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

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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) B1 and B2 (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-
Interaural 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 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
CLICK LATERALIZATION WITH INTERAURAL DISPARITY

Peak II Interaural Latency Disparity

![Graphs showing scatter plots with linear regression lines for time and intensity. The graphs illustrate the relationship between interaural latency difference and lateralization for ABEP peak II across IID and ITD conditions.](image)

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

way to overcome intersubject orientation variability is to compare, within subjects, orientation changes across lateralizations. If IID and ITD were processed by the same anatomical system, equivalent dipole orientation changes will be the same for equal lateralization changes, whether they were due to IID or to ITD. In addition, if IID and ITD 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 IID or ITD.

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

### Table 1

<table>
<thead>
<tr>
<th></th>
<th>BeI</th>
<th>BeII</th>
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<tbody>
<tr>
<td></td>
<td>IID</td>
<td>ITD</td>
</tr>
<tr>
<td>Slope (cm/deg)</td>
<td>0.25</td>
<td>0.15</td>
</tr>
<tr>
<td>R</td>
<td>0.34</td>
<td>0.23</td>
</tr>
<tr>
<td>P</td>
<td>0.0001</td>
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</tr>
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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 IID and 3 ITD.

ABEP peaks I and II reflect afferent activity in the
CLICK LATERALIZATION WITH INTERAUDIAL DISPARITY

Peak III Interaural Latency Disparity

Fig. 4. Scatter plots of the correlations between click lateralization and interaural afferent latency difference for ABEP peak III across IID and ITDs. The results of linear regression show highly significant correlations with a slope for IID 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 IID and ITD, 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 IID 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 B_{X} and B_{Z} were estimated (Pratt et al., 1987, 1995; Polyakov and Pratt, 1994) for the seven binaural stimulus conditions (symmetrical, as well as 3 IID and 3 ITD). 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 IID conditions and for 3 ITD. Further details of the recording and signal analysis methods are provided elsewhere (Polyakov and Pratt, 1996).
BINARURAL INTERACTION COMPONENTS
INTERAURAL INTENSITY DISPARITY

Grand Averaged Across 13 Subjects, 11/sec, ca. 65 dB nHL clicks

Fig. 5. The 'X', 'Y' and 'Z' channels (bottom), as well as the 3-CLT of the Be complex (corresponding to the BICs P1-P2), estimating the equivalent dipoles Be and BeII, in response to symmetrical (solid line) and the largest IID of this study (broken line), grand averaged across all subjects. Tick marks on the 'X', 'Y' and 'Z' waveforms show the latency range for which the corresponding 3-CLTs were derived. Different IIDs (and hence lateralizations) were associated with different orientations of BICs equivalent dipoles.

3. Results

The psychophysical lateralization estimates were consistent within subjects, across repetitions of the same stimulus condition, within the measurement error of pointing with a finger (±5 mm). The binaurally symmetrical clicks were invariably indicated to come from the midline of the scalp.

The 'Z' channels of monaurally evoked ABEPs, grand averaged across all subjects, from the IIDs and ITDs of this study are presented in Figs. 1 and 2, respectively. Note the larger interaural afferent latency differences with increasing interaural disparities. Scatter plots of click lateralization as a function of interaural afferent latency disparity for peak II across IIDs and ITDs are presented in Fig. 3. The results of linear regression analysis are summarized on each scatter plot. Note the highly significant correlations, and the slope which was more than double for IIDs than for ITDs. Similarly, the correlations between lateralization and
BINAURAL INTERACTION COMPONENTS
INTERAURAL TIME DISPARITY

Grand Averaged Across 13 Subjects, 11/sec, 65 dB nHL clicks

Fig. 6. The 'X', 'Y' and 'Z' channels, as well as the 3-CLT of the Be complex (corresponding to the BICs P1–P2), estimating the equivalent dipoles Be and Be₁, in response to symmetrical (solid line) and the largest ITDs of this study (broken line), grand averaged across all subjects. Different ITDs (and hence lateralizations), were associated with different orientations of BICs equivalent dipoles.

Interaural afferent latency disparity for peak III across IID and ITD are presented in Fig. 4. Here too, correlations were highly significant, and the slope was almost double for IID than for ITD. The corresponding slopes for peaks II and III were not significantly different.

