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The relationship between auditory brainstem response and behavioral thresholds in normal hearing infants and adults *

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The nature of age-related improvements in auditory sensitivity was explored by comparing behavioral and auditory brainstem response (ABR) thresholds in 3- and 6-month-old infants and in adults. Thresholds were estimated for tone pips at 1, 4, and 8 kHz, presented at a rate of 13.3/s. The time course of development of the two response measures was compared, and the correlation between thresholds for individual subjects was examined. Infant ABR threshold was adultlike at all frequencies, even among 3-month-olds. Infant behavioral thresholds were elevated relative to adult thresholds. Between 3 and 6 months, significant improvement occurred in the 8-kHz behavioral threshold, but no improvement occurred at other frequencies. This difference between ABR and behavioral measures in developmental time course suggests that peripheral sensitivity is not a major determinant of behavioral threshold elevation during infancy. The correlation between behavioral and ABR thresholds was significant at 4 kHz for 3-month-olds and at 8 kHz for adults. This suggests that variability in sensory function at these frequencies contributes to both behavioral and ABR thresholds, although other factors are likely to be involved as well.

Auditory sensitivity; Auditory development

Introduction

By some measures, auditory sensitivity continues to mature during human infancy. Auditory brainstem response (ABR) thresholds for frequency-specific stimuli do not reach adult values until some time after 28 weeks chronological age (Folsom and Wynne, 1986; Klein, 1984). Behavioral thresholds for frequency-specific stimuli are reported to decline progressively during infancy (e.g., Schneider et al., 1980; Sinnott et al., 1983; Trehub et al., 1980, 1991; Werner and Gillenwater, 1990), and in some cases well into childhood (e.g., Schneider et al., 1986; Trehub et al., 1988; Yonshige and Elliott, 1981). However, recent reports suggest that evoked otoacoustic emissions are adultlike in most respects by full-term birth (e.g., Bonfils et al., 1992; Norton and Widen, 1990). A common interpretation of these results is that the ear is mature by the end of gestation, but that neural immaturities limit sensitivity during infancy and childhood (e.g., Eggermont, 1985; Schneider et al., 1989).

An alternative explanation is that evoked potential and behavioral thresholds are elevated during infancy and childhood as a result of factors that are unrelated to auditory sensitivity. It is known that the ABR is highly dependent on neural synchrony: The ABR may be abnormal or absent in neurological disorders which disrupt neural synchrony, even when the behavioral audiogram is normal (e.g., Jacobson et al., 1987). If neural synchrony is immature in infants, then a higher intensity may be required to elicit an ABR even if sensitivity is adultlike. Immature neural synchrony is also cited as an explanation for prolonged response latencies and lower response amplitudes typically observed in infants as late as 24 months of age (e.g., Eggermont and Salamy, 1988; Gorga et al., 1989). Along the same lines, behavioral measures of infant sensitivity are notoriously susceptible to the effects of state of arousal, motivation, and attentiveness. This reputation is consistent with data showing that infants' thresholds can be reduced dramatically by procedures that increase motivation (Olsho et al., 1988; Trehub et al., 1981) and to a lesser extent by manipulations of attention (Primus and Thompson, 1985). By this line of reasoning, 'true' infant thresholds are lower than those estimated by either evoked potential or behavior; sensitivity may even be mature by birth.

One approach to deciding whether elevated ABR and behavioral thresholds actually reflect immaturity within the auditory nervous system is to ask whether

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the results of developmental studies using ABR and those using behavioral sensitivity measures converge (Garner et al., 1956). In other words, if the two measures yield the same pattern of development, despite the fact that the 'nuisance variables' affecting them are quite different, it suggests that threshold development can be explained by age-related change in auditory sensitivity. By nuisance variables, in this context, we mean any variable that affects the response that is not directly related to the auditory capacity of interest. They would include variables such as electrode impedance for the ABR and state of arousal for behavior. Although a variable such as neural synchrony may be directly related to some auditory capacities (e.g., Hendler et al., 1990), if we are interested in absolute sensitivity, neural synchrony is generally thought of as an ABR nuisance variable (e.g., Klein, 1986).

