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Confirmation of G. von Békésy's Theory of Paradoxical Wave Propagation along the Cochlear Partition by Means of Bone-Conducted Auditory Brainstem Responses

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Key Words
Auditory brainstem responses · Boneconduction · Traveling wave · Paradoxical wave propagation · High-pass noise masking

Abstract
In order to investigate the propagation time of the traveling wave in the cochlea after boneconduction stimulation of the inner ear, bone-conducted auditory brainstem responses (ABRs) were recorded in 6 normally hearing subjects after masking the basal cochlear region using high-pass filtered noise. As in air-conducted ABRs, Jewett V wave latency is delayed corresponding to the propagation time of the traveling wave front traversing the desynchronized hair cell region. These results support the theory of paradoxical wave propagation proposed by von Békésy in 1952, who postulated that wave motion always starts from the stiffest part of the basilar membrane, independent of the location of the vibrating force. In addition, we also found a latency delay of the Jewett V wave of bone-conducted ABRs in 8 patients with high-frequency hearing loss which corresponded to the severity of their hearing impairment.

Introduction

By transient stimulation of the ear with short acoustic stimuli, the synchronization of action potentials in the acoustic nerve is high enough to evoke synchronous electric activity in the tracts and nuclei of the auditory pathway which can be recorded from the human scalp as auditory brainstem responses (ABRs) consisting of 6 waves, Jewett I–VI, occurring between 2 and 10 ms after stimulus onset [1].

Every form of hearing impairment gives rise to characteristic changes in the ABR pattern. High-frequency cochlear hearing losses result in a latency shift corresponding to the time taken for the cochlear traveling wave front to pass the damaged cochelar region. In flat hearing losses, the waves have normal latency but a raised threshold corresponding to the degree of the hearing loss. In conductive hearing loss, air-conducted ABRs appear with prolonged latencies and raised thresholds, whereas bone-conducted ABRs have normal latency and threshold [2].

A valid estimation of the air-bone gap can be derived from the comparison of ABR thresholds and latencies for air- and bone-conducted clicks. Since their first description by Mauldin and Jerger [3], bone-conducted ABRs

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have frequently been cited in the literature with uniform emphasis on the feasibility and reliability of this method for use in pediatric audiology, especially for the diagnosis of malformations [4–8].

Until recently, bone-conducted ABRs have not been used to obtain additional information about the transmission of bone-conducted sound to the inner ear. Von Békésy [9] postulated in 1952 that due to the hydromechanical properties of the cochlear partition, a traveling wave always originates from the stiffest portion of the basilar membrane at its basis, even if the cochlea is excited in an artificial way at any place, e.g. by placing a bone vibrator on the bones of the skull.

The aim of this study was to investigate time and direction of the cochlear traveling wave resulting from bone-conducted ABRs. So far, estimation of cochlear traveling time has only been done with air-conducted ABRs using high-pass filtered noise masking by Don and Eggermont [10]. They observed an increase in latency of Jewett waves I, III and V with successive desynchronization of the basal cochlear sensory cells with high-pass filtered noise [10]. Similar results should be obtained for bone-conducted ABRs, if, as postulated by von Békésy, the traveling wave always passes from the basal to the apical part of the cochlea, even if the sound is transmitted to the inner ear via the skull using a bone vibrator.

Methods and Material

To conduct our experiments we proceeded in the following order and used the following number of probands.

At first a calibration of the bone conduction receiver had to be done. For this aim we determined the mean bone conduction behavioral threshold of 11 normally hearing subjects ranging in age between 18 and 26 years. As a next step we determined the latency-intensity functions for both air- and bone-conducted ABRs. This series was performed with a group of 20 normally hearing subjects (using only one ear in each person) ranging in age between 16 and 26 years. Mean and standard deviation of both air- and bone-conducted potentials were determined and displayed graphically. The masking series with high-pass filtered noise was performed with 6 normally hearing volunteers between 22 and 42 years who showed bone-conducted potentials with high amplitudes and steep peaks. Finally both air- and bone-conducted potentials were recorded in 8 patients between 32 and 65 years with various degrees of basocochlear hearing loss and compared with the latency-intensity functions of the 20 normally hearing subjects.

