Dichotic listening revisited: Trial-by-trial ERP analyses reveal intra- and interhemispheric differences

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ABSTRACT

The dichotic listening (DL) paradigm is often used to assess brain asymmetries at the behavioral level. The aim of this study was to evaluate the dynamic temporal and topographical characteristics of event related potentials (ERPs) obtained with diotic and dichotic consonant–vowel (CV) stimuli from the same subjects. We used a novel approach in which we concurrently analyzed on a trial-by-trial basis ERP parameters during trials that resulted in a right ear advantage (REA) or left ear advantage (LEA) or that were presented under diotic (homonymous) conditions. CV syllables were used as auditory stimuli (/ba/, /da/, /ga/, /ka/, /pa/, /ta/). The EEG measurements were performed with 64 channels by mainly focusing on the N1P2, N2P3 and late negativity (LN) components. Overall, behavioral data revealed a clear REA. The central area showed higher amplitudes than the other locations for N1P2 responses. Additionally, responses were faster for the diotic, compared to the dichotic conditions. The LN had shorter latencies in trials resulting in a REA, compared with those producing a LEA. This result makes it likely that the overall REA is a time-bound effect, which can be explained by the structural theory of Kimura. Furthermore, the results demonstrated a specific spatiotemporal shift from central to frontal areas between N1P2 and LN that was pronounced in dichotic trials. This shift points towards the involvement of frontal areas in resolving conflicting input.

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1. Introduction

During evolution, the two hemispheres of the human brain became specialized for different cognitive functions, with speech perception and language processing emerging as the most important left hemispheric function (Hugdahl, 2005a; Thomsen, Rimol, Ersland, & Hugdahl, 2004). One frequently used method to study such language asymmetry is dichotic listening (DL) (Hine & Debener, 2007; Hugdahl, 2005b; Toga & Thompson, 2003). Although the notion of a 'dichotic' stimulus was originally introduced by Trimble (1931), the classic DL test was developed by Broadbent (1954) and later linked to hemisphere-specific functions by Kimura (1961). The test follows a typical sequence of events, in which a dichotic or diotic (homonym; HOM) stimuli is presented followed by the subject reporting what they heard, usually out of a list of six syllables or two tones (Brancucci et al., 2005; Hugdahl, 2005a, b). The behavioral results of this simple, non-invasive proce-

dure indicate an overall hemispheric dominance effect (Ahonniska, Cantell, Tolvanen, & Lyytinen, 1993; Kimura, 1961). In addition to the so-called "nonforced" condition, forced left ear and forced right ear conditions are commonly applied (Hugdahl et al., 2000; Jäncke, Buchanan, Lutz, & Shah, 2001; O'Leary, 2005). Over time, further dichotic tests have been introduced to address-specific issues. For example, the fused dichotic words test (Wexler & Halwes, 1983), consisting of pairs of monosyllabic rhyming words, was developed to minimize order of report problems and attentional manipulations (Asbjørnsen & Bryden, 1996). Moreover, a one-, two-, and three-pair dichotic digit test has been used to assess performance with increased age (Strouse & Wilson, 1999).

Because of its ability to distinguish which hemisphere processes-specific sounds, the use of DL has become widespread in studies of brain asymmetry (Penna et al., 2006). For example, when non-speech stimuli, such as musical or environmental sounds, are used, a left ear advantage (LEA) is evident (Penna et al., 2006). By contrast, when speech sounds are presented, the DL test reveals a right ear advantage (REA) that highly correlates with data from the Wada-test (Hugdahl, Carlsson, Uvebrant, & Lundervold, 1997) and is related to speech sound processing of the left temporal lobe (Tervaniemi & Hugdahl, 2003). Such findings are supported by a large body of DL research (e.g., Berlin, Lowe-Bell, Cullen, &

Thompson, 1973; Hugdahl, 2005a; Jäncke et al., 2001; Jäncke & Shah, 2002; Penna et al., 2006; Sandmann et al., 2007).

The DL task can be studied using electrophysiological as well as behavioral methods, as electrophysiological techniques allow high temporal resolution based on electroencephalography (EEG) signals obtained non-invasively. The early evoked potentials of the auditory system include auditory brainstem responses (ABR), and middle latency responses (MLR). After the first 100 milliseconds (ms) the auditory processing is assumed to enter the "cognitive" domain (Hillyard & Kutas, 1983; McPherson, 1996). The first negative deflection is commonly called N1 (N100) and has been related to processes in discriminating auditory spectro-temporal characteristics (Eichele, Nordby, Rimol, & Hugdahl, 2005) and also to early attention triggering processes (Chait, Simon, & Poeppel, 2004; Fabiani, Gratton, & Federmeier, 2007; McPherson, 1996). This waveform is followed by a positive deflection, known as P2 (P160) (McPherson, 1996). Together these two waveforms can be analyzed as a single entity known as the N1P2 complex (Barry, Kirkaikul, & Hodder, 2000; Carrillo-de-la-Peña, 2001). Early cognitive N2 and P3 responses are possibly related to inhibitory mechanisms with a fronto-central location (Falkenstein, Hoormann, & Hohnsbein, 2002; Nicholls, Gora, & Stough, 2002). N2P3 responses also occur with the oddball paradigm (Hillyard & Kutas, 1983). It has been proposed that a later negativity (LN, N450), occurring later than 200 ms after stimulus onset (Fabiani et al., 2007; Korpilahti, Krause, Holopainen, & Lang, 2001; Yasin, 2007) is an indicator of more complex higher cognitive processing. The source of the N450 is suggested to be the parahippocampal anterior fusiform gyrus (Fabiani et al., 2007; McPherson, 1996). In linguistic paradigms, high amplitude of the N450 is often observed when an ambiguous word appears at the end of a sentence (Fabiani et al., 2007). Recently, with respect to early processing, Eichele, Nordby et al. (2005) pointed to latency differences in the N1 time window between centrotemporal locations corresponding to perceptual differences of a DL task, and Sandmann et al. (2007), exploring the effect of temporal cues in CV syllables, reported that voiced syllables resulted in larger N1 fronto-central responses when compared to voiceless counterparts.

Converging evidence in the field of DL strongly suggests that the REA arises through mechanisms postulated by Kimura's structural model. According to this model, REA has been interpreted as resulting from rigid bottom up neural connections (Hugdahl, 2005b), that is the contralateral projections of the ascending auditory system consist of more fibers and consequently produce more cortical activity than the ipsilateral projections. In addition, stronger activity in the contralateral system inhibits the processing on the ipsilateral side (Yasin, 2007). However, the neural processes that differ between dichotic and diotic stimuli are not yet fully understood, and it is likely that different contributions of bottom–up and top–down processes (Sætrevik & Hugdahl, 2007) and attentional mechanisms (Hiscock, Inch, & Kinsbourne, 1999; Hugdahl et al., 2000; Jäncke et al., 2001; Petkov et al., 2004), as well as response competition and conflict monitoring (Greenwald & Jerger, 2003; Hertrich, Mathiak, Lutzenberger, & Ackermann, 2003) play a decisive role. Thus, various levels of cognitive information processes interact during DL tasks (Hugdahl, 2005a; Thomsen et al., 2004).