To put it a little more formally, let $\Theta_{\text{ABR}} = \psi + \nu_{\text{ABR}}$, where Θ_{ABR} is the ABR threshold for a given individual, ψ is 'true' threshold sensitivity and ν_{ABR} is the threshold elevation caused by ABR nuisance variables (e.g., background noise, neural synchrony, head size), and let $\Theta_{\text{BEH}} = \psi + \nu_{\text{BEH}}$, where Θ_{BEH} is the behavioral threshold for the same individual and ν_{BEH} is the threshold elevation caused by behavioral nuisance variables (e.g., state of arousal, attentiveness, motivation). If ν_{ABR} and ν_{BEH} are unrelated – a reasonable assumption – then Θ_{ABR} and Θ_{BEH} will only co-vary when ψ varies. Obviously, ψ only reflects sensitivity through the brainstem level; if Θ_{BEH} reflects immaturities of the auditory nervous system rostral to the brainstem, then the variance due to those immaturities will be included in the nuisance variable ν_{BEH} in this analysis.

There are three meaningful ways that Θ_{ABR} and Θ_{BEH} can co-vary. First, it is possible that $\Theta_{\text{ABR}} = \Theta_{\text{BEH}}$. This seems an unlikely outcome, as in general, $\Theta_{\text{ABR}} > \Theta_{\text{BEH}}$ among adults (e.g., Gorga et al., 1988); moreover, it would only occur if the effects of the respective nuisance variables were equal as well. Second, mean Θ_{ABR} and mean Θ_{BEH} may vary in parallel with age. If ν_{ABR} and ν_{BEH} are random variables, then their effects should cancel out when we average across individuals, even when the amount of variance due to nuisance factors is high. Thus, one should be able to show that mean Θ_{ABR} and mean Θ_{BEH} vary with age in a similar way, as long as ψ varies with age. Third, and finally, Θ_{ABR} and Θ_{BEH} may be positively correlated, such that individuals with high Θ_{ABR} tend to have high Θ_{BEH} . Clearly, $\Theta_{\text{ABR}} = \Theta_{\text{BEH}}$ is a special case of this condition, but correlations could be identified in any case where the relative values of Θ_{ABR} and Θ_{BEH} remained constant across individuals. The size of the correlation would reflect the proportion of variance common to the two measures (i.e., sensitivity). Of course, if the amount of variance due to ν_{ABR} or ν_{BEH}

is very high or if the amount of variance due to ψ is very low, then a significant correlation between Θ_{ABR} and Θ_{BEH} may be difficult to demonstrate. While the amount of variance in ψ is rather low among normal-hearing adults, it might be higher during development because rate of development tends to vary across individuals (e.g., Gottlieb, 1971). Thus, the relative values of Θ_{ABR} and Θ_{BEH} at a given age, the extent and timing of change in mean Θ_{ABR} and mean Θ_{BEH} with age, as well as the correlation between these thresholds in individual subjects all provide means for assessing how peripheral and brainstem neural immaturities limit sensitivity during development.

In general, previous analyses of ABR and behavioral measures in infants and children have addressed the issue of whether the ABR is an appropriate technique for screening or for diagnosis of hearing loss. Thus, few studies have actually compared the development of the two measures or examined the correlation between them. Kaga and Tanaka (1980) measured click-evoked ABR thresholds for a group of infants, as well as 'reflexive responses' for 1- to 4-month-olds and 'conditioned orientation responses' (COR) for infants older than 4 months. The stimuli for the behavioral measures were pure tones of 0.5, 1, 2, and 4 kHz. ABR and behavioral thresholds decreased in parallel, until about 7 months, when ABR thresholds reached an asymptote. Behavioral thresholds did not reach an asymptote until 10 months. Ruth, Horner, McCoy and Chandler (1983), in contrast, used click-evoked ABR, behavioral observation audiometry (BOA; similar to Kaga and Tanaka's 'reflexive responses') with a speech stimulus, and pure-tone visual reinforcement audiometry (VRA; similar to Kaga and Tanaka's COR) to estimate threshold in a group of 1- to 12-month-olds; VRA was only performed for infants older than 4 months of age. In agreement with Kaga and Tanaka, Ruth et al. reported that BOA thresholds decreased with age, reaching an asymptote at 7 months. VRA thresholds did not decrease between 4 and 7 months, but did decrease between 7 and 9 months, remaining asymptotic thereafter. ABR thresholds were stable over the entire range of ages tested. Although the results differ to some extent, both of these studies suggest a different time course of development for ABR and behavioral thresholds, which in turn suggests that nuisance factors (including more central auditory immaturities or neural synchrony) are important contributors to these thresholds. Unfortunately, the fact that the stimulus used to evoke the ABR was different from the stimulus used to evoke a behavioral response makes it difficult to interpret the differences in developmental course reported for these measures. Furthermore, because the same method has not been used to assess behavioral response across an age range, the sources of improvement in behavioral threshold are not clear.