The acoustic stimuli were transmitted via a Beyer DT 48 headphone and a Bosch BKH 10 bone vibrator with a weight of 205 g and a contact area of 1.85 cm^2. The Bosch bone vibrator showed the best frequency response characteristics among several bone conduction receivers (Radioear B 71, Oticon A 20, Precitronic KH 70, Beoton, Bosch BKH 10) tested on a Bruël & Kjær Artificial mastoid (type 4930). The stimulus levels were referenced to the mean bone conduction behavioral threshold of 11 normally hearing adults. The bone conduction receiver was positioned on the forehead with a rubber band and a constant static force of the conductor's own weight. The click stimuli were generated by an acoustic stimulator (ZLE, ASTT 020-H) with alternating polarity, a repetition frequency of 24/s and an impulse duration of 0.1 ms. We used a bipolar click with a waveshape of the first-time derivation of a Gaussian curve. Two-channel ABR recordings were made (ZLE, A062) using Ag/AgCl cup electrodes between vertex and ipsilateral mastoid with the ground electrode on the left clavicle.

Table 1. Latency (ms) and standard deviation (SD), of Jewett V latency for air (AC)- and bone (BC)-conducted ABRs of 20 normally hearing subjects

Stimulus level dB nHL	AC		BC	
	latency	SD	latency	SD
50	6.37	0.36	7.11	0.34
45	6.54	0.37	7.36	0.38
40	6.78	0.39	7.55	0.43
35	6.98	0.42	7.83	0.49
30	7.28	0.53	8.09	0.50
25	7.56	0.63	8.25	0.58
20	7.92	0.55	8.63	0.68
15	8.25	0.67	9.16	0.74
10	8.40	0.69	–	–

Since there are no general guidelines for contralateral masking, we adopted the following procedure: The nontested ear was masked with air-conducted white noise 10 dB above the level of the bone-conducted click stimuli; however, the maximal masking level was not allowed to exceed 50 dB above normal hearing level (dB nHL) to avoid overmasking.

The latencies and amplitudes of the Jewett V wave for air- and bone-conducted stimuli were analyzed in a control group of 20 normally hearing ears. Measurements had to be limited to 50 dB nHL due to the distortion of bone-conducted ABRs when using higher stimulus levels. The measurements of the control group lasted approximately 1.5 h per subject, the number of averages was 2,000–6,000 (close to the threshold region). The amplification varied between 350,000 and 500,000. ABRs for air and bone conduction were elicited at stimulus levels between 50 and 10 dB nHL using 5-dB steps.

The masking series was performed in 6 normally hearing adults ranging in age from 22 to 42 years. In order to desynchronize the basal sensory cells, the test ear was masked by air-conducted high-pass filtered noise via a headphone. The contralateral ear was totally masked by white noise. The ABRs were evoked by bone-conducted stimuli with sound pressure levels between 30 and 50 dB nHL in 5-dB steps using the paradigm described above. At first the latency of wave V was determined without masking, then the sound pressure level of the band-pass noise (high pass = 20 Hz, low pass = 20 kHz) was calibrated in such a way that ABRs could no longer be recorded. The cutoff frequencies of the high-pass noise were varied according to the frequency of critical bands after Zwicker and Farsl [11]:

Table 2. Mean and standard deviation (SD), of Jewett V latency (ms) for bone-conducted ABRs in relation to high-pass cutoff frequency at different stimulus levels of 6 normally hearing subjects

