephalography (EEG), spectral coherence, directed transfer function (DTF), functional coupling.

Dichotic listening (DL) consists in the simultaneous presentation of two different auditory stimuli to either ear (Bryden, 1988). This technique has been successfully used in the study of hemispheric functional asymmetries (Tervaniemi and Hugdahl, 2003). It has been shown that subjects with left-hemispheric language lateralization are faster and more accurate in reporting verbal items presented at right than left ear (Kimura, 1961; Studdert-Kennedy and Shankweiler, 1970), while they exhibit a left ear advantage for tasks involving the recognition of complex tones, music or environmental sounds (Kallman and Corballis, 1975; Boucher and Bryden, 1997; Brancucci and San Martini, 1999, 2003).

Functional neuroimaging studies of regional cerebral blood flow have elucidated fine spatial details of brain structures involved in DL such as bilateral primary auditory areas (Hugdahl et al., 1999, 2000; Lipschutz et al., 2002; Jäncke et al., 2003), orbitofrontal and hippocampal paralimbic belts (Pollmann et al., 2004), prefrontal cortex (Lipschutz et al., 2002; Thomsen et al., 2004), and splenium of the corpus callosum (Pollmann et al., 2002).

In parallel, electroencephalographic (EEG) and magnetoencephalographic studies have shown fine time evolution of activity in auditory areas during DL (Ahonniska et al., 1993; Yvert et al., 1998; Wioland et al., 1999; Mathiak et al., 2000, 2002; Greenwald and Jerger, 2003). It has been observed that auditory event-related potentials are related to ear advantage for dichotic complex tones (Tenke et al., 1993). Namely, subjects with strong left ear advantage for dichotic stimuli had late positive event-related potentials (P350 and P550, about 300–600 ms post-stimulus) with greater amplitude over right than left auditory area. On the contrary, these potentials had greater amplitude over left than right auditory area in subjects with little or no left ear advantage for dichotic stimuli. More recently, earlier auditory evoked magnetic fields (M100, about 90–120 ms post-stimulus) have been found to be modulated during DL. In particular, M100 amplitude over right auditory cortex progressively increased when complex monotic tones of increasing intensity were given to ipsilateral (right) ear (Brancucci et al., 2004). The increase of ipsilateral M100 was abolished when a competing complex tone of constant intensity was delivered dichotically to the contralateral (left) ear. Remarkably, the inhibition of ipsilateral

M100 was not observed when contralateral and ipsilateral tones were not competing, i.e. when they had distant fundamental frequencies. This might be due to a possible inhibitory effect of contralateral over ipsilateral sensory pathway. Such an occlusion mechanism would be exerted in cortical auditory areas, as the dichotic effects were observed at M100 but not earlier M50 component. This explanation is in line with the structural theory of DL (Kimura, 1967) and previous behavioral evidence (Sidtis, 1981, 1988) demonstrating that ear advantage for dichotic stimuli is a function of the spectral overlap of the two stimuli. Namely, stimulus pairs having high spectral overlap (i.e. competing tones having near fundamental frequencies) yield stronger ear effects when compared with stimulus pairs having low spectral overlap (i.e. distant fundamental frequencies).

Taken together, the mentioned results suggest that the two auditory cortices do not respond with the same features during DL of competing tones. Therefore, it is conceivable that this different activity of auditory cortices during DL of complex non-verbal tones is associated with a reduced coordination or coupling between them, possibly due to an increased influence of right (dominant for non-verbal tones) over left auditory cortex. Such a functional coupling would be allowed by direct inter-hemispherical connections between auditory cortices, revealed by several studies in the cat, rat, monkey and man (Diamond et al., 1968; Pandya et al., 1969; Cipolloni and Pandya, 1985, 1989; Vaughan, 1983; De Lacoste et al., 1985; Code and Winer, 1986; Alexander and Warren, 1988; Bozhko and Slepchenko, 1988; Arnault and Roger, 1990).

The present study focused on functional coupling between bilateral auditory cortices and on possible influence of right over left auditory cortex during DL. The experimental design included dichotic and (control) monotic pairs of complex tones, which were presented during EEG recordings. These tone pairs were formed by either near (i.e. competing) or distant (i.e. non-competing) fundamental frequencies. Functional coupling between auditory cortical areas was evaluated by two different techniques, namely spectral coherence and directed transfer function (DTF). The analysis of EEG coherence is a method to quantitatively measure the linear dependency between the activities of two brain regions. It is a large-scale measure, which depicts dynamic functional interactions between electrode signals. High coherence between two EEG signals would indicate an increased functional interplay between the underlying cortical sources (Walter, 1968; Shaw, 1984; Rappelsberger, 1998; Petsche and Etlinger, 1998). It has been directly shown that functional connectivity between the auditory cortices is supported by the corpus callosum, in that inter-hemispheric coherence decreases in patients with agenesis of the corpus callosum when compared with healthy subjects (Quigley et al., 2003). Compared with EEG coherence analysis, the analysis of DTF is a method to estimate from EEG data the direction of the modeled information flow between two brain regions (Kaminski and Blinowska, 1991; Kaminski et al., 1995; Korzeniewska et al., 2003). This technique has been previously used to

study the propagation direction of temporal epileptic activity (Fraszczuk et al., 1994), the information flow direction during voluntary movements (Babiloni et al., 2004c), short-term memory (Babiloni et al., 2004a), and sleep (De Gennaro et al., 2004), as well as the functional relationships among hippocampus, entorhinal-piriform area, subiculum and lateral septum in the rat (Korzeniewska et al., 1997).