Traditionally, DL studies mostly represent behavioral experiments that are, unfortunately, rarely analyzed by electrophysiological means. Among the existing electrophysiological studies, the classical approach is to categorize the groups of subjects according to their responses as REA or LEA subjects. However, such grouping overlooks the fact that subject's responses vary over trials; a subject who mostly selects right ear input may still switch to the left side in some trials. These trial-to-trial changes can reveal dynamic processes that we address in the present study. One critical goal of the current work was to uncover mechanisms altering the responsiveness of the two hemispheres during dichotic stimulation. Accordingly, the present study was designed to allow concurrent analyses of REA and LEA and HOM responses in a within-subject design. In order to assess the on-line response evaluation, the design required the construction of an interactive stimulus unit, marking data continuously in the EEG to subsequently categorize it into subgroups. Additionally, we sought to analyze the EEG signature of the conflicting nature of the dichotic stimuli in comparison to diotic trials. Achieving this task requires the analysis of later time windows.

2. Methods

2.1. Subjects

A total of 60 healthy subjects (behavioral main group; mean age 23.38 years, 30 female) participated voluntarily in the DL study after having given informed written consent. A subgroup of 20 subjects (mean age: 21.15, 10 females) formed the electrophysiological subject pool. The subjects were mainly students at the University of Dokuz Eylül (DEU) Medical Faculty, Izmir. They reported no history of any neurological and psychiatric conditions and all were native Turkish speakers. The experimental procedure was approved by the Local Ethics Committee. Furthermore, all subjects were screened with audiometric testing (0.125, 0.250, 0.500, 0.750, 1, 1.5, 2, 3, 4, 6, and 8 kHz with SibelMED, AC-50D) to ensure normal hearing in both ears. None of the subjects had a hearing threshold greater than 20 dB or interaural difference greater than 10 dB on any frequency.

2.2. Handedness and laterality index

The Edinburgh Handedness Questionnaire (Oldfield, 1971) was used to assess handedness. Participants who received more than 60 points on the questionnaire were identified as "right handed persons" and all others as "non-right handed persons", classifying 49 subjects of the main (behavioral) group and 15 of the electrophysiology subgroup as right handed.

The subject's dichotic laterality index (LI) was calculated as (1):

$$\text{laterality index (LI)} = \frac{\text{correct right ear responses} - \text{correct left ear responses}}{\text{correct right ear responses} + \text{correct left ear responses}}$$

$$\times 100 \tag{1}$$

By definition, the index varies between -100 and $+100$ and has positive values for REA and negative values for LEA (Eichele, Nordby et al., 2005; Hugdahl, 2005b; Penna et al., 2006; Rimol, Eichele, & Hugdahl, 2006).

2.3. Procedure

The stimulus pairs were presented through closed system SONY headphones (model CDR50) at 80 dB. As in the definition of Trimble (1931), the dichotic presentation is defined as the simultaneous presentation of two non-identical syllables in each trial to the right and left ear. The stimulation set also consisted of diotic (HOM) stimuli which consisted of two identical sounds. Stimuli were digitally recorded natural complex speech sounds produced by an adult Turkish male baritone voice. The classical consonant–vowel (CV) syllables were used /ba/, /da/, /ga/, /ka/, /pa/, /ta/ with a mean duration of 350 ms. The basic sound characteristics such as intensity of the auditory stimuli (CV syllables) were tested with a Brüel&Kjaer Precision Sound Level Meter Type 2232.

While forming dichotic syllables, spectral temporal envelopes of the syllables were matched. The differences between the voice onset time of the voiced (/ba/, /da/, /ga/) and voiceless stop consonants (/pa/, /ta/, /ka/) were identified and controlled for voice onset time (VOT). All possible combinations of the CV pairs were applied to both ears, thus cancelling out potentially confounding effect(s) of VOT-induced variability on Auditory Evoked Potentials (AEPs)/Auditory Event-Related Potentials (AERPs) responses.

Six homonym pairs and 30 possible combinations of the six CV syllables were used which resulted in 36 possible pairs. In order to be able to observe possible differences between right hand and left hand responses, the participants were presented with 72 (one round for right hand and one round for left hand 2 × 36 × 2 CV pairs in counter balanced order) dichotic syllable pairs, for a total of 144 stimuli. Since there were no significant differences between the right and left hand responses, the EEG epochs of both hand responses were combined in the electrophysiological analysis. In order to minimize the aural differences between channels, the headphones were reversed for half of the participants. The interstimulus interval was varied randomly between 5.17 and 6.17 s during EEG recording (Fig. 1). Consequently, the experimental set-up of this study was designed such that the button-press would not be commenced before a 2-s period with the help of a light indicator.

2.3.1. The stimulus set-up/system

We used a recently developed stimulus application system designed for the DL paradigm: The Embedded Interactive Stimulus Design (EMISU). For the purpose of
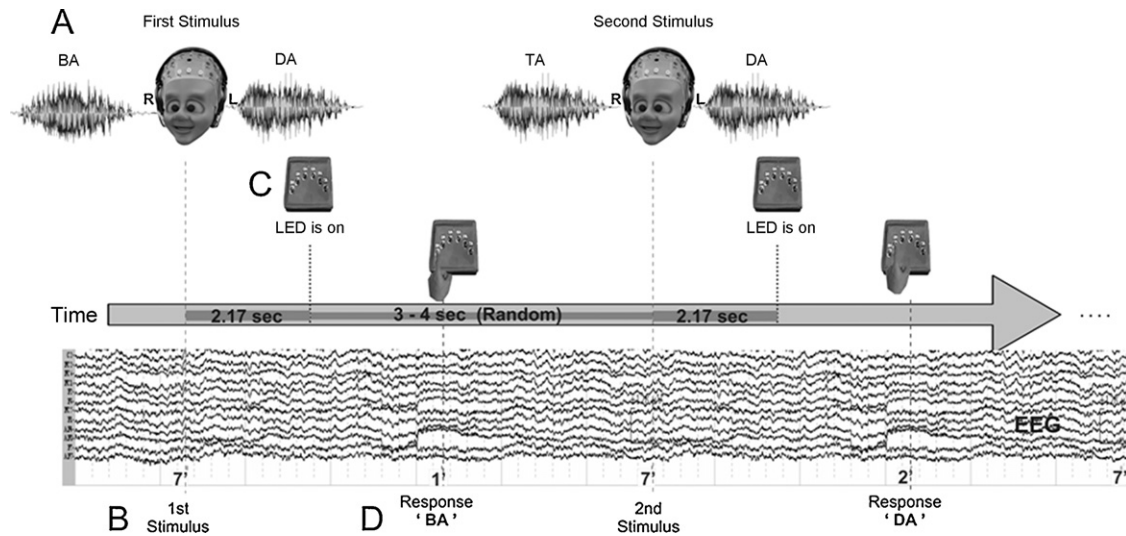
Fig. 1. The recording and stimulation scheme during the dichotic listening paradigm. The different pairs are presented (A) and the stimulus point is marked by 7′ in the bottom of (B) as 'first stimulus'. About 2.17 s (sec) later the light (LED) signal prompts the subject to make a selection on the keypad (C). The choice is marked real-time with 1′ (D). Following these, 2nd stimulus is applied to continue the cycles.

conducting the DL experiments, a microcontroller-based hardware and its software were developed in the DEU Biophysics Laboratory. The system is capable of marking the time point on the EEG record at which the dichotic stimulus is sent to the person in real time. Additionally, it can coregister the responses of the individual to the dichotic stimulus via a six button custom keypad (attributed to /ba/, /da/, /ga/, /ka/, /pa/, /ta/). Furthermore, it can represent a behavioral report related to the responses of the person to the stimuli on-line, thereby allowing the recording and processing of different response conditions on the same head (Ozgoren et al., 2008).

