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Evidence for separate processing in the human brainstem of interaural intensity and temporal disparities for sound lateralization

Hillel Pratt *, Andrey Polyakov, Leonid Kontorovich

Evoked Potentials Laboratory, Behavioral Biology, Gutwirth Bldg., Technion-Israel Institute of Technology, Haifa 32000, Israel

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Abstract

Sound lateralization can be induced by interaural intensity disparities (IIDs) or by interaural temporal disparities (ITDs). The purpose of this study was to indicate whether IIDs and ITDs are processed by the same central units that detect interaural disparity in timing of afferent activity. If sound lateralization to intensity and time cues was determined by the same afferent latency disparity detectors in the brainstem, lateralization would be the same, regardless of whether latency disparity was induced by IIDs or ITDs. Moreover, the disparity detectors, and thus their dipole equivalents, would be the same for equal lateralizations, whether induced by IIDs or ITDs. Auditory brainstem evoked potentials (ABEPs) were recorded in response to monaural and binaural clicks, with a variety of IIDs and ITDs. Peak II (proximal auditory nerve activity), peak III (input to the superior olivary complex), and binaural interaction components (BICs) Be_I and Be_{II} (binaurally activated upper pons) were identified and their latencies measured. The psychophysical lateralization of the clicks (in cm from vertex) was also measured in response to the same binaural stimuli. The correlations between interaural afferent latency disparities (difference in corresponding peak latencies originating in each ear) and psychophysical click lateralization were calculated. Similarly, the correlations with click lateralization of the BICs equivalent dipole latency as well as orientation change (relative to symmetrical clicks) were determined. A strong correlation with lateralization was found for peaks II and III latency disparities, with steeper slopes for IIDs than for ITDs. Moreover, binaural activity across the same lateralizations differed between IIDs and ITDs. These results, therefore, indicate that interaural time and intensity cues are processed by separate systems in the brainstem, both at the afferent convergence level and after interaural disparities are determined.

Keywords: Sound localization; Auditory brainstem; Evoked potential; Human; Click

1. Introduction

Interaural time and intensity differences contribute to the localization and lateralization of a sound source. Sound lateralization involves the comparison of the signals received by the two ears in the central nervous system. The first level of the auditory system that can compare inputs from the two ears is the superior olivary complex (SOC), where afferent impulses from both ears converge for the first time. Neurons in this area respond specifically to interaural time and intensity differences (Brugge and Geisler, 1978; Masterton and Imig, 1984).

Afferent auditory activity, as recorded in auditory brainstem evoked potentials (ABEPs), is delayed with decreasing stimulus intensity at a rate of about 0.5 ms/10 dB at intensities below 60 dB nHL, and at a rate of 0.15 above 60 dB (Hecox and Galambos, 1974; Pratt and Sohmer, 1977; Gorga et al., 1985). Thus, in addition to stimulus timing, intensity can affect afferent latency in the auditory pathway. Therefore, IIDs may be affecting lateralization merely because of the afferent timing disparities associated with them. In other words, interaural time and intensity cues may be processed by the same afferent latency disparity detectors in the brainstem, using the afferent timing disparity as the sole cue for lateralization.

If indeed only one latency disparity measurement system was involved in lateralization, the effects of in-

* Corresponding author. Tel.: (972) 4-8292321; Fax: (972) 4-8229949; E-mail: hillel@tx.technion.ac.il

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teraural afferent latency disparities on lateralization would be the same, regardless of whether they were induced by interaural intensity disparities (IIDs) or by interaural temporal disparities (ITDs). Conversely, different lateralizations by IIDs and ITDs that are associated with the same interaural afferent latency difference would indicate separate systems for time and intensity cues of lateralization.