Stimulus level dB nHL	Without masking		7.7 kHz		6.4 kHz		5.3 kHz		4.4 kHz		3.7 Hz	
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
50	6.99	0.37	7.13	0.40	7.18	0.39	7.34	0.46	7.57	0.31	7.73	0.36
45	7.21	0.38	7.63	0.41	7.66	0.43	7.83	0.51	7.97	0.53	8.10	0.39
40	7.42	0.39	7.82	0.38	8.03	0.43	8.11	0.43	8.23	0.51	8.61	0.63
35	7.68	0.37	8.05	0.41	8.28	0.55	8.36	0.62	8.52	0.66	9.29	0.59
30	8.01	0.51	8.28	0.59	8.59	0.61	8.82	0.77	9.23	0.92	9.46	0.93

Stimulus level dB nHL	3.2 kHz		2.7 kHz		2.3 kHz		2.0 kHz		1.7 kHz	
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
50	8.55	0.36	9.32	0.65	9.72	0.51	10.30	0.39	10.70	0.52
45	8.56	0.44	9.74	0.62	10.22	0.72	11.42	0.71	11.12	0.62
40	8.78	0.58	9.63	0.83	10.51	0.52	11.01	0.54	–	–
35	9.82	0.72	10.20	1.01	–	–	–	–	–	–
30	10.58	0.66	11.10	0.68	–	–	–	–	–	–

7.7 kHz; 6.4 kHz; 5.3 kHz; 4.4 kHz; 3.7 kHz; 3.2 kHz; 2.7 kHz; 2.3 kHz; 2.0 kHz, 1.7 kHz; 1.5 kHz, 1.3 kHz; 1.1 kHz. The number of averages was 2,000–7,000 (close to threshold region); the measurements of this series lasted approximately 5–7 h per subject.

Results

Firstly the latency and amplitude of the Jewett V wave to air- and bone-conducted stimuli were obtained in 20 normally hearing subjects. Bone-conducted ABRs could be evaluated down to 15 dB nHL, air-conducted ABRs down to 10 dB nHL. Table 1 shows the mean and standard deviation of Jewett V latency for both air and bone conduction. Bone-conducted ABRs could be recorded in 12 of 20 subjects up to a stimulus level of 15 dB nHL. Only in 2 subjects was it possible to record ABRs at 10 dB nHL. Four subjects showed a threshold of 20 dB nHL and 2 a threshold of 25 dB nHL. For air conduction, reproducible measurements were possible down to stimulus levels of 10 dB nHL in 13 normally hearing adults. In 5 subjects potentials could be registered down to 15 dB nHL and in 2 subjects down to 20 dB nHL. The latency of bone-conducted ABRs was prolonged by 0.7–0.9 ms in comparison to air-conducted ABRs. The standard deviation of bone-conducted ABRs approximately equaled that of air-conducted ABRs. The latency shift with decreasing stimulus level was different. A decreasing stimulus level was different. A decrease in stimulus level from 50 to 15 dB nHL led to a latency increase of 1.88 ms for air conduction and 2.25 ms for bone conduction.

In order to study the propagation time effect of the traveling wave in the cochlea during bone-conducted stimulation of the inner ear, bone-conducted ABRs were recorded in 6 normally hearing adults using simultaneous masking by high-pass filtered white noise. Table 2 shows the absolute latency values at stimulus levels between 30 and 50 dB nHL in relation to the cutoff frequency of the high-pass noise. At high stimulus levels, bone-conducted ABRs could be recorded up to a high-pass cutoff frequency of 1.7 kHz, while at low stimulus levels the threshold for evoking ABRs was reached at a higher cutoff frequency, i.e. at 30 dB nHL at 2.7 kHz. Figure 1 shows the relative Jewett V latency shift (in relation to the latency without masking) at the different stimulus levels. One can see that the curves are approximately parallel. In the high-frequency region they are flat, while in the medium-frequency region their steepness increases. Figure 2 shows the ABRs of one subject. Here also the latency increases markedly with decreasing high-pass cut-off frequency.