2.4. EEG recordings

Participants listened to the dichotic syllables in an electrically shielded, acoustically isolated, and dimly lit room. While their electroencephalography (EEG) was recorded continuously, they were seated in a comfortable chair, with their eyes open. Neuroscan data acquisition system (Scan 4.3, Neuroscan, Synamps, USA) was used for EEG recording. The Ant EEG Cap (Waveguard cap system, Netherlands), which consists of 64 Ag/AgCl electrodes (channels) was placed on the participants' heads according to a modification of the International 10–10 system. Electrode impedances were kept at less than 5 kΩ. Electrooculogram (EOG) electrodes were placed above and below the left eye (vertical EOG) and at the outer canthus of the left and right eyes (horizontal EOG). EEG channels were referenced to linked ear lobe electrodes ($A1 + A2$), and as a ground electrode, AFz was assigned.

Continuous EEG activity was taken with a sampling rate of 1 kHz, filtered between 0.15 and 70 Hz, and stored to the hard disc for offline analysis. In offline analyses, the merged epochs of the right and left hand responses were used together, as they did not differ. The epochs which were higher than $\pm 50 \,\mu V$ in EOG channel were automatically rejected. ERP/EP response measurement was done visually and separately for the epochs of LEA, REA, and HOM stimuli, and the number of the epochs for these situations were kept equal for each participant. The selected epochs were averaged and automatically baseline corrected, using prestimulus interval and digitally band pass filtered at 1–30 Hz (6 dB/octave). For the figure presentations, the grand averages of evoked potentials of 20 participants were used.

In this report, 9 electrodes (F_3, F_4, C_3, C_4, C_Z, T_7, T_8, P_7, and P_8) were chosen out of 64 electrode sites corresponding to frontal, central, temporal and parietal regions of interest, covering a number of areas that turned out to be central in DL studies (Ahonniska et al., 1993; Davidson & Hugdahl, 1996; Eichele, Nordby et al., 2005; Eichele, Specht et al., 2005; Hugdahl et al., 2000; Jäncke & Shah, 2002; Jerger & Martin, 2004). Furthermore, the sweeps were epoched from −1000 ms prestimulus to +1000 ms poststimulus. The time windows were chosen to represent the major peaks of the responses. Accordingly, N1P2, N2P3 and late negativity (LN) wave complexes were studied. The latency reporting was conducted in accordance with the prominent peaks (N1 (136–147 ms), P3 (344–375 ms) and LN (440–519 ms), respectively) of the wave complexes in three time windows.

2.5. Statistical analysis

SPSS 11.0 (SPSS Inc., USA) was used for statistical analysis. For the behavioral data analysis, DL responses were subjected to a repeated measures three-way ANOVA, with EARADVANTAGE (RE, right ear correct reports; LE, left ear correct reports;

blend errors) as within-subject factors. Following a significant effect in the repeated measures, ANOVA's post hoc analysis with Bonferroni correction was used for comparison of the differences between the correct ear responses or ear advantages.

For the electrophysiological analysis, peak-to-peak maximum amplitude and latency of responses were analyzed for each time window (N1P2, N2P3, and LN) by means of repeated measures ANOVAs, including CONDITION (three levels: REA, LEA, and HOM), ELECTRODE (9 levels: F_3, F_4, C_Z, C_3, C_4, T_7, T_8, P_7, and P_8) and LATERALITY (two levels: left and right) as within-subject factors. Greenhouse–Geisser correction was applied. Following a significant effect in the repeated measures, ANOVA's post hoc analysis with Bonferroni correction was used for the comparison of the differences between the electrodes. Bilateral electrodes for laterality effect (F_3–F_4; C_3–C_4; T_7–T_8; P_7–P_8) and ipsilateral electrodes for anterior/posterior processing (F_3–P_7; F_3–T_7; F_4–P_8; F_4–T_8) were evaluated. For the post hoc analyses of laterality, comparisons of the electrode pairs, t-tests (two tailed) were applied.

Besides these analyses, to investigate the relationship between regional interaction, four regions of interest (**ROI**) were defined as frontal (F_3 and F_4), central (C_3, C_4, and C_Z), parietal (P_7 and P_8) and temporal (T_7 and T_8). Mean amplitude of these ROI were analyzed for each time window (N1P2, N2P3, and LN) by means of a repeated measures ANOVAs, including the two within-subject factors CONDITION (three levels: REA, LEA, and HOM) and REGION (four levels: frontal, central, temporal, and parietal). In order to demonstrate overall latency analyses, each of these three condition's latency values were grouped. Furthermore, Pearson correlation coefficients were used to assess the test–retest reliability per DL test (First DL Test Laterality Index (LI) vs. Second DL Test LI).

3. Results

3.1. The effectiveness of the experimental set-up and design

The current experimental design illustrated its efficacy during recording and offline analyses. The supporting features behind this argument are that the present set-up enabled behavioral reports to be used as feedback for the EEG system, allowing subgroupings of ERPs concurrently for REA, LEA and HOM types. Additionally, the ERPs were free of artifacts for the larger time windows (−1000 to 1000 ms), permitting a later time window analysis.

3.2. Behavioral data

3.2.1. Laterality index

The mean ($\pm$S.D.) laterality index (as calculated according to the formula above (1)) of the 20 subjects that formed the electrophysiological group, was 23.75% (± 22.6). Seventeen subjects (85% of subjects) had a positive LI (REA mean value = 32.3% (± 15.2)
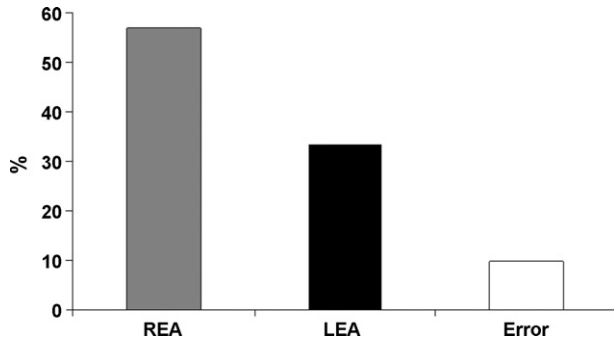
Fig. 2. The histogram derived from 60 subjects that depicts the behavioral grand average ear advantage distribution. REA, black; LEA, gray; blend errors, white color.

and the remaining 3 subjects had a negative index (LEA mean value = − 10.7% (±10.6)).

3.2.2. Dichotic listening behavioral results

In the overall statistical analysis of ear advantage scores of the 60 subjects (83.33% of subjects had positive LI), the ANOVA showed a significant main effect of EAR ADVANTAGE ($F(1.19, 70) = 116.57$, $p < 0.001$). The post hoc analysis showed significantly higher right ear correct responses (REA = right ear advantage) 56.82% (±16.32) than left ear correct responses (LEA = left ear advantage) 33.32% (±16.39), and blend errors (errors + unanswered cases) 9.86% (±8.05) ($p < 0.001$) (Fig. 2).

Upon closer examination for handedness effects, the ear advantage resulted in 33.65% (±15.60) LEA, 57.11% (±15.02) REA for right handed subjects and 33.33% (±20.35) LEA, 54.09% (±21.22) REA for left handed subjects.

3.2.3. Test–retest reliability

In order to determine the retesting accuracy of the modified DL paradigm, we recruited 10 randomly selected subjects approximately 4 months later for the retesting procedure. The analysis showed a high test–retest reliability of the modified DL paradigm. The correlation between DL Test 1 and DL Test 2 was significant ($n = 10$, $r = 0.87$, $r^2 = 0.76$, and $p < 0.05$).

3.3. Electrophysiological findings

The electrophysiological data sets that were (concurrently) obtained from the same subjects were divided into three conditions: LEA, REA, and HOM, respectively. The repeated designed ANOVA analyses were performed (Section 2.5) separately in three time windows: N1P2, N2P3, and LN.