Binaural interaction in humans has been evaluated by deriving the difference waveform between the algebraic sum of ABEPs which had been recorded in response to monaural stimulation of the right or left ear, and potentials which had been recorded in response to binaural stimulation (Dobie and Berlin, 1979). The binaural interaction components (BICs) thus derived are dependent on the integrity of the binaurally innervated neurons in the brainstem (Wada and Starr, 1983a,b,c). BICs may be associated with the psychoacoustic functions of localization and lateralization, as was suggested by their dependence on interaural time and intensity disparities (Dobie and Berlin, 1979; Furst et al., 1985, 1995; Jones and Van der Poel, 1990). In an

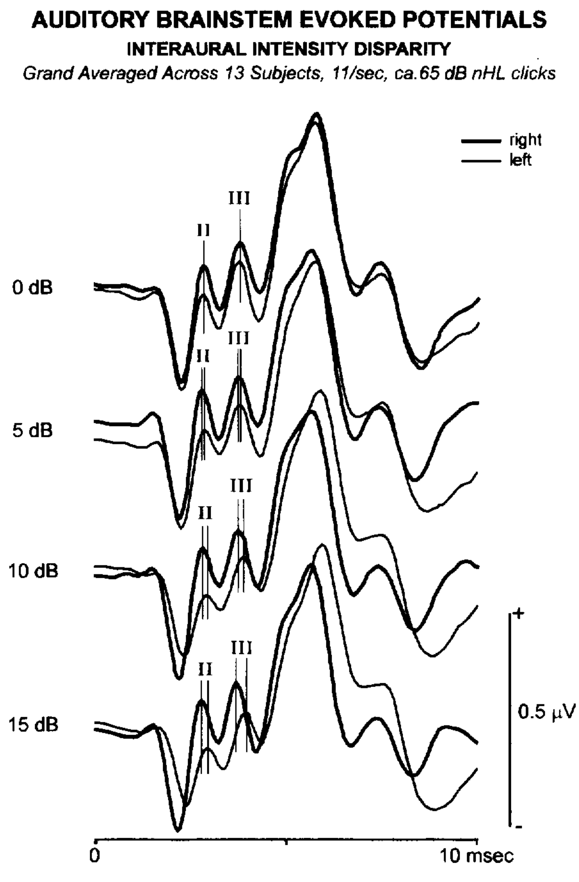

Fig. 1. The 'Z' channel of monaurally evoked ABEPs, grand averaged across all subjects, in response to the IIDs of this study. The tick marks denote the peaks measured, and the horizontal distance between corresponding marks represents the interaural afferent latency difference. Interaural afferent latency differences increased with increasing IIDs.

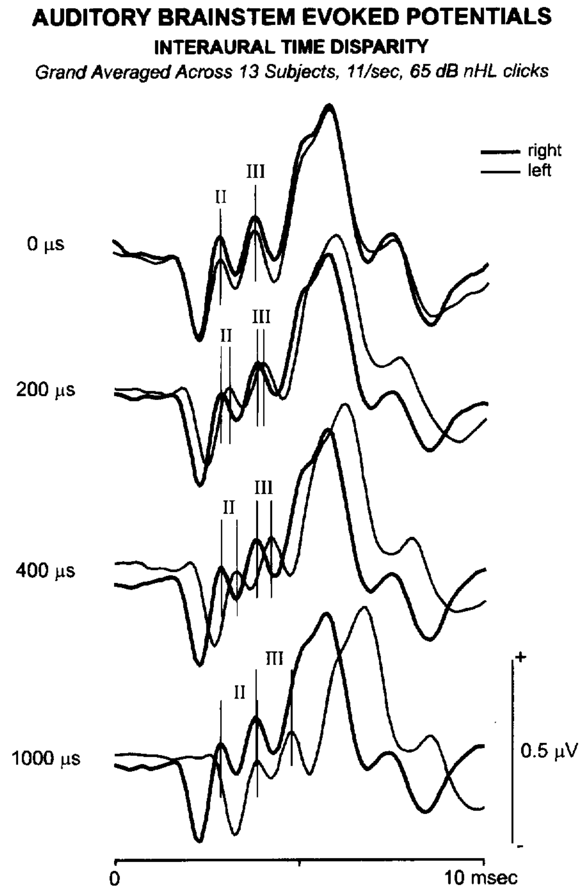

Fig. 2. The 'Z' channel of monaurally evoked ABEPs, grand averaged across all subjects, in response to the ITDs of this study. The tick marks denote the peaks measured, and the horizontal distance between corresponding marks represents the interaural afferent latency difference. Interaural afferent latency differences increased with increasing ITDs.

earlier report we suggested that human BICs may be associated with the SOC (Polyakov and Pratt, 1994). The effects of varying ITDs and IIDs on BICs have been studied in both animals and humans (Dobie and Berlin, 1979; Arslan et al., 1981; Prasher et al., 1981; Wrege and Starr, 1981; Rosenhamer and Holmkvist, 1983; Gerull and Mrowinski, 1984; Furst et al., 1985; Sontheimer et al., 1985; Jones and Van der Poel, 1990).