As one can see from figure 1, the maximal latency shift was almost 4 ms (3.94 ms at a threshold frequency of 1.7 kHz at 45 dB nHL) and, in addition, it was independent of the stimulus level. Above a cutoff frequency of 3.7 kHz, the continuous desynchronization of the basal sensory cells was associated with a relatively small increase in latency, while between 3.7 and 2.3 kHz the curves became steeper.

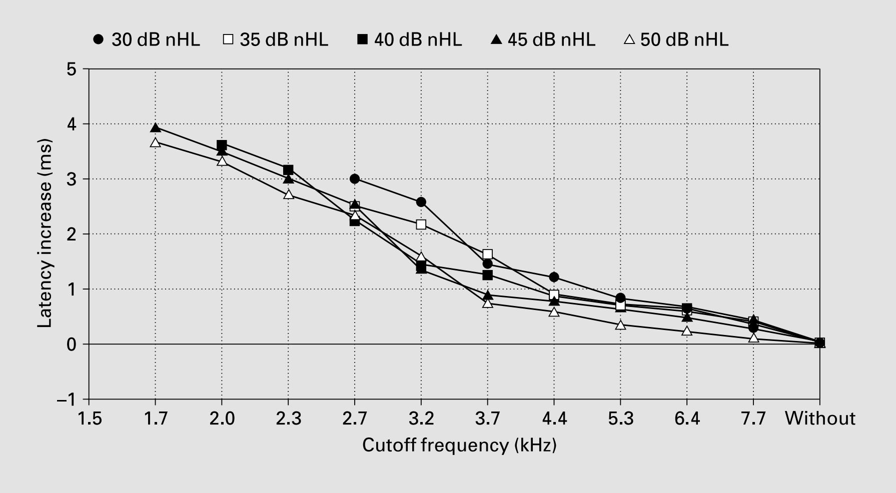

Fig. 1. Relative Jewett V latency shift depending on high-pass cutoff frequency.