The specific working hypothesis of the present study was that dichotic stimulation with competing tones induced an atypical functional coupling between the two auditory cortices, as revealed by a decrease of EEG coherence and an increase of DTF from right to left auditory cortex during dichotic stimulation with near compared with distant complex tones.

EXPERIMENTAL PROCEDURES

Subjects

Fifteen healthy volunteers were recruited (age range of 26–31 years, five females). They were right-handed (Edinburgh Inventory). None of them had auditory impairments as shown by auditory functional assessment. No differences (± 5 dB) of hearing threshold at 250 and 400 Hz were found between left and right ears. All subjects gave their written informed consent according to the Declaration of Helsinki and could freely request an interruption of the investigation at any time. The general procedures were approved by the local Institutional Ethics Committee.

Auditory stimuli

Two dichotic and two monotic complex tone pairs were used (Table 1). The two dichotic stimuli were constituted by *i*) tone A (261 Hz, middle C; 60 dBA) delivered at the left ear and tone B (293 Hz, middle D; 60 dBA) delivered at the right ear (A and B have 'near' fundamental frequencies) and by *ii*) tone A delivered at the left ear and tone E (391 Hz, middle G; 60 dBA) delivered at the right ear (A and E have 'distant' fundamental frequencies). Similarly, the two monotic stimuli (delivered at the right ear) were constituted by *i*) tones A and B and by *ii*) tones A and E. These tones were synthesized on a Pentium 166 PC with Sound Blaster audio card (Creative, Model AWE 32; Microwave, Rome, Italy), by means of CSound language (Vercoe, 1992) for sound synthesis. Sampling rate was 44100 Hz and amplitude resolution 16 bit. Spectral composition and amplitude envelope were the same for all tones. Spectrum was composed by eight harmonic components with the following relative amplitudes: 1, 0.8, 0.6, 0.5, 0.4, 0.3, 0.2, and 0.1. The tones lasted 500 ms and had a rise and fall-time of 50 ms. To ensure that no transients or undesired

Table 1. The stimuli used in the present experiment

Condition ear	Dichotic		Monotic, Right
	Left	Right	
Near fundamental frequencies	Tone A 261 Hz	Tone B 293 Hz	Tones A and B 261 and 293 Hz
Distant fundamental frequencies	Tone A 261 Hz	Tone E 391 Hz	Tones A and E 261 and 391 Hz

They are complex tones (eight harmonic components) presented at 60 dBA. Tone pairs with near fundamental frequencies are considered as 'competing,' whereas tone pairs with distant fundamental frequencies are considered as 'non-competing.' Monotic stimuli were presented at the right ear.

EXPERIMENTAL PARADIGM

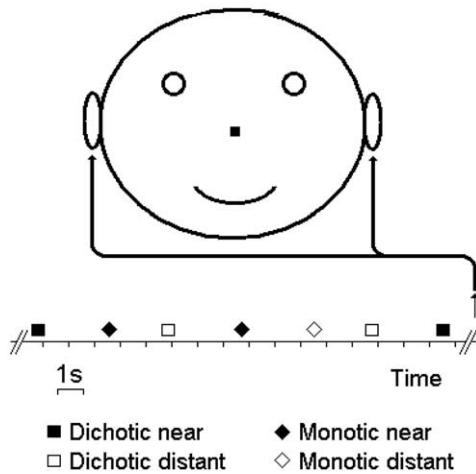


Fig. 1. Sketch of the experimental paradigm. A series of dichotic and monotic tone pairs, having near or distant fundamental frequencies, was presented to the subjects in a pseudorandomized order. Duration of the stimuli was 500 ms. Inter-stimulus interval varied randomly between 2500 and 3500 ms.

alterations were present in the stimuli, they were recorded from the earphones and re-analyzed.

Experimental procedure

Within an electrically shielded and soundproof chamber, subjects lay on a bed and listened passively to a pseudo-randomized sequence of four stimulus pairs (Fig. 1). The pseudo-randomization was performed in order to reduce possible sequence effects and changes of attention across the experiment. Experimenters ascertained by an interview that all subjects could clearly distinguish the near compared with distant dichotic and monotic tone pairs. No recognition task was required of the subjects during the EEG recordings. Each of the four stimuli was presented 80 times for a total of 320 presentations. Inter-stimulus interval varied randomly between 2500 and 3500 ms. The recording session was segmented in four blocks of 80 stimuli (1 min inter-block pause). Before each recording block, subjects were asked to maintain a constant level of attention during the whole session.