Accordingly, in the overall statistical analysis of amplitude of the **N1P2 window**, the ANOVA showed ELECTRODE ($F(1.9, 36.11) = 33.75$, $p < 0.001$), LATERALITY ($F(1, 19) = 7.11$, $p < 0.05$) main effects and ELECTRODE × LATERALITY ($F(1.76, 33.52) = 8.23$, $p < 0.01$) interaction. These effects and further post hoc results are explained in the following sections.

The overall statistical analyses of amplitude of the **late time (LN) window** indicated significant effects for ELECTRODE ($F(2.12, 40.28) = 28.06$, $p < 0.001$) and LATERALITY ($F(1, 19) = 20.91$, $p < 0.001$) main effects. Additionally, the ANOVA showed ELECTRODE × LATERALITY ($F(2.13, 40.36) = 4.95$, $p < 0.05$) and ELECTRODE × CONDITION ($F(4.24, 80.64) = 4.57$, $p < 0.01$) interactions. In the overall analyses of latency of the **LN**, a significant main effect of CONDITION ($F(1.33, 25.29) = 8.70$, $p < 0.01$) was found.

3.3.1. Amplitudes of ERPs in three time windows

The mean amplitudes of N1P2, N2P3, and LN responses of 20 subjects in 9 electrode sites (Fig. 3) during LEA, REA, and HOM are provided in Table 1.

3.3.1.1. Early time window (N1P2) results.
Peak-to-peak maximum amplitudes of N1P2 were analyzed for the three conditions LEA, REA, and HOM. The largest response amplitudes were observed for each condition at the central locations during N1P2. The repeated measures ANOVAs on N1P2 responses revealed a significant effect for ELECTRODE in REA ($F(3.76, 71.48) = 20.93$, $p < 0.001$), in LEA ($F(2.88, 54.67) = 28.65$, $p < 0.001$), and in HOM ($F(2.53, 48) = 28.66$, $p < 0.001$) conditions, indicating an increased N1P2 response at central recording sites. The Bonferroni post hoc comparisons revealed differences between electrode sites as the following:

During the LEA trials, the C_Z amplitude was found to be higher than F_3 ($p < 0.001$), F_4 ($p < 0.001$), C_3 ($p < 0.01$), C_4 ($p < 0.05$), T_7 ($p < 0.001$), T_8 ($p < 0.001$), P_7 ($p < 0.001$), and P_8 ($p < 0.001$) amplitudes for N1P2 results.

The left temporal hemisphere (T_7) N1P2 amplitude was lower than that of the ipsilateral left central hemisphere (C_3) ($p < 0.001$). The right temporal hemisphere (T_8) N1P2 amplitude was lower than that of the ipsilateral right central hemisphere (C_4) ($p < 0.001$). The left parietal hemisphere N1P2 amplitude was lower than that of the ipsilateral fronto-central hemisphere (P_7–F_3, $p < 0.05$; P_7–C_3, $p < 0.001$). The P_8 amplitude of N1P2 results was lower than the C_4 N1P2 results ($p < 0.001$).

To investigate the relationship of laterality interactions during the LEA, a post hoc t-test revealed higher right hemispheric N1P2 ERP amplitudes compared to those of the left hemisphere in LEA conditions (T_7–T_8, $t(19) = 3.68$, p (two tailed) <0.01).

During the REA trials, the C_Z electrode's amplitude of N1P2 was higher than that of F_3 ($p < 0.001$), F_4 ($p < 0.01$), C_3 ($p < 0.001$), C_4 ($p < 0.01$), T_7 ($p < 0.001$), T_8 ($p < 0.001$), P_7 ($p < 0.001$), and P_8 ($p < 0.001$). Fronto-central location N1P2 amplitudes were higher than the ipsilateral parietal location amplitudes (F_3–P_7, $p < 0.01$; C_3–P_7, $p < 0.001$; F_4–P_8, $p < 0.05$; C_4–P_8, $p < 0.001$). At the left and the right temporal hemisphere, the amplitude of N1P2 was lower than the ipsilateral central hemisphere's N1P2 amplitudes (C_3–T_7, $p < 0.001$; C_4–T_8, $p < 0.001$).

The right temporal N1P2 amplitude was higher than that of the left temporal location amplitude ($p < 0.05$). Post hoc t-tests revealed higher right hemispheric N1P2 ERP amplitudes when compared to left hemispheric ones in REA conditions (T_7–T_8, $t(19) = 2.09$, p (two tailed) <0.001; P_7–P_8, $t(19) = 4$, p (two tailed) <0.01).

During the homonym (HOM) condition and for the N1P2 results, post hoc test showed that C_Z was higher than F_3 ($p < 0.01$), F_4 ($p < 0.01$), C_3 ($p < 0.01$), C_4 ($p < 0.01$), T_7 ($p < 0.001$), T_8 ($p < 0.01$), P_7 ($p < 0.001$), and P_8 ($p < 0.001$). Left temporal N1P2 amplitudes were lower than left central N1P2 results ($p < 0.01$).

Both left and right frontal hemisphere responses were higher than ipsilateral parietal hemisphere responses (F_3–P_7, $p < 0.001$; F_4–P_8, $p < 0.05$). Right and left parietal location amplitudes were lower than central location amplitudes (for each comparison $p < 0.001$).

Post hoc t-tests revealed higher right hemispheric N1P2 ERP amplitudes when compared to those of the left hemisphere in the HOM condition ($\mathbf{T_7}$–$\mathbf{T_8}$, $t(19) = 2.56$, p (two tailed) <0.05).

3.3.1.2. ROI comparison of N1P2.
The repeated measures ANOVAs of the N1P2 responses for **ROI** revealed a significant effect for REGION (frontal, central, temporal, parietal) in REA ($F(2.19, 41.57) = 40.18$, $p < 0.001$), in LEA ($F(1.87, 35.71) = 30.64$, $p < 0.001$), and in HOM ($F(1.80, 34.19) = 30.48$, $p < 0.001$). These effects reflected that for all three conditions (LEA, REA, and HOM), the N1P2 amplitude of the
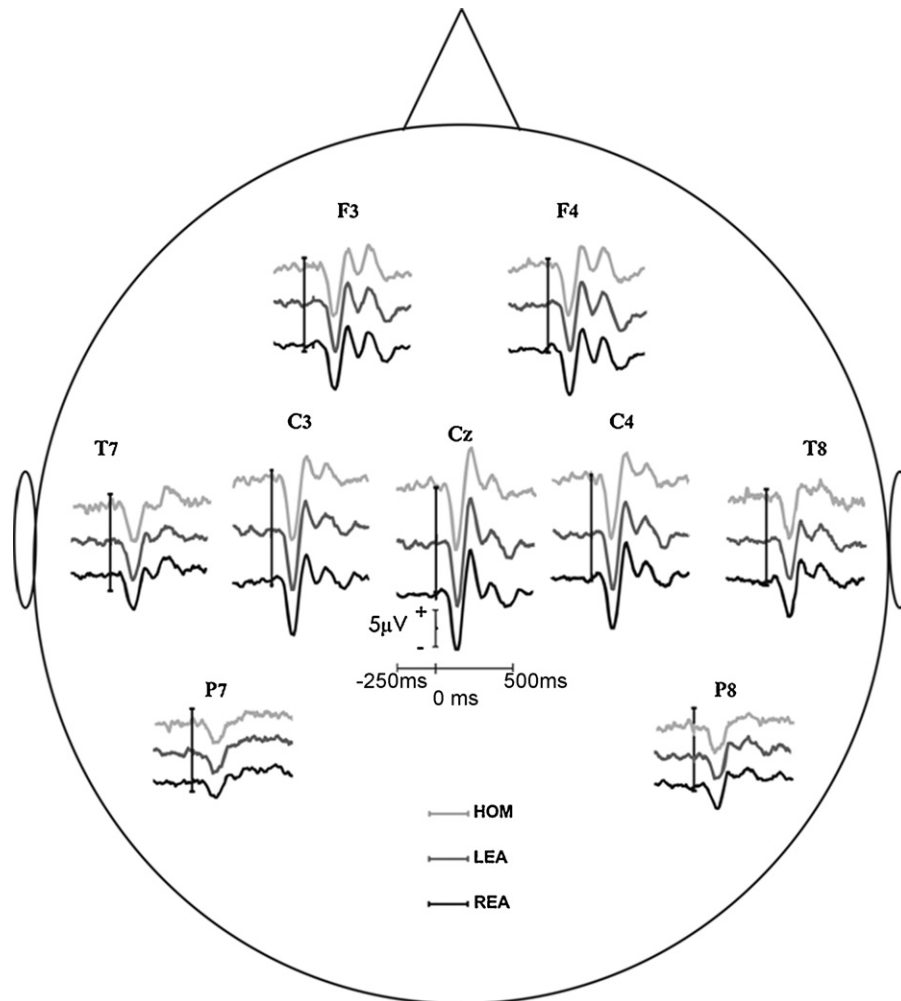
Fig. 3. The whole head ERP waveforms averaged across 20 individuals. For the sake of simplicity only 9 electrodes are shown. The upper waveforms indicate the diotic condition (HOM, gray), the middle waves represent the LEA (dark gray) and the lower ERPs correspond to REA (black) responses. The vertical lines in each graph represent the stimulus time (0 ms) and the poststimulus of 700 ms is displayed. The vertical axis represents amplitudes (μV) with positive towards upper direction (scale of 5 μV displayed).