In an earlier study (Polyakov and Pratt, 1996), three-channel Lissajous' trajectories (3-CLTs) were used to estimate the centrally located dipole equivalent of the BICs of ABEPs to clicks with ITDs or IIDs. The most remarkable finding was a significant change in dipole orientations across stimulus conditions. The changes in dipole orientations, across stimulus conditions, were suggested to indicate spatio-topic organization in the human brainstem. However, whether intensity and time cues are represented separately remained unresolved because dipole orientations were too variable to distinguish orientations of dipoles in response to intensity disparities from those to time disparities. One

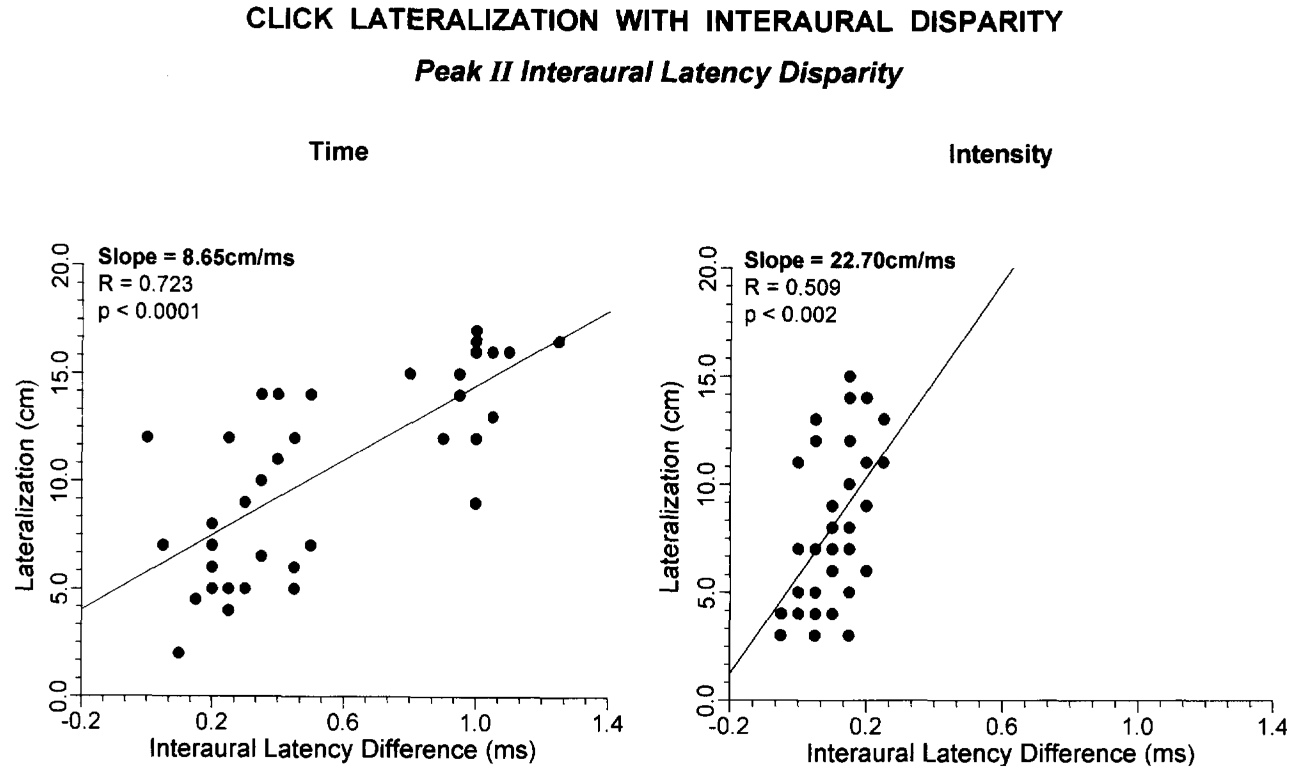

Fig. 3. Scatter plots of the correlations between click lateralization and interaural afferent latency difference for ABEP peak II across IIDs and ITDs. The results of linear regression show highly significant correlations with a slope for IIDs that is more than double that for ITDs.