Subject's attentional level across the different conditions could be a possible confound. Therefore, we estimated it by means of calculation of baseline alpha power across conditions (baseline alpha power is considered as sensitive to subject's mental state; Klimesch 1999). Values of baseline alpha power were statistically analyzed by repeated measures ANOVA with Condition as factor (monotic near, monotic distant, dichotic near, dichotic distant).

EEG recordings and preliminary data analysis

During the mentioned auditory stimulations, EEG data were recorded from T3, T4 and Cz electrode sites placed according to an augmented 10–20 system (bandpass: 0.05–100 Hz, sampling rate: 256 Hz). Linked-ears served as a reference. Electrode impedance was kept lower than 5 kOhm. Two electro-oculographic channels were used to monitor eye movements and blinking (same recording features of EEG data). All data were recorded in continuous mode.

Collected EEG data were segmented in single trials each spanning from –1000 to +4000 ms, the zero time being the onset of auditory stimulus. Single trials were discarded when associated

with head movements, eye movements or blinking. About 70 EEG trials were accepted for each stimulus condition and for each subject.

To perform coherence and DTF analysis of the artifact-free EEG data, we preliminarily removed phase-locked activity (i.e. auditory evoked potential) with a mathematical technique based on weighted inter-trial variance calculation. Briefly, the procedure was the following. A correction factor was calculated for each EEG single trial by cross-correlation between the evoked potential and the ongoing EEG of that single trial. This factor was used to weight the subtraction of the auditory evoked potential from that EEG single trial. A similar technique has been successfully used in previous studies (Kalcher and Pfurtscheller 1995; Babiloni et al., 2004b).

Estimation of functional coupling: analysis of EEG coherence

EEG coherence is a normalized measure of the coupling between two signals at any given frequency (Rappelsberger and Petsche, 1988; Halliday et al., 1995; Babiloni et al., 2004a,c). The coherence values were calculated for each frequency bin by:

$$Coh_{xy}(\lambda) = \frac{|f_{xy}(\lambda)|^2}{f_{xx}(\lambda)f_{yy}(\lambda)}$$

which is the extension of the Pearson's correlation coefficient to complex number pairs. In this equation, f denotes the spectral estimate of two EEG signals x and y for a given frequency bin (λ). The numerator contains the cross-spectrum for x and y (f_{xy}), while the denominator contains the respective auto-spectra for x (f_{xx}) and y (f_{yy}). For each frequency bin (λ), the coherence value (Coh_{xy}) is obtained by squaring the magnitude of the complex correlation coefficient R . This procedure returns a real number between 0 (no coherence) and 1 (maximal coherence). According to current standards, the EEG coherence values were subjected to hyperbolic tangent transformation to make the coherence values Gaussian. Of note, the statistical analysis considered only EEG data from subjects showing coherence values above statistical threshold posed at $P < 0.05$, i.e. statistically significant coherence values. The calculation of the statistical threshold level for coherence was made according to Halliday and collaborators (1995), taking into account the number of single valid EEG trials used as an input for the analysis of EEG coherence.

Here EEG coherence was computed among EEG data recorded at T3, T4 and Cz electrode sites ('10–20' international system). The between-electrode EEG coherence was calculated at 'baseline' period (from –1000 ms to zero time, zero time being the auditory stimulus onset) as well as 'event' period (from zero time to +1000 ms). The computation of EEG coherence from data segments of 1000 ms yielded a frequency resolution of 1 Hz. Frequency bands for EEG coherence analysis were delta (1–3 Hz), theta (4–7 Hz), alpha (8–12 Hz), beta (13–30 Hz), and gamma (31–42 Hz), according to previous studies (Tiihonen et al., 1989; Gerloff et al., 1998; Mima and Hallett, 1999; Tecchio et al., 2003). For the statistical analysis, mean event-related EEG coherence (ErCoh) within each band was used, namely the mean difference between coherence at event and baseline periods. It should be stressed that the magnitude of ErCoh is usually smaller than the absolute coherence values. However, it has the advantage to take into account the inter-subject variability of baseline coherence.

Estimation of the direction of functional coupling: DTF analysis

DTF was used to estimate the direction of the information flow between left (T3) and right (T4) auditory cortices in the frequency bands of interest. DTF is a multivariate autoregressive mathematical model that probes both spectral and directional features of the

functional coupling between two EEG electrodes (Kaminski and Blinowska, 1991; Kaminski et al., 1995; Korzeniewska et al., 2003). For each possible direction, DTF yields a normalized value ranging from 0 (no directed information flow) to 1 (maximally directed information flow). In the present study, two directions were considered: T3 toward T4 and T4 toward T3. DTF data analysis was performed in four steps: (i) computation of DTF for each direction in the baseline and event periods, (ii) computation of event-related DTF, i.e. the difference between DTF during baseline and event periods for each direction (event-related DTF), (iii) computation of the difference between the two event-related DTF directions (dependent variable used for statistical analysis), (iv) statistical analysis (see next section).