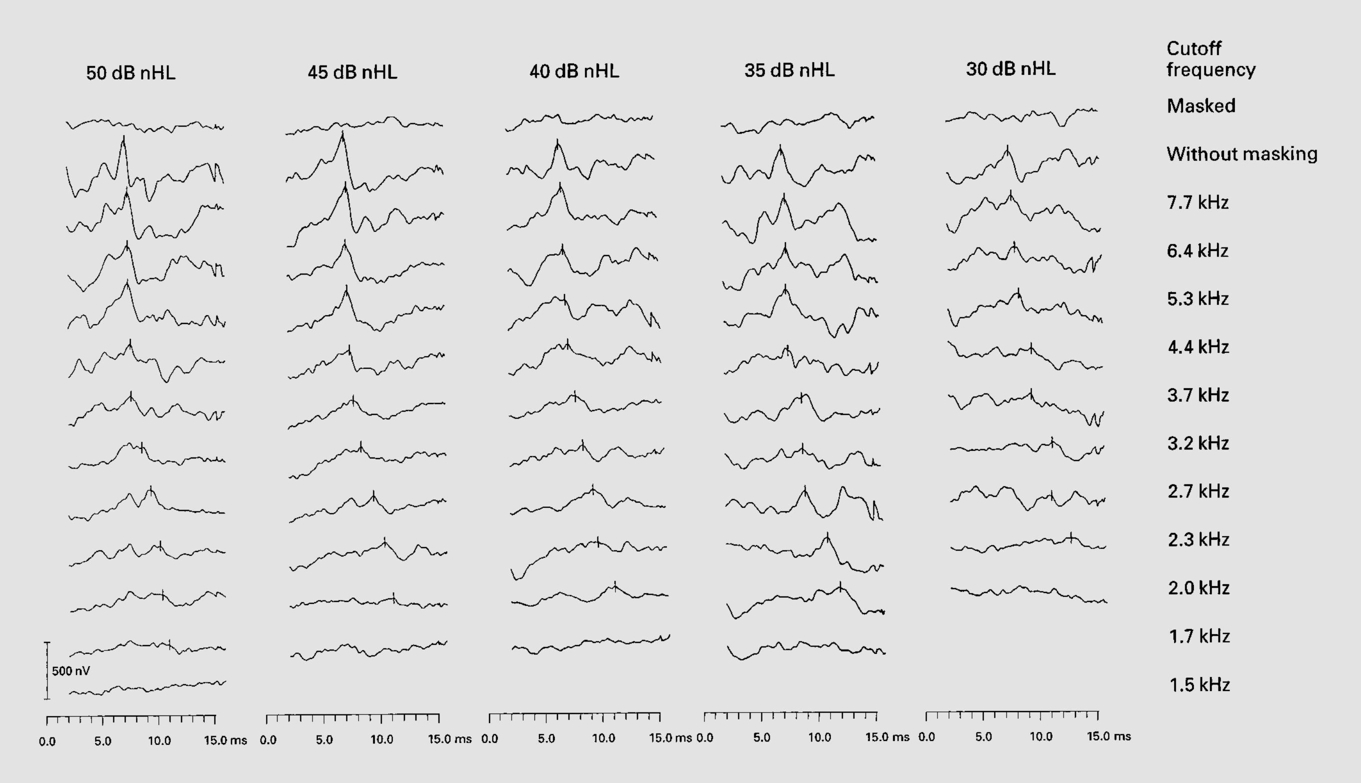

Fig. 2. ABRs of one subject during high-pass noise masking.

In summary it can be said that the latency of bone-conducted ABRs masked by high-pass filtered noise increases overproportionally with successive desynchronization of the basal cochlear sensory cells. This increase in latency is independent of the stimulus level. Masking the part of the cochlea which represents the high frequencies results in a minor latency shift, while with increasing masking the latency shift increases rapidly. To further confirm this experiment in patients with cochlear hearing impairment both bone- and air-conducted ABRs were