To our knowledge, only one study has examined the correlation between ABR and behavioral thresholds in infants. Sasama (1990) compared click-evoked ABR thresholds to 2–4 kHz pure-tone COR thresholds in 39 children aged 4 months to 3.5 years. Sasama reported an astounding correlation of 0.95 between the two thresholds. On the face of it, this result would lead to the conclusion that nearly all of the variance in threshold during childhood is the result of improving sensitivity. There are some aspects of the results, however, that call this conclusion into question. For example, Sasama calculated the correlation between ABR and COR thresholds for the entire group of children; that is, different ages were considered together. Because the nuisance variables that contribute to the ABR threshold and the nuisance variables that contribute to the behavioral threshold both decline with age, looking at correlations across large age ranges may introduce a correlation between nuisance variables that violates the assumption that these variables are unrelated and inflates the correlation between the thresholds. Furthermore, it is puzzling that some of the subjects in this so-called 'normal group' had both ABR and COR thresholds in excess of 90 dB nHL. Finally, as was the case with the other studies comparing ABR and behavioral thresholds, the use of different stimuli to evoke the two responses is problematic; although neural elements responding in the 2–4 kHz range are the major contributors to the click-evoked response in adults, this does not appear to be the case in infants (e.g., Folsom and Wynne, 1986; Klein, 1986).

The present study took the 'convergent operations' approach to the development of auditory sensitivity. Behavioral and ABR thresholds were estimated for the same subjects, 3-month-olds, 6-month-olds and adults. A single behavioral method was applied to the two infant groups. To avoid interpretative difficulties, the same stimuli were used to elicit both brainstem and behavioral responses. Because both ABR and behavioral thresholds have been reported to mature at different rates for different frequencies (e.g., Folsom and Wynne, 1986; Klein, 1984; Olsho et al., 1988; Schneider et al., 1989), the relationship between these thresholds was examined at three frequencies. Both the correlations between measures within an age group and the pattern of age differences in average threshold for the two measures were examined at each frequency.

Method

Subjects

The subjects were 190, 3-month-olds, 125, 6-month-olds, and 40, 18- to 30-year-olds. Infants were tested within 2 weeks of the 3-month or 6-month birthday. All subjects met the following criteria for inclusion: 1) no

family history of congenital hearing loss or other risk factors for hearing loss; 2) normal developmental course, including term birth; 3) healthy on test date; 4) normal tympanometry results on test date; 5) no more than two prior episodes of ear infection and at least two weeks since treatment for last ear infection was completed; 6) identifiable click-evoked ABR at 20 dB nHL. Of these subjects, 123, 3-month-olds, 77, 6-month-olds, and 31 adults provided behavioral thresholds; 96, 3-month-olds, 66, 6-month-olds, and 91 adults provided ABR thresholds; and 77, 3-month-olds, 48, 6-month-olds, and 23 adults provided both behavioral and ABR thresholds.

Stimuli and apparatus

The stimuli were digitally generated tone pips at either 1, 4, or 8 kHz. Each tone pip had 3-cycle rise, 1-cycle plateau, and 3-cycle fall. Tone pips were repeated at a rate of 13.3/s. Using a fixed number of cycles in the rise and fall phase meant that the rise time varied as a function of frequency. Rise time does affect ABR amplitude and latency, but the effects of rise time are equivalent for infants and adults (Folsom and Aurich, 1987). The primary interest here was to examine age differences within frequency condition; the differences in rise time across frequency should not affect those comparisons.

Etymotic ER-1 insert phones were used to present the stimuli for both behavioral and ABR thresholds; the foam ear tips were trimmed to fit the infants' ear canals. Monaural (right ear) stimulation was used to elicit both behavioral responses and the ABR. Peak SPL (pSPL) was measured at the output of the Etymotic sound delivery tube with a Zwislocki coupler fit with a commercially available adaptor and a sound level meter set to 'peak hold'. Acoustic spectra of the tone pips, measured in the coupler, are shown in Fig. 1. The acoustic spectra of the phones used for behavioral and ABR recording were indistinguishable. All thresholds were obtained in double-walled sound attenuating booths.

A microcomputer generated tone pips, controlled external attenuators, filters, and gates, and kept track of responses for the behavioral threshold estimates. ABRs were recorded with gold-plated surface electrodes in a forehead (noninverting)–ipsilateral mastoid (inverting)–contralateral mastoid (ground) configuration. Interelectrode impedance was less than 3 k Ω . The response waveform was amplified and filtered (0.03–3.0 kHz). A high-speed, 12-bit A/D converter (Data Translation 2821) under the control of a microcomputer scanned the waveform at 256 points in 15.36 ms.