Statistical analysis

ErCoh (dependent variable) between T3 and T4 sites for each subject was used as an input for two ANOVAs for repeated measures. The first ANOVA analysis was focused on ErCoh associated with dichotic stimuli. The second (control) ANOVA analysis was focused on ErCoh associated with monotic stimuli. The factors for each ANOVA analyses were 'Frequency distance' (near fundamental frequencies formed by A and B tones; distant fundamental frequencies formed by A and E tones) and 'Band' (delta, theta, alpha, beta, and gamma). For control purposes, the same analyses were performed on ErCoh at T3-Cz and T4-Cz electrode pairs. The working hypothesis predicted a specific effect on T3-T4 ErCoh of 'Frequency distance' for dichotic but not monotic stimuli. We did not perform an overall ANOVA including all three electrode pairs and both dichotic and monotic stimulations for two reasons: in the present case, the global number of factors (3) and levels ($2 \times 2 \times 5$) would be too high with reference to the amount of subjects ($n=15$). Furthermore, a unique ANOVA would have compared EEG variables related to the unpaired condition 'number of ears stimulated,' namely one in the monotic condition and two in the dichotic condition.

Event-related DTF (dependent variable) between T3 and T4 sites for each subject was used as an input for ANOVA for repeated measures. The ANOVA design had two factors: 'Dichotic stimuli' (near, distant) and 'Bands' (delta, theta, alpha, beta, and gamma).

RESULTS

Coherence spectra

Table 2 reports baseline and event absolute EEG coherence values (T3–T4 electrode pair) and statistical thresh-

olds ($P<0.05$, computed according to Halliday et al., 1995) in the four experimental conditions (dichotic near, dichotic distant, monotic near, and monotic distant). Mean baseline coherence values were 0.215 ± 0.025 in the delta band, 0.153 ± 0.021 in the theta band, 0.148 ± 0.013 in the alpha band, 0.092 ± 0.011 in the beta band, and 0.101 ± 0.016 in the gamma band. On the whole, absolute coherence values were relatively low in magnitude but above the corresponding statistical thresholds ($P<0.05$) at both baseline and event periods. This was true for all EEG frequency bands (see Table 2).

Fig. 2 illustrates across subjects ($n=15$) mean EEG coherence spectra in baseline and event periods for the dichotic and monotic conditions and for both near and distant complex tones (T3–T4 electrode pair). Compared with the baseline, event EEG coherence increased at all frequency bands when the dichotic tone pair was constituted by stimuli having distant fundamental frequencies (261 and 391 Hz, see left down panel), but not when the dichotic tone pair was constituted by competing stimuli having near fundamental frequencies (261 and 293 Hz, see left up panel). In the monotic condition, there was a global increase of EEG coherence in event period when compared with baseline period. This was true for both distant and near fundamental frequencies of the tone pairs.

Statistical results relative to ErCoh values

Repeated measures ANOVA analysis for dichotic stimuli pointed to a main effect of 'Frequency distance' ($F_{1,14}=4.620$; $P<0.05$) indicating that ErCoh between T3 and T4 electrode sites was lower with near (competing) than distant fundamental frequencies of the tone pairs, regardless frequency band. This result emerges in Fig. 3 showing across subjects ($n=15$) mean ErCoh values in the dichotic and monotic conditions at all frequency bands. Of note, these ErCoh values were small in amplitude, as expected by the fact that they result from a difference between absolute coherence values at baseline and event.

Table 2. Statistical thresholds of coherence and mean coherence values at baseline and event

Coherence at baseline					Threshold	Coherence at event				
Delta	Theta	Alpha	Beta	Gamma	Mean±st. error	Delta	Theta	Alpha	Beta	Gamma
Dichotic near										
0.210	0.128	0.147	0.089	0.112	0.046	0.188	0.122	0.135	0.080	0.120
0.020	0.014	0.019	0.016	0.015	0.003	0.021	0.021	0.021	0.018	0.006
Dichotic distant										
0.192	0.152	0.137	0.098	0.100	0.046	0.214	0.189	0.151	0.104	0.117
0.029	0.019	0.009	0.012	0.024	0.003	0.021	0.022	0.008	0.021	0.017
Monotic near										
0.228	0.150	0.146	0.080	0.105	0.045	0.240	0.152	0.141	0.093	0.103
0.019	0.019	0.007	0.006	0.005	0.003	0.016	0.022	0.012	0.003	0.003
Monotic distant										
0.228	0.181	0.163	0.103	0.086	0.045	0.195	0.163	0.145	0.118	0.104
0.033	0.030	0.017	0.012	0.019	0.003	0.029	0.030	0.020	0.021	0.022

Values refer to the four experimental conditions and to the five EEG bands. Second row for each condition reports standard errors.

