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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.

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 procedure 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, &

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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):

$$\text{laterality index (LI)} = \frac{\text{correct right ear responses} - \text{correct left ear responses}}{\text{correct right ear responses} + \text{correct left ear responses}} \times 100 \qquad (1)$$

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