way to overcome intersubject orientation variability is to compare, within subjects, orientation changes across lateralizations. If IIDs and ITDs were processed by the same anatomical system, equivalent dipole orientation changes will be the same for equal lateralization changes, whether they were due to IIDs or to ITDs. In addition, if IIDs and ITDs were processed by the same neurons, the latency of BICs associated with the same lateralization should be the same, and that latency should vary similarly across lateralizations, regardless of whether they were obtained with IIDs or ITDs.

The purpose of this study was to determine whether IIDs and ITDs are analyzed by the same interaural afferent latency disparity system, or whether ITDs and IIDs are processed by separate systems in the human brainstem.

Table 1
Correlations of psychophysical lateralization with orientation change (re binaurally symmetrical clicks) of BICs equivalent dipoles Be_I and Be_{II}, to ITDs and IIDs

	Be_I		Be_{II}	
	IIDs	ITDs	IIDs	ITDs
Slope (cm/deg)	0.25	0.15	0.20	0.15
R	0.341	0.233	0.355	0.264
$P<$	0.0001	0.0001	0.0001	0.0001

Interaural intensity disparities tended to have slightly steeper slopes.

2. Methods

Auditory brainstem evoked potentials were recorded, and their BICs derived, from 13 normally and symmetrically hearing adults. BICs were derived by subtracting the response to binaural clicks from the algebraic sum of monaural responses. Potentials were recorded in response to alternating polarity clicks, presented at a rate of 11/s with interaural time differences of 0, 0.2, 0.4 or 1.0 ms and an intensity of 65 dB nHL, or isochronic to both ears with interaural intensity differences of 5, 10 or 15 dB (65 dB nHL ± 2.5, 5.0 and 7.5 dB, respectively). The binaural clicks were always the simultaneous presentation of the monaural left and right clicks used to derive BICs, with the same interaural intensity or time disparities. Three recording channels, from three differential electrode pairs which were orthogonal to each other, were used. The recording channels were: nasion-inion ('X'), left-right mastoids ('Y'), vertex-cervical spinous process VII ('Z').

Psychophysical click lateralization was obtained for each binaural stimulus condition by measuring the distance (in cm) from the vertex to the point on the scalp that subjects pointed to as the source of the clicks. In all, seven lateralization conditions, corresponding to the binaural stimulus conditions, were evaluated psychophysically: binaurally symmetrical clicks, 3 IIDs and 3 ITDs.