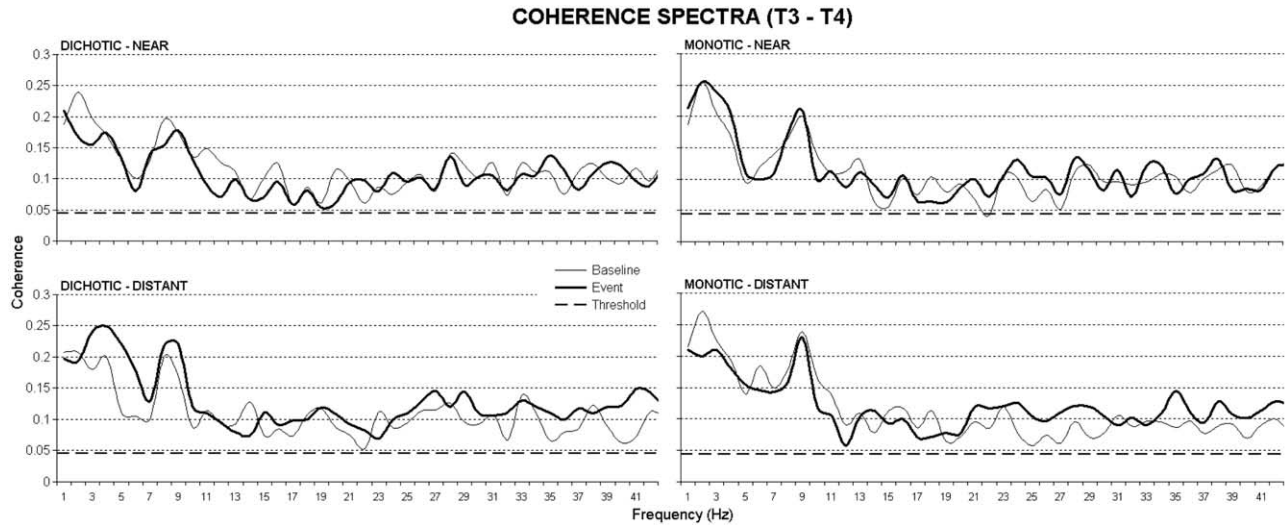


Fig. 2. Across subjects mean EEG coherence spectra (T3–T4) in the baseline and event periods for the dichotic and monotic conditions and for both near and distant stimuli. Frequency bands of interest for further analysis were: delta (1–3 Hz), theta (4–7 Hz), alpha (8–12 Hz), beta (13–30 Hz), and gamma (31–42 Hz). The subsequent statistical analysis was performed on ErCoh values, i.e. on the differences between event and baseline coherence.

The specificity of the above statistical result was confirmed by no statistically significant effect found in the ANOVA analysis for the monotic stimuli ($P > 0.05$).

As a control analysis of subjects' attentional state, repeated measures ANOVA with baseline alpha power as a dependent variable and 'Condition' as factor (monotic

near, monotic distant, dichotic near, dichotic distant) showed no statistically significant effects ($P > 0.05$). These results indicated that baseline spectral power in the alpha range did not significantly differ among the mentioned experimental conditions.

Control analysis for spatial specificity

In order to control for spatial specificity of the present result, we calculated coherence and ErCoh also for T3–Cz and T4–Cz electrode pairs. Fig. 4 shows coherence spectra and mean ErCoh values between T3 and Cz as well as between T4 and Cz electrode pairs. It can be observed that absolute coherence values are higher than those between T3 and T4, due to a reduced distance between the electrodes. However, no significant effects ($P > 0.05$) were found in the ANOVA for either electrode pair.

Descriptive and statistical results of DTF

Regarding near dichotic stimuli, event-related DTF data showed that, in seven subjects, T4 toward T3 direction prevailed over the opposite direction, especially at beta and gamma bands. In four subjects, the prevailing direction was that from T3 to T4 with a complex inter-individual pattern relative to the different EEG bands. The remaining four subjects showed no prevailing direction between T3 and T4 at most EEG bands.

Distant dichotic stimuli were associated with event-related DTF data showing that, in two subjects, T4 toward T3 direction prevailed over the opposite direction. In three subjects, the prevailing direction was from T3 to T4. In the remaining 10 subjects, no prevailing direction was shown. In all cases, there was a complex inter-individual pattern relative to the different EEG bands.