The 'X', 'Y' and 'Z' channels, as well as the 3-CLT of the Be complex (corresponding to BICs P1–P2) in response to binaurally symmetrical clicks and to the largest interaural disparities of this study, grand averaged across all subjects, are presented in Figs. 5 and 6, for IID and ITD, respectively. Different lateralizations, as measured in the psychophysical estimates, were associated with different orientations of BICs equivalent dipoles Be and Be₁. Lateralization as a function of orientation change of BICs equivalent dipole (re binaurally symmetrical clicks), presented highly significant correlations (Table 1), with slightly steeper slopes for intensity than for temporal disparities, but this difference in slopes did not attain significance. The slopes for lateralization as a function of dipole latency of Be and Be₁ were only significant for temporal but not intensity interaural disparities (Table 2).
4. Discussion

Lowering click intensity delays afferent activity from the affected ear. With binaural stimulation, this would result in a similar lateralization as when full intensity clicks to the affected ear are delayed. Thus, IIDs and ITDs may have a common mechanism in sound lateralization – their effect on afferent interaural timing difference. The purpose of this study was to examine whether binaural disparities were analyzed separately for intensity and temporal cues, or whether both cues are based on the interaural timing disparity of afferent activity from the two ears.

Psychophysical click lateralizations were therefore correlated with interaural latency disparities of proximal auditory nerve compound action potentials (peak II) and with the input volley to the SOC (peak III). The correlations associated with IIDs were compared to those with ITDs to assess whether they indicated the same processing. The binaurally symmetrical clicks were always judged by the subjects to be in a midline position but these data were not included in the graphs which only depict binaural disparities. The discrepancy showing consistent deviation of the intercept from a '0' midline position indicates that linear regression may not have been the best description of the functions. However, for the purpose of this study, comparing IIDs with ITDs, linear regression suffices, particularly in view of its high significance.

The correlation of lateralization with interaural afferent latency disparities had slopes which were approximately double for IIDs than for ITDs (Figs. 3 and 4). This difference would suggest that interaural afferent latency disparities that result from IIDs are twice as effective in lateralizing sound as the disparities from ITDs. Such a difference indicates different processing of temporal and intensity cues.

An alternative explanation of these results may suggest that only one type of processing takes place, but that the cue is not the latency but the amplitude of the afferent volley. This suggestion is unlikely because both IIDs and ITDs result in lateralization, and only IIDs are associated with interaural amplitude disparities. A modification of this suggestion could include a combined evaluation of interaural afferent volley latency and amplitude disparities. The data of this study cannot rule out this possibility, but it too includes different processing of interaural temporal cues (which do not include afferent volley amplitude disparities) and intensity cues (which include both latency and amplitude disparities in the afferent volley). This combined processing of latency and amplitude attributes by the same processor seems more unlikely in view of the BICs equivalent dipole analysis.

If intensity and temporal cues were processed by the same interaural disparity analyzer, the latency and orientation of its equivalent dipole would vary across interaural disparities in the same manner, regardless of whether disparity was achieved by IIDs or ITDs. To assess this possibility, lateralization was correlated with the latencies of BICs BeI and BeII and their dipoles’ orientation changes. When lateralization was correlated with orientation changes of the BICs equivalent dipoles, slightly steeper slopes were observed for intensity than for temporal disparities (Table 1). This difference in slopes is unlikely to result from orientation changes due to intensity differences associated with IIDs. The intensity differences involved (15 dB or less) are too small to cause orientation changes in the equivalent dipoles of ABEPs (Martin et al., 1986). The difference in slopes for IIDs and ITDs was not large enough to indicate a significant difference.

The difference between equivalent dipoles associated with binaural interactions with ITDs and IIDs was more pronounced when their latencies were compared: the slopes for lateralization as a function of dipole latency of BeI and BeII were only significant with ITDs but not with IIDs (Table 2). This difference in latency changes of binaural activity between ITDs and IIDs suggests that temporal cues are processed by binaural neural elements with different latencies for different lateralizations, whereas lateralization due to IIDs does not involve latency change in binaural units. This, again, could indicate different neural processing of time and intensity cues resulting in different temporal output patterns of activity.

In conclusion, electrophysiological measures associated with IIDs and ITDs were differently correlated with psychophysical lateralization, suggesting separate processing of these cues in the human brainstem at the convergence of afferent activity from either ear as well as after interaural disparities are determined in the upper pons.

References


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