Each averaged response at threshold was based on 2048 stimulus presentations. The choice of number of stimulus presentations per response represented a

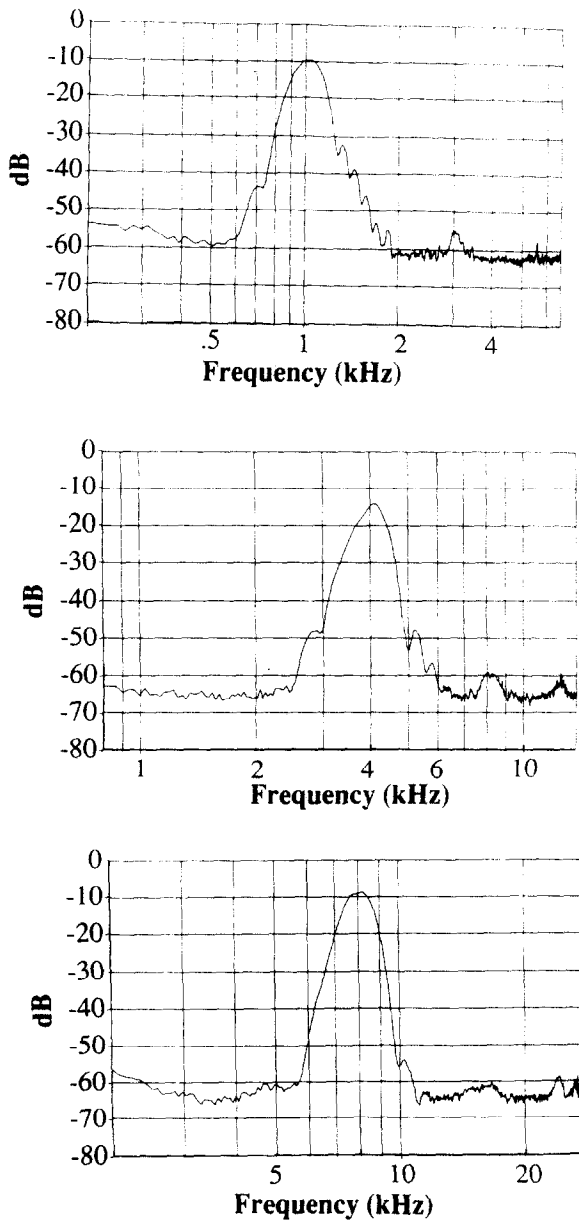


Fig. 1. Amplitude spectra of tone pips. Top panel, 1 kHz; middle panel, 4 kHz; bottom panel, 8 kHz.

trade-off between optimizing signal-to-noise ratio and the need to collect data from unsedated infants as quickly as possible. There is no doubt that increasing the number of presentations would yield lower threshold estimates (e.g., Elberling and Don, 1987). However, in previous work (e.g., Rickard, 1988) we have found that 2048 presentations were sufficient to estimate threshold reliably, and other work indicates that increasing the number of repetitions from 2000 to 4000 repetitions would be expected to reduce threshold by 5 dB or less (Don et al., 1984). Thus, although the ABR thresholds reported here may be slightly higher than they would have been had we used a greater number of stimulus presentations per response, we do not believe the effect is substantial.

Procedure

Each infant was tested at one frequency for both behavioral and ABR measures. Preliminary results suggested that 1-kHz behavioral and ABR thresholds were unrelated in 3-month-olds. Because we hypothesized that correlations should not 'reappear' at subsequent ages, ABR thresholds for 6-month-olds were only collected at 4 and 8 kHz. Each adult was tested at all three frequencies on both measures.

Somewhat different threshold 'search' procedures were used for behavioral and ABR thresholds, as described in detail in the following paragraphs. Using a different algorithm to estimate a threshold will change the threshold by a few dB, but it should be kept in mind that 'threshold' is in any case arbitrarily defined. As long as one algorithm is used to estimate behavioral threshold for all subjects, and one algorithm is used to estimate ABR threshold for all subjects, the relationship between the two should not be affected by the choice of algorithm. The only exception would be in the case where the two thresholds are expected to be equal. As mentioned in the Introduction, we did not expect that to be the case.