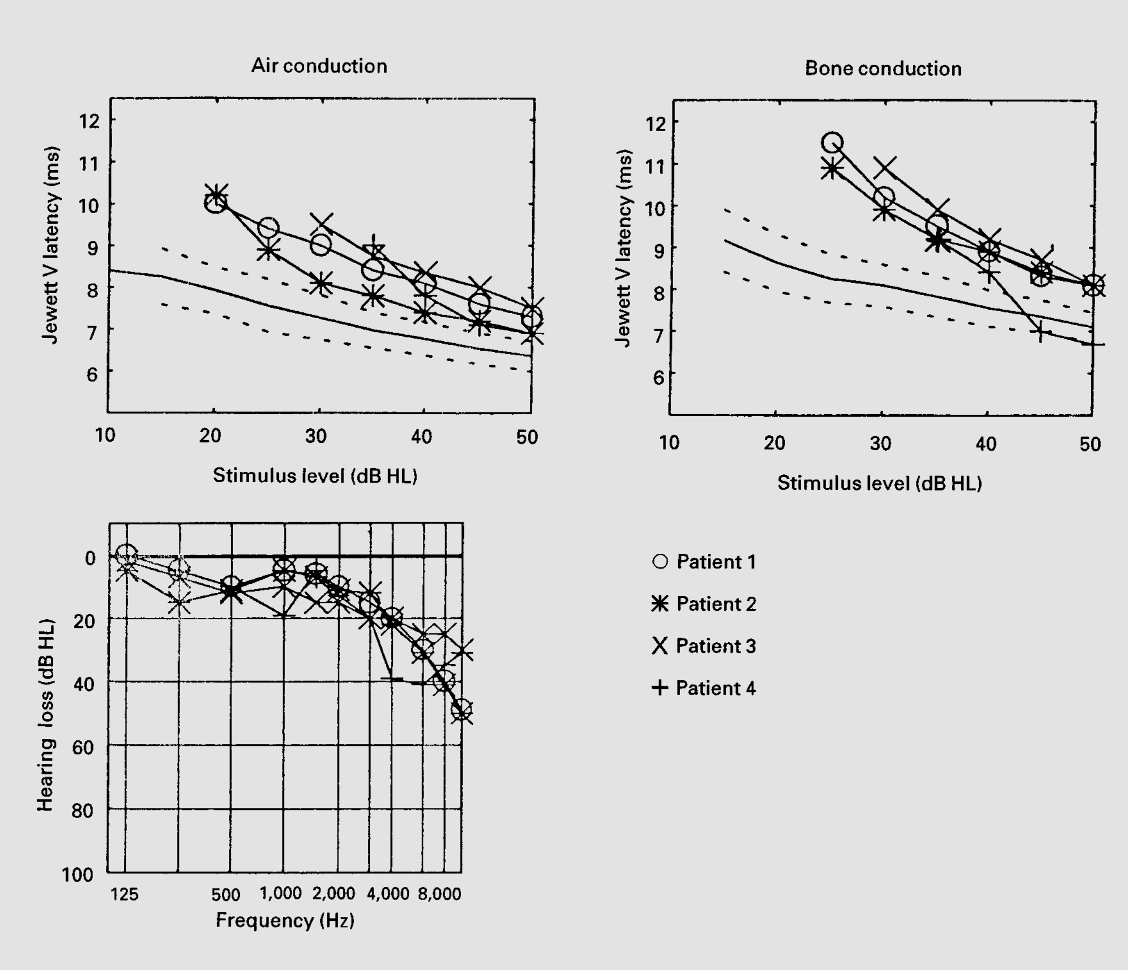

Fig. 3. Audiogram and ABR latency of patients 1–4 with basocochlear hearing impairment in relation to Jewett V latency-intensity functions of normally hearing subjects as presented in table 1. Mean = Bold line; standard deviation = dashed lines.

measured in 8 patients with high-frequency hearing loss. Figures 3 and 4 show the relations between stimulus level and Jewett V latency in 8 patients which are arranged according to the onset of the high-frequency hearing loss in the audiogram. In both types of stimulation there is a significant latency shift close to threshold which is more than 2.5 standard deviations from the median value of the 20 normally hearing subjects. In 5 of 8 patients, ABR stimulus thresholds were higher for bone conduction than for air conduction (see patients 1, 2, 5, 6, and 8 in fig. 3 and fig. 4) in 3 patients (see patients 3, 4, and 7 in fig. 3 and fig. 4) they were equal. The absolute latency of the Jewett V wave at threshold was higher for bone conduction than air conduction in 7 patients and approximately equal in 1 patient (see patients 5 in fig. 4).

Discussion

Even now the mechanism by which sound is conducted via the skull bones is not completely understood in its complexity. What is still unclear is how adequate stimuli are generated in the final common pathway of all sound components in the inner ear. The conduction theory of Bezold [12], which attributed the stimulation of the inner ear via bone conduction solely to the effects of the ossicular chain, must be regarded as obsolete. Von Békésy [13] proved experimentally that the frequency location and distribution on the basilar membrane is identical for both types of stimulation. At 400 Hz, he could make the perception of a bone-conducted tone completely disappear by application of an air-conducted tone which had an