central region was significantly higher than those of temporal, parietal, and frontal regions. The amplitude of the parietal region was significantly lower than those of frontal and temporal regions (all comparisons are at least significant at the 0.05-level, Fig. 4A).

3.3.1.3. Intermediate time window (N2P3) results. In general, repeated measures ANOVAs showed that the N2P3 window did not provide significant differences between the LEA, REA, and HOM conditions. Only for the laterality measure, the post hoc *t*-test

revealed higher left hemispheric N2P3 ERP amplitudes when compared to right hemispheric ones in the HOM condition (T_7–T_8, $t(19) = 4.01$, p (two tailed) <0.001).

3.3.1.4. Late time window (LN) results. Peak amplitudes of LN were analyzed for all three conditions (LEA, REA, and HOM). The largest amplitudes of responses were observed at the frontal locations for LEA and REA. The repeated measures ANOVAs on LN responses revealed a significant effect for ELECTRODE in REA

Table 1
Amplitudes of responses in three conditions and three time windows. N1P2, N2P3, and LN response mean amplitudes (μV) and standard deviations of 20 subjects at 9 electrode positions during LEA, REA, and HOM ($n = 20$).

| Electrodes	LEA mean amplitudes (μV)			REA mean amplitudes (μV)			HOM mean amplitudes (μV)		
	N1P2	N2P3	LN	N1P2	N2P3	LN	N1P2	N2P3	LN
F_3	10.5 ± 4.4	5.2 ± 2.8	−3.9 ± 2.4	10.3 ± 4.0	5.6 ± 2.5	−3.6 ± 2.3	11.2 ± 4.4	6.0 ± 2.7	−2.5 ± 2.2
F_4	10.7 ± 4.3	5.4 ± 2.9	−4.3 ± 2.4	10.7 ± 3.6	5.2 ± 1.9	−4.3 ± 2.5	11.2 ± 4.8	5.7 ± 2.4	−3.6 ± 2.8
C_Z	15.5 ± 5.3	5.1 ± 2.7	−3.8 ± 2.8	15.4 ± 4.9	4.7 ± 2.6	−3.8 ± 2.7	15.2 ± 6.1	5.8 ± 2.3	−2.9 ± 2.3
C_3	13.2 ± 4.1	5.6 ± 2.7	−1.8 ± 2.6	12.6 ± 4.0	5.2 ± 2.7	−2.3 ± 2.1	13.2 ± 4.6	5.6 ± 2.8	−1.8 ± 2.4
C_4	13.1 ± 4.4	5.3 ± 3.2	−2.7 ± 2.4	13.1 ± 4.6	4.6 ± 2.6	−2.6 ± 2.2	12.8 ± 4.8	5.2 ± 2.7	−2.1 ± 2.2
T_7	8.0 ± 2.8	5.1 ± 1.7	−1.4 ± 2.0	7.6 ± 2.7	5.5 ± 2.4	−1.8 ± 1.9	7.9 ± 2.1	5.9 ± 2.1	−1.1 ± 1.4
T_8	10.0 ± 3.4	4.8 ± 2.3	−2.8 ± 2.1	9.9 ± 4.0	4.9 ± 2.0	−2.9 ± 1.6	9.2 ± 2.6	4.2 ± 1.6	−2.9 ± 1.7
P_7	6.1 ± 2.0	4.4 ± 1.5	−0.2 ± 1.4	5.5 ± 2.2	4.6 ± 2.0	−0.5 ± 1.4	5.4 ± 2.6	5.1 ± 2.1	−0.9 ± 1.4
P_8	6.9 ± 2.4	5.6 ± 2.5	−1.1 ± 1.7	7.0 ± 2.7	4.8 ± 2.4	−1.2 ± 1.5	6.8 ± 2.2	4.8 ± 2.0	−1.8 ± 1.7
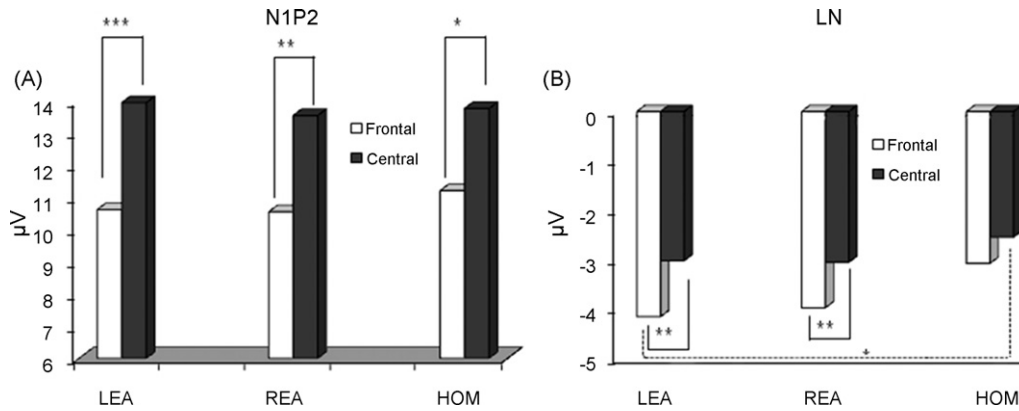
Fig. 4. The histogram of amplitudes of LEA, REA, and HOM conditions for two time windows (A) N1P2 and (B) LN ($*p < 0.05$; $**p < 0.01$; $***p < 0.001$). The dark gray color represents the grouped central responses; white color indicates grouped frontal responses.

