

Research paper

Interaural delay-dependent changes in the binaural difference potential of the human auditory brain stem response

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Abstract

Binaural difference potentials (BDs) are thought to be generated by neural units in the brain stem responding specifically to binaural stimulation. They are computed by subtracting the sum of monaural responses from the binaural response, $BD = B - (L + R)$. BDs in dependency on the interaural time difference (ITD) have been measured and compared to the Jeffress model in a number of studies with conflicting results. The classical Jeffress model assuming binaural coincidence detector cells innervated by bilateral excitatory cells via two delay lines predicts a BD latency increase of $ITD/2$. A modification of the model using only a single delay line as found in birds yields a BD latency increase of ITD . The objective of this study is to measure BDs with a high signal-to-noise ratio for a large range of ITDs and to compare the data with the predictions of some models in the literature including that of Jeffress. Chirp evoked BDs were recorded for 17 ITDs in the range from 0 to 2 ms at a level of 40 dB nHL for four channels (A1, A2, PO9, PO10) from 11 normal hearing subjects. For each binaural condition 10,000 epochs were collected while 40,000 epochs were recorded for each of the two monaural conditions. Significant BD components are observed for ITDs up to 2 ms. The peak-to-peak amplitude of the first components of the BD, DP1-DN1, is monotonically decreasing with ITD. This is in contrast with click studies which reported a constant BD-amplitude for ITDs up to 1 ms. The latency of the BD-component DN1 is monotonically, but nonlinearly increasing with ITD. In the current study, DN1 latency is found to increase faster than $ITD/2$ but slower than ITD incompatible with either variant of the Jeffress model. To describe BD waveforms, the computational model proposed by Ungan et al. [Hearing Research 106, 66–82, 1997] using ipsilateral excitatory and contralateral inhibitory inputs to the binaural cells was implemented with only four parameters and successfully fitted to the BD data. Despite its simplicity the model predicts features which can be physiologically tested: the inhibitory input must arrive slightly before the excitatory input, and the duration of the inhibition must be considerably longer than the standard deviations of excitatory and inhibitory arrival times to the binaural cells. With these characteristics, the model can accurately describe BD amplitude and latency as a function of the ITD.

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1. Introduction

The interaural time difference (ITD) is one of the most important cues used by the auditory system for azimuthal sound localization (Rayleigh, 1907; Stevens and Newman, 1936; Wightman and Kistler, 1992). The first site of binaural interaction in the mammalian auditory system is the superior olivary complex (SOC) where ITD-sensitive neurons reside. Neurons in the medial superior olive (MSO) predominantly receive excitatory inputs from both cochlear nuclei. These EE-cells are sensitive to ITDs of the fine

Abbreviations: ABR, auditory brain stem response; ACT, acoustic cross talk; B, evoked response to binaural stimulation; BD, binaural difference potential; EE, excitatory–excitatory; IC, inferior colliculus; IE, inhibitory–excitatory; ITD, interaural time difference; L, evoked response to monaural left stimulation; LL, lateral lemniscus; LSO, lateral superior olive; MER, middle ear reflex; MNTB, medial nucleus of the trapezoid body; MSO, medial superior olive; nHL, normal hearing level; R, evoked response to monaural right stimulation; SNR, signal-to-noise ratio; SOC, superior olivary complex; SPL, sound pressure level

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structure of a stimulus in the low-frequency range (<1500 Hz) (Goldberg and Brown, 1968; Yin and Chan, 1990). On the other hand, cells in the lateral superior olive (LSO) primarily receive contralateral inhibitory and ipsilateral excitatory inputs. These IE-cells are sensitive to interaural level differences at higher frequencies (>1500 Hz) (Boudreau and Tsuchitani, 1968; Goldberg and Brown, 1969), but also for ITDs of the stimulus envelope (Joris and Yin, 1995; Joris, 1996; Batra et al., 1997a,b; Joris and Yin, 1998). Furthermore, Tsuchitani (1988a) found that LSO neurons are as well sensitive to ITDs of transients, i.e., to interaural time-of-arrival differences of high-frequency stimuli. The subsequent stages of the mammalian brain stem as the lateral lemniscus (LL) and the inferior colliculus (IC) also exhibit strong ITD sensitivity (Kuwada et al., 1987; Yin et al., 1987; McAlpine et al., 1996; Fitzpatrick et al., 2002; Joris et al., 2004).