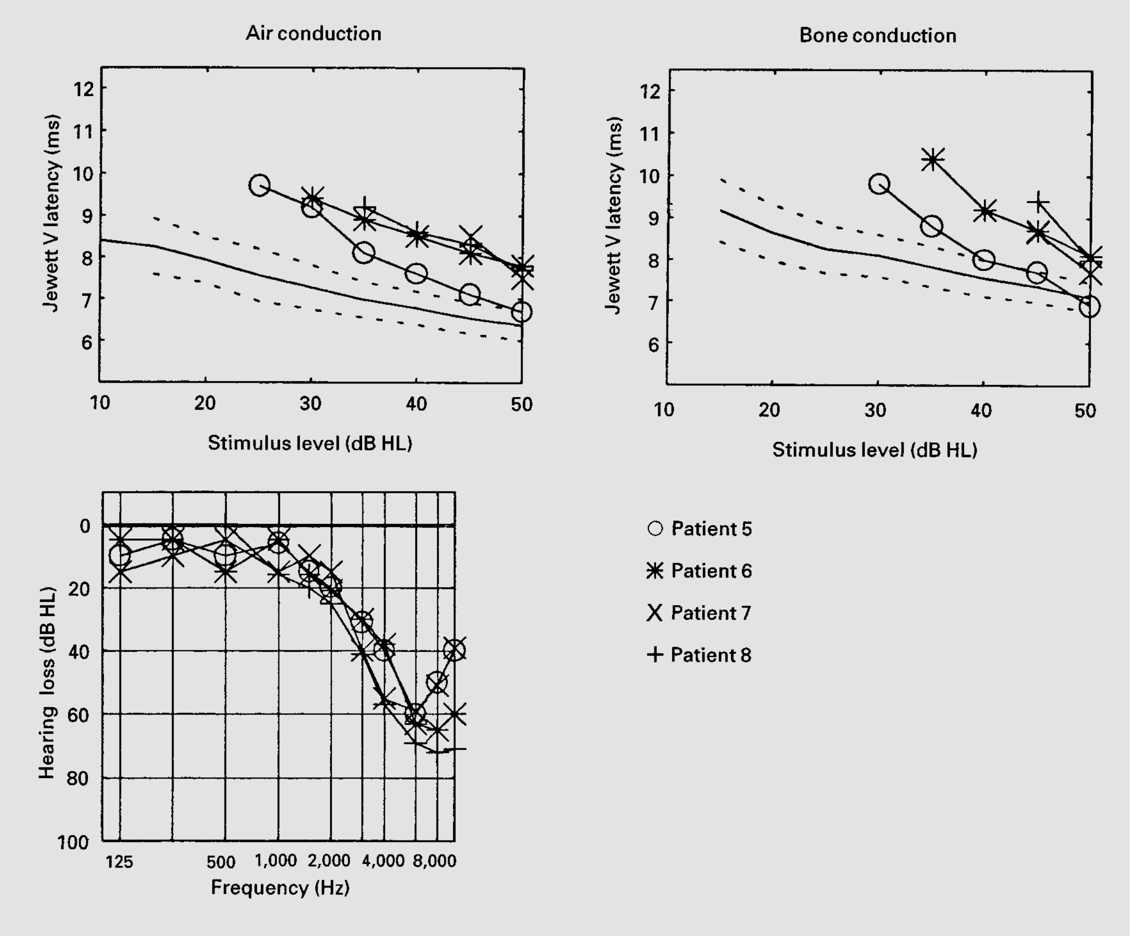

Fig. 4. Audiogram and ABR latency of patients 5–8 with basocochlear hearing impairment.

identical frequency but a different phase and amplitude. Obviously, interference and extinction of two waves of identical frequency and amplitude at a phase shift of 180° must have occurred. Additionally, von Békésy [13] could show that, due to the decreasing stiffness gradient of the basilar membrane, the wave propagation in the cochlea always spreads from the basal to the apical areas, even if initiated by bone-conducted stimuli, and is therefore independent of the source of stimulation. He could also demonstrate this phenomenon in the cochlea of human cadavers. If the stimulation was induced by an artificial stapes implanted at the apical end of the cochlea, the direction of wave propagation did not change. Based on these findings, von Békésy [13] talked of 'paradoxical wave propagation along the cochlear partition'.