The ANOVA analysis including the factors 'Dichotic stimuli' (near, distant) and 'Bands' (delta, theta, alpha,

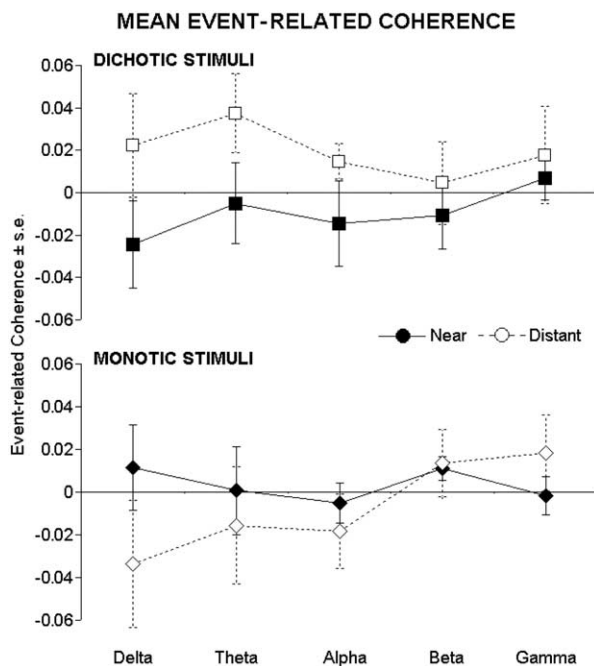


Fig. 3. Across subjects mean (\pm standard error) ErCoh values in dichotic and monotic conditions. Each graph includes ErCoh values obtained presenting tone pairs having distant (non-competing) vs. near (competing) fundamental frequencies. Statistical analyses showed that, in the dichotic but not monotic condition, there was a decrease of ErCoh when the dichotic stimulus was composed by competing compared with non-competing tone pairs.