($F(3.76, 71.4) = 20.93$, $p < 0.001$) and in LEA ($F(3.53, 67.13) = 22.40$, $p < 0.001$), indicating an increased LN response at frontal recording sites. Bonferroni post hoc comparisons revealed the differences between electrode sites. Additionally, the repeated measures ANOVAs for LN responses of **ROI** revealed a significant effect for REGION in REA ($F(2.04, 38.83) = 19.32$, $p < 0.001$) and in LEA ($F(1.87, 35.48) = 21.06$, $p < 0.001$) (Fig. 4B).

LEA trials: When the LN responses were compared, the mean amplitudes of F3 were higher than those of the T_7 ($p < 0.01$) and of the P_7 ($p < 0.001$). F4 amplitudes were higher than both of T_8 and P_8 (F_4–T_8, $p < 0.01$; F_4–P_8, $p < 0.001$). The P_8 amplitude was lower than that of C_4 ($p < 0.05$). C_Z LN amplitudes were higher than those in P_7 ($p < 0.001$), P_8 ($p < 0.01$), and T_7 ($p < 0.05$). To investi-

gate the relationship between right and left electrodes, post hoc t-tests revealed higher right hemispheric LN ERP amplitudes when compared to those of the left hemispheric during LEA trials (**C_3–C_4**, $t(19) = 2.91$, p (two tailed) <0.01; **T_7–T_8**, $t(19) = 2.82$, p (two tailed) <0.05; **P_7–P_8**, $t(19) = 3.25$, p (two tailed) <0.01). At a broader level, the LN amplitudes of the frontal **ROI** were higher than those of temporal ($p < 0.01$), parietal ($p < 0.001$), and central ($p < 0.01$). The parietal region amplitudes were lower than those of the central ($p < 0.01$) and temporal regions ($p < 0.001$) (Fig. 4B).

REA trials: When the relationship between the amplitudes was analyzed for 9 electrodes, it was shown that LN amplitudes of the left and right frontal electrodes were higher than those of the ipsi-lateral parietal electrodes ($p < 0.001$). At C_Z, the LN amplitude was
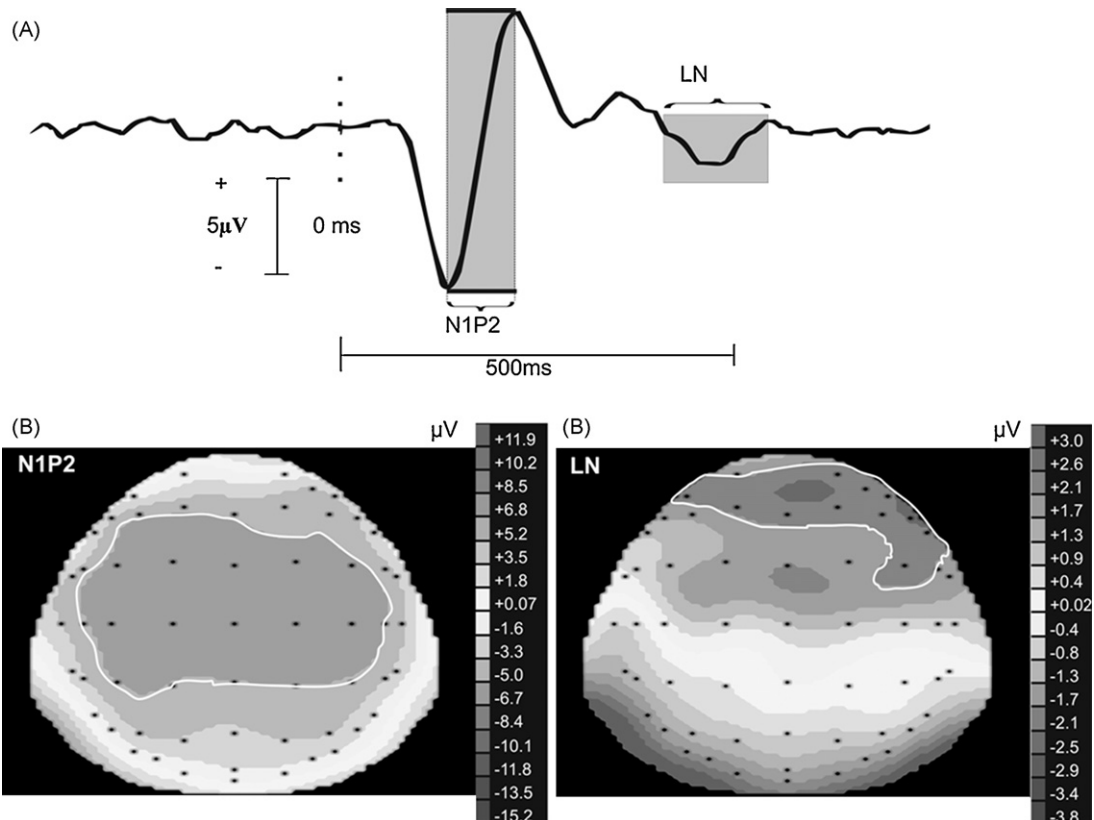

Fig. 5. The grand average of dichotic listening response waveform and its corresponding map during REA condition. (A). The evoked potential indicates the N1P2 and LN sections. (B) The N1P2 2D map and (C) LN 2D map. The amplitude is presented by means of a graded scale; the corresponding highest peak effect is shown by means of a white contour line.

Table 2
The N1P2, N2P3 and late negativity (LN) response mean latencies (ms) and standard deviations of 20 subjects in 9 electrodes during LEA, REA, and HOM ($n = 20$).

Electrodes	LEA mean latencies (ms)			REA mean latencies (ms)			HOM mean latencies (ms)		
	N1	P3	LN	N1	P3	LN	N1	P3	LN
F_3	142.2 ± 10.1	367.2 ± 21.8	506.7 ± 55.0	141.4 ± 19.5	363.7 ± 23.6	484.5 ± 47.0	142.7 ± 20.8	371.1 ± 20.4	476.8 ± 32.9
F_4	142.5 ± 11.8	368.4 ± 23.3	493.5 ± 52.5	146.5 ± 20.1	359.2 ± 18.7	488.2 ± 50.8	136.9 ± 19.1	365.4 ± 17.6	476.5 ± 24.2
C_Z	137.4 ± 8.0	361.8 ± 25.6	496.7 ± 52.9	140.3 ± 12.9	364.0 ± 28.1	477.4 ± 52.5	134.4 ± 14.7	374.4 ± 19.6	473.5 ± 47.7
C_3	140.5 ± 8.6	359.0 ± 31.9	465.9 ± 39.5	142.2 ± 13.5	353.0 ± 33.1	445.3 ± 35.1	139.8 ± 14.7	361.3 ± 15.8	443.7 ± 35.5
C_4	139.3 ± 9.7	357.6 ± 35.4	469.1 ± 39.7	136.2 ± 14.7	358.4 ± 23.6	445.8 ± 35.1	138.5 ± 16.3	362.6 ± 25.2	440.0 ± 34.8
T_7	147.3 ± 17.9	363.2 ± 32.7	490.6 ± 56.6	146.6 ± 16.8	375.4 ± 34.3	481.8 ± 47.1	146.1 ± 18.9	365.6 ± 17.9	468.7 ± 43.3
T_8	147.2 ± 15.1	359.7 ± 25.8	519.8 ± 42.2	141.9 ± 31.2	353.7 ± 27.7	491.3 ± 55.2	142.9 ± 20.7	361.5 ± 22.2	466.8 ± 39.6
P_7	136.8 ± 30.8	363.5 ± 34.5	464.1 ± 63.6	137.7 ± 22.5	350.6 ± 29.5	431.3 ± 40.2	141.8 ± 27.0	367.5 ± 23.1	447.4 ± 51.8
P_8	141.5 ± 28.7	353.7 ± 30.0	478.4 ± 48.7	136.9 ± 12.7	344.7 ± 32.7	440.3 ± 34.5	140.7 ± 23.0	355.6 ± 27.1	449.1 ± 45.1