ABRs are suitable for the measurement of paradoxical wave propagation by non-invasive means. Both types of stimulation are associated with short latency at high and prolonged latency at low stimulus levels. This latency shift associated with decreasing stimulus levels can be attributed to a shift of the main focus of stimulation towards apical portions of the cochlea. As a result of the decreasing stiffness of the basilar membrane, the amplitude which is necessary to initiate sensory transduction is reached only in apical portions. The latency shift of the Jewett V wave is dependent on the stimulus level for both air conduction and bone conduction. This argues in favor of a similar mechanism for the spread of excitatory impulses in the cochlea for both stimulation modalities. The difference in the latency shift (table 1) between air and bone conduction is known from the literature [3, 7, 14, 15]. As a probable cause for this difference, it is assumed that an alteration of the potential evoking stimulus occurs on the pathway through the skull as a result of resonance and phase shifts caused by the skull bones.

By successive desynchronization of the basal sensory cells using high-pass filtered noise, an increase in the latencies of the ABRs occurs which is independent of the stimulus level (fig. 1). When only those parts of the basilar membrane are masked which respond to high frequencies, the increase in latencies is small. Latency increases remarkably as soon as medium regions of the basilar membrane are masked. If these results are compared to the latency shifts of air-conducted ABRs, which were studied under the same experimental conditions [16], one can recognize that also there, the masking of the high-frequency cochlear regions showed a lesser and the masking of the middle-frequency cochlear regions showed a greater increase in latency. In both cases (bone and air conduction) the latency shifts were independent of the stimulus levels (compare with fig. 1). With air conduction however, ABRs can be recorded even at very low cutoff frequencies (down to 0.51 kHz), whereas with bone conduction no potentials are discernible under a cutoff frequency of 1.7 kHz.

Comparable results were presented by Stürzebecher et al. [17], who used bone-conducted tone pulses masked by notched noise to create frequency-specific ABRs. He observed a latency shift of wave Jewett V with decreasing carrier frequency, which was shorter, but comparable to our results. However, masking was done via a bone vibrator and not via a headphone as in this study. In their experiments with high-pass noise masking, Don and Eggermont [10] described a similar behavior of air-conducted ABRs. They observed a rapid drop in amplitude for waves I and III and an increase in latency shifts for waves I, III and V when the cutoff frequency became lower than 2 kHz [10].

The time delay of ABRs evoked by bone conduction stimulation which is associated with simultaneous masking of the basal sensory cells by high-pass filtered noise can only be explained by the fact that integration of oscillation energy in the inner ear triggers a traveling wave via the bones of the skull which, due to the stiffness gradient, spreads from the basal to the apical portions of the cochlea. As a result of the continuing desynchronization, the main point of excitation is moved towards the apex and so propagation time effects occur. This is in agreement with the hypothesis of von Békésy [9], which says that bone-conducted stimulation of the inner ear also leads to the development of a traveling wave spreading from a basal to apical direction.

Corresponding results were found in the group of patients with basocochlear hearing loss reported here. For both air- and bone-conducted stimulation, all patient showed a significant latency shift of wave Jewett V in the region close to threshold, which was more than 2.5 standard deviations of the normally hearing subject sample at the threshold of potential extinction. The latency shift increased according to the onset and the steepness of the high-frequency hearing loss in the audiogram. Bone-conducted ABRs showed higher thresholds and longer latencies in most cases. For both stimulation modalities, the delay of Jewett V latency can be explained as a result of propagation time effects caused by basocochlear traveling waves traversing defective hair cells.

The results presented in this study show that after continuous desynchronization of the basal sensory cells using high-pass filtered noise in normally hearing subjects, as well as in patients with basocochlear hearing loss, the Jewett V latency increases in both air and bone conduction ABRs. This leads to the conclusion that the stimulation of the inner ear via the bones of the skull evokes a traveling wave which, as in air conduction, travels from the base to the apex.

The presented data obtained by an objective measuring method substantiate von Békésy's hypothesis of paradoxical wave propagation that states that traveling waves always spread on the basilar membrane from a basal to apical direction independent of the source of the entrance of energy. Thus, the data also confirm his assumption formulated already in 1932: '... we can be sure that the basilar membrane is moved by a bone-conducted tone the same way as by an air-conducted tone ... and that, in addition, another way of acoustic nerve stimulation doesn't exist' [9].

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