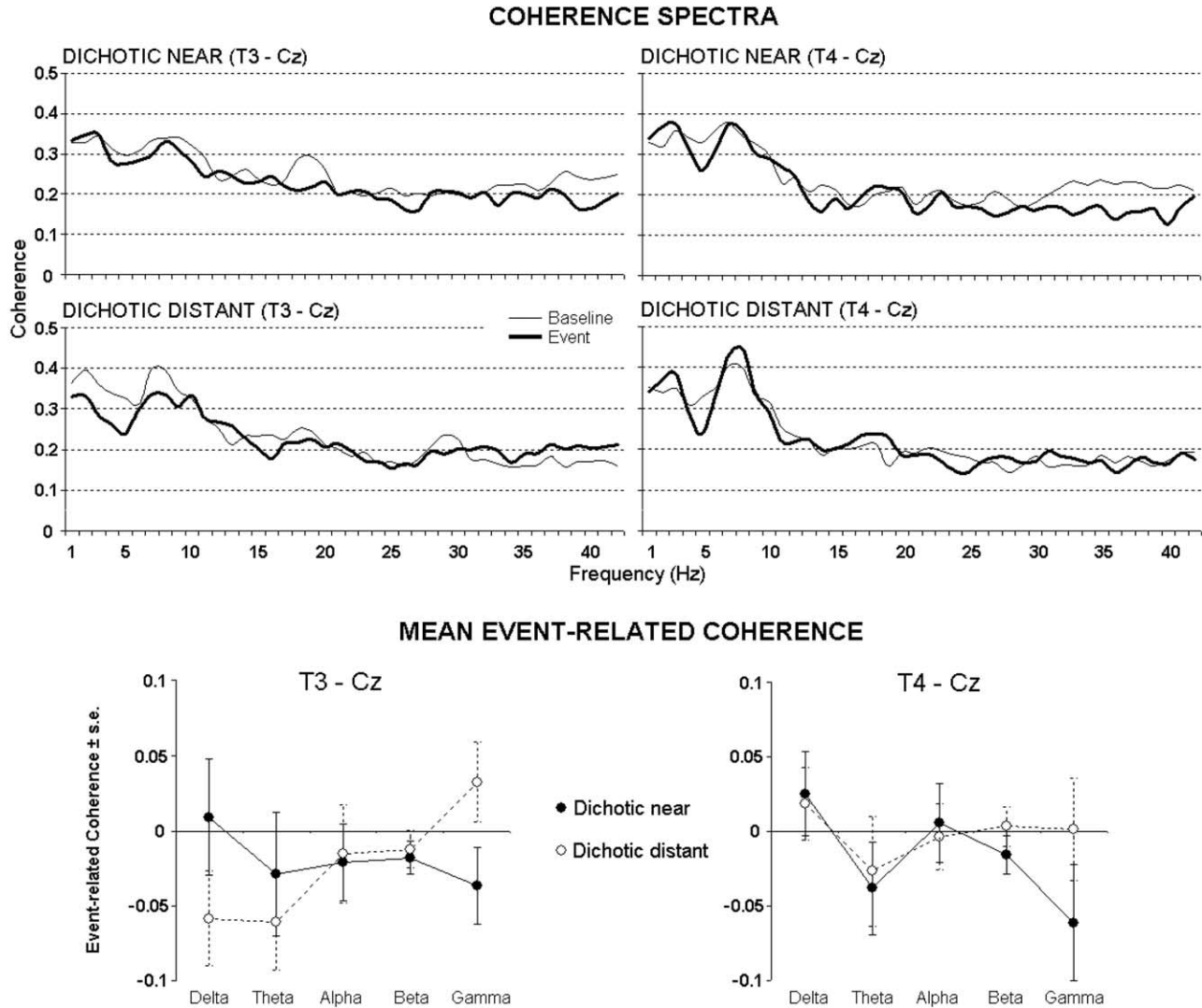


Fig. 4. Control analyses. *Top:* Across subjects mean EEG coherence spectra (left: T3–Cz; right T4–Cz) at baseline and event periods for the dichotic near and distant stimuli. *Bottom:* across subjects mean (\pm standard error) ErCoh values for T3–Cz electrode pair (left) and T4–Cz electrode pair (right) for the dichotic near and distant stimuli. No statistically significant effects are shown by these control analyses, thus confirming the spatial specificity of the results regarding the T3–T4 electrode pair.

beta, and gamma) showed no statistically significant results ($P > 0.05$).

DISCUSSION

In the present study, we tested whether the inter-hemispheric functional coupling between auditory cortices decreases during DL, as revealed by EEG coherence and DTF analyses. Results showed a decrease of inter-hemispheric functional coupling across all frequency bands of interest when the dichotic pair was composed by tones having near (competing) than distant fundamental frequencies tones. This was a specific effect, since no change of inter-hemispheric functional coupling was seen when monotic pairs with tones having distant or near fundamental frequencies were presented and no change of coherence was observed between control electrode pairs (T3–Cz and T4–Cz). Furthermore, these results were not

due to uncontrolled changes of subject's motivation and attention across the different conditions (i.e. dichotic near, dichotic distant, monotic near, and monotic distant). Indeed, the dichotic and monotic stimuli were pseudo-randomized across the experiment. In addition, we observed that baseline alpha power (a reliable indicator of subject's mental state) remained stable throughout the conditions. Finally, the present results were not biased by uncontrolled variations of reference electrode. In the present study, the stimuli of the different conditions were intermingled, with brief inter-stimulus intervals of 2500–3500 ms during EEG recordings. Therefore, it is unlikely that uncontrolled variations of the reference electrode occurred systematically and specifically together with dichotic and competing stimuli.

It should be stressed that the present EEG coherence values at baseline and event were somewhat low. This

was due to the large distance between the two temporal recording sites at which EEG data for the coherence analysis were recorded. It was also due to the preliminary removal of the auditory evoked potentials (i.e. neural activity phase locked to the auditory stimulus) before the computation of the coherence, in order to investigate brain rhythms non-phase-locked to the stimulus (Pfurtscheller and Lopes da Silva, 1999). Previous findings have shown that EEG coherence between electrodes is inversely proportional to the inter-electrode distance (Thatcher et al., 1986). Furthermore, the preliminary removal of the evoked potential is in line with recent guidelines on the study of brain rhythmicity (Pfurtscheller and Lopes da Silva, 1999) and provides absolute and event-related coherence values lower than those obtained computing the coherence from event-related potentials (Yamasaki et al., 2005). Finally, it should be also stressed that the present coherence values were low but statistically significant ($P < 0.05$). Indeed, the coherence values of each subject were significantly higher than statistical threshold as computed with the procedure suggested by Halliday et al. (1995).

In the present study, the dichotic effects on coherence were not specific for EEG frequencies. From a statistical point of view, the coherence at all frequency bands similarly decreased during the DL of competing than non competing tones. This result is at odds with the idea that the power of EEG at different frequency bands is associated with peculiar cognitive functions. In reality, there is no general consensus on that idea. Previous evidence has shown that sensorimotor, attentional, and memory processes are all related to the modulation of gamma power at about 40 Hz (Basar et al., 2001; Engel and Singer, 2001; Tecchio et al., 2003), but also to the modulation of beta, alpha, and theta power (Klimesch, 1999; Pfurtscheller and Lopes da Silva, 1999; Stam et al., 2002). It can be speculated that cognitive processes are associated with the parallel modulation of different EEG rhythms within proper neural networks. The functional specificity of these different EEG rhythms might be affected by the extension and kind of the neural networks engaged (Pfurtscheller and Lopes da Silva, 1999; Von Stein and Sarnthein, 2000). At the present stage of research, it should be stressed that variations of EEG band power across the physiological events do not directly indicate the level of cooperation among nodes of the neural networks. Conversely, estimation of functional coupling by EEG coherence or non-linear techniques can roughly disclose the level of cooperation among cerebral areas (Babiloni et al., 2004a, 2004d). On the whole, the present results indicate that DL is correlated with the functional coupling of right and left auditory cortices (functional coupling) as a function of the features of the stimuli (competing vs. non competing) and that such a functional coupling reflects a modulation of the EEG rhythms at all main frequency bands.