higher than LN amplitudes at P_7 ($p < 0.001$) and P_8 ($p < 0.01$). The C_Z LN amplitude was higher than the T_7 amplitude ($p < 0.001$). C_3 and C_4 amplitudes were higher than P_7 and P_8 (C_3–P_7, $p < 0.001$; C_4–P_8, $p < 0.05$). Post hoc *t*-tests revealed higher right hemispheric LN ERP amplitudes when compared to those of the left hemisphere during REA trials (**F_3–F_4**, $t(19) = 3$, p (two tailed) <0.01; **T_7–T_8**, $t(19) = 4.14$, p (two tailed) <0.01; **P_7–P_8**, $t(19) = 2.82$, p (two tailed) <0.05). When the relationships between the amplitudes were analyzed for **ROI**, it was found that the LN amplitude of the frontal region was higher than those of the temporal ($p < 0.05$) and the central ($p < 0.01$) one. The parietal region amplitudes were lower than those of the frontal ($p < 0.001$) and temporal regions ($p < 0.05$) (Fig. 4B).

The topographic mapping during the **REA** condition in two time windows is shown in Fig. 5. Here, during the early time window (N1P2) activity patterns were more pronounced in central than in frontal areas. In the same condition, LN responses were dominant in frontal compared to central areas (see Figs. 3–5).

HOM condition: There were no significant differences between LN amplitudes for frontal and central electrodes (Fig. 4B). To assess the laterality effects, post hoc *t*-tests revealed higher right hemispheric LN ERP amplitudes when compared to left hemispheric ones in HOM conditions (**F_3–F_4**, $t(19) = 2.59$, p (two tailed) <0.05; **T_7–T_8**, $t(19) = 3.38$, p (two tailed) <0.01; **P_7–P_8**, $t(19) = 2.89$, p (two tailed) <0.01).

3.3.2. Latency of ERP in three time windows

The latency values of N1P2, N2P3, and LN wave complexes were analyzed according to N1, P3, and LN latencies. The resulting mean latencies of 20 subjects at 9 electrode positions during LEA, REA, and HOM are presented in Table 2.

According to the analyses of the **latencies** of the **first (N1P2)** and the **second (N2P3) time window** for LEA, REA, and HOM conditions, there were no significant differences between the 9 electrode positions. The repeated measures ANOVAs on **LN latency responses** revealed a significant effect for CONDITION ($F(1.33, 25.29) = 8.70$, $p < 0.01$) and for ELECTRODE ($F(2.61, 49.66) = 25.31$, $p < 0.001$). In the post hoc analysis for the REA condition, LN latencies of the P_7 were shorter than those of the F3 ($p < 0.01$), and latencies of the P_8 were shorter than of C_4 ($p < 0.05$).

The **overall latency values** were also grouped for each condition. **In the late time window (LN)**, the repeated measures ANOVAs of these groups revealed a significant effect for CONDITION ($F(1.87, 334.65) = 19.26$, $p < 0.001$) (Fig. 6). As shown in Fig. 6, the LEA latency values were significantly longer than those of REA and HOM (for each comparison, $p < 0.001$) (Fig. 6).

4. Discussion

The aim of this study was to investigate the dynamic perceptual and cognitive processes during DL by means of electrophysiological analyses. To address these goals, early and late time windows

were studied during diotic conditions and during dichotic trials that resulted in either a LEA or REA. With the help of a novel interactive stimulus unit, the present report marks the first study to concurrently analyze these dynamic responses. We found that the early time window (N1P2) ERPs reveal a central higher activity pattern for all three conditions. However, the late time window (LN) ERPs demonstrate a larger frontal-activity pattern for dichotic, compared to diotic stimuli. Thus, our data reveal an initial activation of both sensory and attentional systems irrespective of input type, followed by shifts to a larger frontal dominance for the conflicting input. The second important feature obtained from the present study is that the late time window latency of ERPs of the LEA was longer than that of the REA, indicating faster processing of trials that result in a REA.

4.1. Behavioral data

In a DL study with Norwegian participants, Hugdahl (2005b) reported that the right ear has a sex-independent advantage (48%) over the left ear (35%). Similar results were obtained in a German (Bethmann, Tempelmann, Bleser, Scheich, & Brechmann, 2007), Spanish (Azañón-Gracia & Sebastián-Gallés, 2005), and Italian sample (Morra, Martini, Cornacchia, Tobey, & Miller, 1983). Even when using click consonant stimuli to African subjects, a REA could be revealed (Best & Avery, 1999). The present study reports similar findings in the Turkish population (56.82% REA and 33.32% LEA), supporting the universality of DL test results across different cultures and languages (Hugdahl, 2005a). Furthermore, the test/retest reliability of our study was similar to Hugdahl and Hammar (1997) and Azañón-Gracia and Sebastián-Gallés (2005) studies. Besides, a LEA is usually elicited during listening of complex tones, musical and environmental sounds (Brancucci et al., 2005; Hugdahl, 2005b; Penna et al., 2006).

As predicted, the diotic condition revealed fewer error rates than the dichotic condition. Thus, diotic stimuli can be regarded as "**easy**"
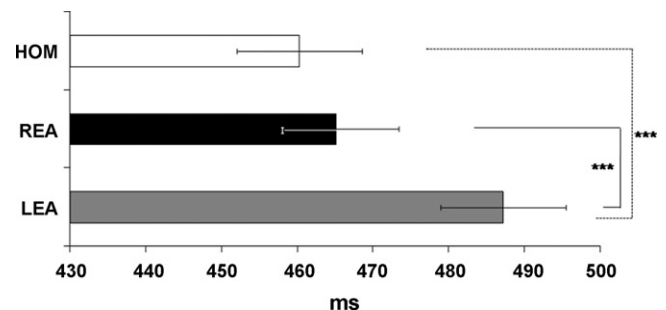

Fig. 6. The comparison REA, LEA, and HOM mean latencies at LN. The gray color indicates LEA, black REA, white diotic (HOM) conditions (***$p < 0.001$). Thin capped horizontal bars represent standard errors for each group.

and dichotic stimuli as "**difficult**". Furthermore, the six dichotic CV syllable pairs show different degrees of laterality effects (Bayazıt, Öniz, Özgören, & Güntürkün, 2008), possibly resulting from differences in voice onset time (VOT) between the syllables used (Rimol et al., 2006; Sandmann et al., 2007; Zaehle, Jäncke, & Meyer, 2007). VOT is the length of time that passes between the release of a consonant and the onset of voicing, defined by the vibration of the vocal folds. Certainly, this DL-parameter deserves further investigation. The present study design controlled these possibly confounding acoustic effects by ensuring the homogenous distribution and symmetrical presentation of every single CV pair. Further control could be achieved by incorporating attention-dependent parameters into the design, as attention and stimulus properties have been found to be important factors (Hugdahl et al., 2000; Lipschutz, Kolinsky, Damhaut, Wikler, & Goldman, 2002; O'Leary, 2005; Zaehle et al., 2007).

4.2. Electrophysiological results

The early and late responses N1P2 and LN revealed significant differences between conditions. While the early components appear primarily related to bottom up sound processing mechanisms, the late components seem to reflect several aspects of cognitive processes (Hillyard & Kutas, 1983; McPherson, 1996).