ABEP peaks I and II reflect afferent activity in the

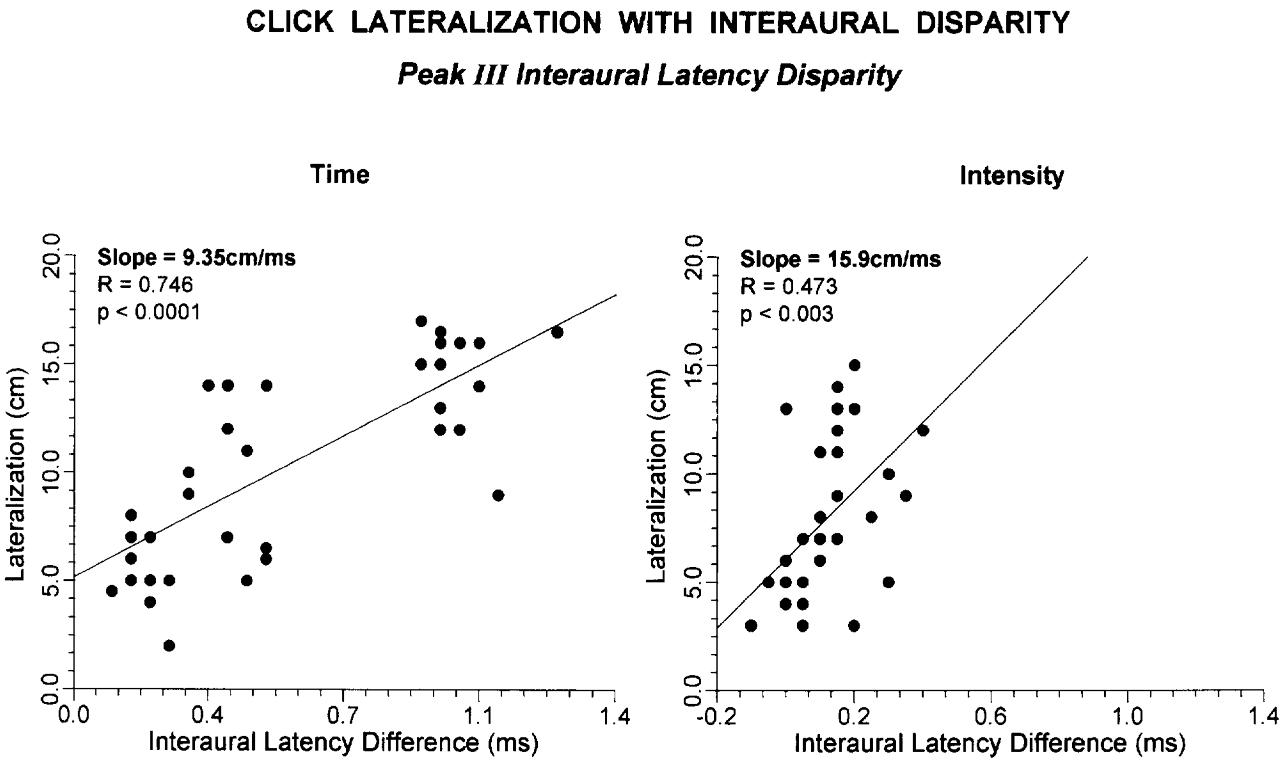

Fig. 4. Scatter plots of the correlations between click lateralization and interaural afferent latency difference for ABEP peak III across IIDs and ITDs. The results of linear regression show highly significant correlations with a slope for IIDs that is almost double that for ITDs.

intracochlear and proximal portions of the auditory nerve, respectively. Peak II latency was thus measured to represent afferent input to the brainstem. Peak III is the latest peak that does not include binaural interaction components, and was thus selected to represent afferent input to the binaural processor in the brainstem. Thus, peak latencies of ABEP components II and III from the 'Z' channel were determined for each monaural stimulus condition. From these peak latencies the interaural afferent latency differences, between ABEPs to left ear and right ear stimulation, for peak II and peak III in each of the IIDs and ITDs, were derived. In all, seven interaural afferent latency disparities were computed for each peak: for symmetrical clicks to right and left ear, as well as 3 disparities corresponding to the 3 IIDs and 3 disparities for the 3 ITDs.

Peak V includes substantial contributions from both monaurally and binaurally evoked activity. It was thus deemed too late for analyzing afferent input to the binaural processor, and contaminated with monaural activity for analyzing the binaurally evoked activity. However, the BICs, which represent purely binaurally evoked activity, were analyzed as indicators of activity after binaural convergence in the brainstem. From the 'X', 'Y' and 'Z' records, the latency, magnitude and orientation of BICs equivalent dipoles Be_I and Be_{II} were estimated (Pratt et al., 1987, 1995; Polyakov and Pratt, 1994) for the seven binaural stimulus conditions (symmetrical, as well as 3 IIDs and 3 ITDs). From the dipole orientations at each stimulus condition, the change (in degrees of included angle) between orientation with symmetrical clicks and the orientation with each interaural disparity condition was computed. Thus, for each dipole, orientation change was determined for 3 IIDs conditions and for 3 ITDs. Further details of the recording and signal analysis methods are provided elsewhere (Polyakov and Pratt, 1996).

Table 2