The present results extend previous DL evidence (Milner et al., 1968; Sparks and Geschwind, 1968; Springer and Gazzaniga, 1975; Hugdahl et al., 1999; Pollmann et al., 2002; Brancucci et al., 2004) by quantifying the functional coupling of two auditory cortices for all main fre-

quency bands of EEG spectrum. This represents a step forward with respect to the simple evaluation of amplitude and latency of EEG or magnetoencephalographic activity evoked by dichotic stimuli. Furthermore, the present results complement previous behavioral evidence demonstrating that small changes in the degree of competition (i.e. spectral overlap) between the dichotic tones significantly affect the magnitude of perceptual asymmetry. Namely, the higher the spectral overlap of the dichotic stimulus, the stronger the left ear advantage for complex tones (Sidtis 1981, 1988) and the stronger the right ear advantage for linguistic sounds (Springer et al., 1978). Consistent results have been obtained with subjects who underwent to temporal lobectomy and hemispherectomy (Berlin et al., 1973).

In the present study, we used DTF technique to investigate whether the direction of estimated information flow between right and temporal electrodes was affected during DL. This technique has been successfully used for the study of functional brain connectivity in previous studies (Kaminski and Blinowska, 1991; Kaminski et al., 1995; Korzeniewska et al., 2003). We observed no statistically significant result at group level when event-related DTF for near (competing) vs. distant dichotic stimuli was compared. During DL of near (competing) vs. distant dichotic stimuli, event-related DTF showed a prevailing direction from T4 (overlying right auditory cortex dominant for complex non-verbal stimuli) to T3 in only seven of 15 subjects. The remaining subjects presented opposite or no preferred direction. At this stage of research, we had to reject the working hypothesis that directionality of information flow from T4 to T3 reflects the prevalence of right (dominant) over left auditory cortex during DL of competing dichotic non-verbal stimuli. Indeed, such a prevalence of right hemisphere has been repeatedly demonstrated in several behavioral studies on DL of complex non-verbal tones similar to those used in the present study (Brancucci and San Martini, 1999, 2003; Brancucci et al., 2005) but its final neural substrate is an open issue. Future studies should re-evaluate this issue using more sophisticated methodology for the estimation of rhythmical activity in auditory cortex, such as high-resolution EEG or magnetoencephalographic techniques.

On the whole, the present results agree with the 'structural theory' proposed originally by Kimura (1967). On the basis of neuropsychological results, she suggested that, during DL, the contralateral neural pathway suppresses the ipsilateral one. In line with this theory, commissurotomy patients had no difficulty reporting words or consonant-vowel syllables presented monaurally to each ear (Milner et al., 1968; Sparks and Geschwind, 1968; Springer and Gazzaniga, 1975). In contrast, they failed to report items presented to left ear when the same stimuli were presented dichotically. The lesion of the posterior part of the corpus callosum (splenium) prevented dichotic sounds to left ear from reaching the left hemisphere via the indirect contralateral route (Pollmann et al., 2002). This indirect contralateral route going through the splenium would permit normal subjects to hear dichotic items in both

ears, even if there is the typical advantage favoring the ear contralateral to the dominant hemisphere for that kind of stimulus. The present EEG coherence results extend the aforementioned 'structural theory,' in that the suggested inhibition of the ipsilateral pathway may be associated with a drop of the functional coordination between the two auditory cortical areas.

CONCLUSION

The present study focused on functional coupling between bilateral auditory cortices and on possible influence of right over left auditory cortex during DL of near (competing) compared with distant complex non-verbal tones. It was hypothesized that dichotic stimulation with competing tones would induce an irregular functional coupling between the two auditory cortices, as revealed by a decrease of EEG coherence and an increase of DTF from right (dominant) to left auditory cortex. The coherence results showed that ErCoh between left and right auditory cortices was generally low in magnitude, as expected by the fact that it derives from the difference between EEG coherence at baseline and event-period. As a main result, ErCoh was significantly lower for all EEG bands of interest during DL of competing than non-competing tone pairs. This was a specific effect, since ErCoh did not differ with monotic competing vs. non-competing stimuli. Conversely, the DTF results showed no influence at group level of right over left auditory cortex during DL. These results suggest a decrease of functional coupling between bilateral auditory cortices during DL of competing non-verbal complex tones, as a possible neural substrate for the lateralization of auditory stimuli during DL.

Future pieces of research should (i) test the generalization of the present findings to other auditory stimuli such as speech, environmental sounds or noise, and (ii) improve the spatial sampling of EEG data for a source analysis aimed at disentangling the role of primary and secondary auditory areas.

Acknowledgments—We thank Matilde Ercolani, Eleonora Merlotti, and Filippo Zappasodi for their technical help. We also thank Prof. Fabrizio Eusebi for his continuous support. This research was principally granted by Fatebenefratelli Association for Research (AFaR).

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(Accepted 17 June 2005)
(Available online 3 October 2005)