The electric activity of the human brain stem can be noninvasively studied with auditory brain stem responses (ABRs, e.g., Jewett et al., 1970; Picton et al., 1974). Specific binaural processing is believed to be reflected by binaural difference potentials (BDs). They are computed as the difference between the binaurally and the sum of monaurally evoked potentials, symbolically $BD = B - (L + R)$ (e.g., Dobie and Norton, 1980; Ito et al., 1988; Jiang, 1996; Riedel and Kollmeier, 2002a). With independent left and right auditory pathways one would obtain $BD = 0$. The amplitude of the binaurally evoked potential is roughly 20% smaller than the sum of the monaurally evoked potentials, i.e., $B < L + R$ (Levine, 1981; McPherson and Starr, 1993; Riedel and Kollmeier, 2002b), resulting in the major negative BD peak named DN1 at or shortly after wave V of the binaural ABR. In studies using the reversed sign convention to compute the BD, the major peak is positive and labeled β (e.g., Levine, 1981; Furst et al., 2004).

The dependence of binaural difference potentials on the ITD has been analyzed in guinea pig (Dobie and Berlin, 1979; Goksoy et al., 2005), cat (Sontheimer et al., 1985; Ungan et al., 1997, 2002) and humans (Wrege and Starr, 1981; Gerull and Mrowinski, 1984; Kelly-Ballweber and Dobie, 1984; Furst et al., 1985, 1990; Jones and Van der Poel, 1990; McPherson and Starr, 1995; Polyakov and Pratt, 1996; Pratt et al., 1997; Brantberg et al., 1999; Riedel and Kollmeier, 2002a; Delb, 2003; Riedel and Kollmeier, 2003; Furst et al., 2004). The results of these studies are partially conflicting and were often interpreted against the background of the model by Jeffress (1948), the prevailing paradigm for azimuthal sound localization for now more than half a century. This model generates a place code for the ITD using an array of coincidence detector cells innervated by excitatory inputs through bilateral delay lines. Postulations regarding the amplitude and the latency of the BD can be derived from the Jeffress model. If BDs would truly reflect the output of Jeffress-like coincidence detector cells, as, e.g., postulated by Jones and Van der Poel (1990) and Furst et al. (2004), a representation of ITDs beyond the physiological range (about ± 0.8 ms in

humans) would be useless and the BD should vanish at those ITDs. Furst et al. (1985) reported a nearly constant β -amplitude for ITDs up to 0.8 ms, and the BD became undetectable for ITDs > 1 ms. These data support the Jeffress model, and the BD was interpreted a physiological correlate of binaural fusion. Only a few studies tested ITDs beyond the physiological range. Wrege and Starr (1981) found significant BDs for ITDs up to 2 ms, while McPherson and Starr (1995) reported a gradually decreasing BD-amplitude up to an ITD of 1.6 ms. In cat with a physiological ITD-range of roughly ± 0.4 ms, Ungan et al. (1997) obtained significant BDs up to ITDs of 1.5 ms.

Regarding the BD latency, the Jeffress model predicts a latency increase (compared to the response to a stimulus with ITD = 0 ms) with half the ITD of the stimulus (Jones and Van der Poel, 1990; Ungan et al., 1997). A modification of the Jeffress model using only a single delay line instead of two as suggested by the projection from the avian nucleus magnocellularis to the nucleus laminaris (Young and Rubel, 1983; Overholt et al., 1992) yields a latency increase of just the ITD of the stimulus (Ungan et al., 1997). The latency increase in human BD studies was reported to be close to the ITD (Wrege and Starr, 1981), close to ITD/2 (Jones and Van der Poel, 1990; Walger et al., 2003) and at intermediate values between ITD/2 and ITD (e.g., Furst et al., 1990; Brantberg et al., 1999; Delb, 2003). In a cat study Ungan et al. (1997) found a nonlinear latency increase between ITD/2 and ITD. They were able to model the amplitude decrease and the latency increase of the BD for a wide range of ITDs with a population model assuming IE-interaction.

With values around 0.2 μ V BD amplitudes of humans are comparatively small, and the above-mentioned contradicting results of human studies may in a great measure be attributed to the low signal-to-noise ratio (SNR) of the BD and to insufficient control of the residual noise. Therefore, the objectives of the present study are to measure the ITD-dependence of the BD with high quality and fine ITD resolution for a wide span of ITDs in and outside the physiological range, to investigate if this dependence can be explained by the LSO model proposed earlier (Ungan et al., 1997), and to compare the results to literature data and models of binaural interaction.

2. Methods

2.1. Subjects

Eleven adults, seven males and four females, ranging in age from 23 to 34 years, participated in this study. Subjects were either paid or volunteers from the staff of the Medical Physics Group at the University of Oldenburg. They were classified as normal hearing by routine audiometry and had no history of audiological or neurological problems.

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