4.2.1. Early time window

In the present study, N1P2 was notably recorded between 108 and 161 ms at C_Z. Formerly, the superior temporal plane and the lateral superior temporal gyrus were suggested to be the source of the N1P2 (McPherson, 1996). The total dipole effects of the synchronous firing of neural clusters generate a maximal N1P2 ERP response at the C_Z on the scalp in auditory paradigms (McPherson, 1996). Both amplitude and latency of N1P2 at C_Z were independent of syllable combination, ear advantage (REA and LEA), or the HOM condition. Recently, Eichele, Nordby et al. (2005) reported that the ERP latencies of the N1P2 ERP components were shorter for REA compared to LEA subjects. In the present study, subjects were not grouped into REA- or LEA-types instead, in what we believe to be the first approach of this kind, ERP responses of trials that resulted in a REA or a LEA, or that were diotic, were evaluated separately on a trial-by-trial basis. This more fine-grained approach did not reveal a differentiation of early time-window amplitudes across REA, LEA and HOM conditions. However, in contrast to the data pattern of the Eichele, Nordby et al. (2005) study, we obtained higher amplitudes in the right temporo-parietal regions compared to the left side. The higher amplitude of the central region did, however, conform to Eichele's study, for LEA, REA, and HOM conditions in the N1P2 window. It is likely that differences in the analyses strategies of the two studies have produced these discrepancies. The detailed analysis of the present study did not reveal an asymmetry in the speed of early stimulus processing between the two hemispheres.

4.2.2. Intermediate time window

The present data reveal higher left compared to right hemisphere amplitude of the N2P3 window within the HOM condition which supports previous work (e.g., Ahonniska et al., 1993). The N2 component is related to error control mechanisms, whereas the P3 component appears to be associated with processing of new information (Fabiani et al., 2007; Falkenstein et al., 2002). One possible implication of this finding is the suggestion that, under natural hearing conditions, a left hemispheric superiority emerges at an early period of processing. The fact that such a finding was not significant under dichotic conditions could be due to the additional processing demand that is created by dichotic stimuli.

4.2.3. Late time window

The N450 or LN is observed in the centro-parietal region (McPherson, 1996) and is related to semantic cognitive processes such as word integration (Fabiani et al., 2007; Hillyard & Kutas, 1983; Kuperberg, 2007; Rhodes & Donaldson, 2008) and conflict monitoring (Swick & Turken, 2002). N450 has also been associated with conceptual or semantic violations of sentences (Fabiani et al., 2007). Naturally, the DL task places a high demand on subjects as they are asked to provide one answer from a set of choices, with performance depending on the continuous focused processing of contradictory results. The consciously perceived syllable during dichotic presentation is possibly resolved by means of neural structures that are also activated in the context of semantic processes, thereby evoking a N450 ERP component.

The overall latency results in the late time window (LN) revealed that LEA had the longest latency, followed by REA and than HOM. This finding indicates that a conflicting input results in longer processing time which itself results in longer latencies for dichotic stimuli, possibly due to increased cognitive load (Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999; Ozgoren, Başar-Eroğlu, & Başar, 2005). Most important is our finding of longer latencies for trials that produce a LEA, compared to those where subjects decide for the right ear input (REA). To understand the relevance of this finding it is necessary to recapitulate the basic assumption of the Kimura-model. According to Kimura (1961), final processing of a syllable heard by the left ear is not accomplished in the right hemisphere; instead, it occurs only after transference via the corpus callosum to the language-dominant left hemisphere (O'Leary, 2005; Pollmann, Lepsien, Hugdahl, & Yves von Cramon, 2004). This transfer is not necessary for syllables heard by the right ear, since they directly enter the left hemisphere. Thus, our data reveal a time-advantage of the right ear input for those trials in which the right ear syllable is consciously perceived, resulting in a REA-trial. LEA trials have the longest latencies because the syllable giving rise to the conscious choice must be transferred from the right to the left hemisphere in order to be properly decoded (Rimol et al., 2006). Our finding of shorter N450 latencies for REA than for LEA, therefore, provides strong support for the structural theory of Kimura (1961). Consequently, it can be speculated that the reason why DL studies produce an overall REA is that semantic language processing must be analyzed by the left hemisphere, resulting in a time-advantage of right ear input. The ear-asymmetry of DL therefore seems to be a time-bound effect.

4.3. Anatomy and functional aspects

The literature provides different views on the functional localization of activation during the performance of DL tasks. DL has been linked to a general left hemisphere dominance in a number of brain imaging studies (Bethmann et al., 2007; Jäncke et al., 2001; Jäncke & Shah, 2002; Thomsen et al., 2004). Recently the DL responses were explored using a low resolution source localization (LORETA), which estimated the intracerebral sources of electrical activation within the perisylvian brain area (Sandmann et al., 2007). The present temporal dynamics could benefit from further techniques with high topographical resolution or even combined applications of EEG and fMRI (Eichele, Specht et al., 2005). Pollmann et al. (2004) found that both right and left ear target detections elicited activation in right posterior areas. Similarly, the present results indicate higher activation of right hemisphere regardless of condition (REA, LEA and HOM) in N1P2 and LN time windows, with a further frontal differentiation, especially in LEA trials.

The results of the present study provide different laterality findings in three time windows. The N2P3 time window marks the left temporal amplitude (left dominance) being larger than the right

temporal amplitude. Additionally, the current N1P2 and LN ERPs point to higher activation levels within the right hemisphere. The ERP amplitude dominance, therefore, was observed to shift from one region to another in time. Our findings point to a transposition of activation in between hemispheres with a time resolution that exceeds fMRI-analyses.

4.4. The centrofrontal shift in the temporal domain

As shown by the current results, the central activity was pronounced for all three groups (REA, LEA and HOM) in the first time window. However, at a later onset (LN), the frontal activity became higher than that of the central generators, a shift especially marked for the dichotic trials. This centrofrontal shift is possibly related to the dichotomous nature of the stimulus input, indicating a significant conflict that has to be resolved by cognitive means. Frontal areas are crucial for this conflict resolution process. Indeed, a recent fMRI study using dichotic presentations reported more activation of areas in the superior temporal gyrus, the middle and inferior frontal gyrus, and the cingulate cortex than during diotic presentations. Thus, it is suggested that the DL procedure involves a cortical network extending beyond primary speech perception areas in the brain to also include the prefrontal cortex (Thomsen et al., 2004). Similarly, Jäncke and Shah (2002) indicated the presence of extended activations in frontotemporal networks during a DL study. Given that, in the present study, the dichotic and diotic ERPs were concurrently obtained from the same individuals, our results reveal a functional interplay between frontal and central areas. Consequently, the frontal activation associated with conflicting input is of the utmost importance, and strongly suggests top down processes.

5. Conclusion

This is the first study that concurrently analyzed the electrophysiological responses in trials resulting in REA or LEA, or under HOM conditions obtained from the same individuals. Using this approach we were able to uncover the dynamic processes that take place during a DL paradigm. Two outcomes are of great importance. First, the analyses of the processing of the REA trials revealed shorter latencies compared to LEA trials. This point supports the structural model of Kimura, in which the callosal transfer is considered as an important factor in producing a REA. Thus, the ear-advantage could be primarily a time-bound effect. Second, while the first time window showed similar ERPs regardless of the condition (REA, LEA and HOM), the conflicting input produced increased frontal area activation at a later stage. One possible explanation for this centrofrontal shift is that frontal areas are involved in conflict resolution for input processed in more posterior cortical areas. Thus, the proper decoding of the simultaneously presented syllables appears to be a phenomenon that requires the interaction of frontoposterior networks.

Acknowledgements

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