Behavioral thresholds

Behavioral thresholds were estimated using the observer-based psychoacoustic procedure (OPP), previously described in detail (e.g., Olsho et al., 1988; Olsho et al., 1987; Spetner and Olsho, 1990; Werner and Marean, 1991). Briefly, the infant was seated on the parent's lap in the test booth. An assistant seated to the infant's left quietly manipulated toys to keep the infant's gaze directed roughly at midline. The parent listened to music and the assistant listened to an observer in an adjacent control room over circumaural headphones. The observer viewed the infant through a window and on a video monitor. When the observer judged that the infant was quiet and attentive, she signaled the computer to begin a trial. Trials lasted approximately 7.5 s. On sound trials, tone pips were presented in 8 groups of 6, separated by 500 ms silent periods. No-sound trials had the same duration, but no sound was presented. The computer presented sound or no-sound trials on a random schedule, and the observer did not know what type of trial was being presented. The observer decided on each trial whether or not a sound had been presented, based on the infant's response. The computer provided feedback to the observer at the end of the trial. When the observer correctly identified a sound trial, a mechanical toy enclosed in a dark plexiglas box was illuminated and activated to reinforce the infant for responding to the sound.

Each session had three phases. In the initial phase, tone pips were presented at a level anticipated to be clearly audible to the subject. The mechanical toy

'reinforcer' was activated on each sound trial for at least 4 s to demonstrate the association between the tone pips and the reinforcer. This phase continued until the observer correctly identified at least 3 of the last 4 sound trials (prior to reinforcer onset) and at least one no-sound trial. In the second phase, the level of the tone pips continued as it had been in the first phase, but the reinforcer was only presented on sound trials if the observer responded correctly, to teach the infant the contingency between response and reinforcer. This phase continued until the observer correctly identified 4 of the last 5 sound trials and 4 of the last 5 no-sound trials. Threshold was estimated in the final phase using an adaptive procedure. Level began approximately 20 dB above anticipated threshold. If the observer was correct on two consecutive trials, the level of the tone pips was reduced on the next trial. If the observer was incorrect on one trial, the level of the tone pips was increased on the next trial. Initial step size was 10 dB and varied over trials according to PEST rules (Taylor and Creelman, 1967). Minimum step size was 1 dB. This phase continued until at least 8 reversals were obtained. Threshold was defined as the average of the last 6 reversals. Thresholds were only included if the standard deviation of the reversals was less than or equal to 10 dB. Adaptive runs in which the level of the stimulus on any trial should have been above the maximum presentation level were also discarded. The appropriate levels for each phase of the experiment were chosen for each frequency after extensive pilot work.

Each infant test session lasted from 20–30 min. Two sessions were scheduled for each infant to obtain one threshold. If an infant did not provide a threshold in the first session, the entire test procedure was repeated in the second. In a few cases, thresholds were obtained in both sessions. The lower of the two thresholds was used for the analysis, but these thresholds were always within 5 dB of each other.

Adult and infant subjects listened under similar conditions. Adults were told to indicate when they 'heard the sound that would make the toy come on.' Although the levels presented were chosen to be appropriate for adults, in other respects the experimental phases and the psychophysical procedure were the same for adults and infants. Adult thresholds were obtained in a single session with breaks between runs and order of frequencies was counterbalanced across subjects.

ABR thresholds

For ABR threshold, both infants and adults were tested in natural sleep. After placement of the electrodes and earphone, adults slept in a reclining chair and infants either slept in the parent's arms or in a crib. Ongoing EEG was monitored throughout the

session; data were collected only during periods of quiet sleep, and recordings were not made during periods of excessive EEG activity. After determining that the subject had an identifiable response to a 20-dB nHL click, a threshold was estimated using a modified method of limits algorithm. The level of the tone pip was set at 20 dB nHL on the first run, then reduced in 10 dB steps until a response was no longer evident, and finally increased in 2 dB steps until the response was reestablished.

Threshold was defined as the lowest level at which Wave V was clearly identifiable. During the recording session, the experimenter made judgments about whether a response was present on each run; the experimenter attempted to ensure that response threshold could be estimated in the range of intensities presented. The final decision about threshold value was made off-line by a scorer who was blind to stimulus condition and subject age. If the scorer could not identify a threshold within the range of stored responses, the data were excluded from further analysis. Both the experimenter and the scorer were experienced at scoring ABR waveforms.

Results

The results are presented in three parts: the behavioral thresholds, the ABR thresholds, and the relationship between the behavioral and ABR thresholds. The effects of age and frequency on thresholds and the interdependence of these effects are of primary interest. Thresholds were collected at only one frequency for each infant, but at all three frequencies for each adult. As a consequence, the effects of age were evaluated separately at each frequency and the effects of frequency were evaluated separately for each age, using analysis of variance and Tukey HSD post hoc pairwise comparisons. To aid in readability, only significance levels for these comparisons are reported. Because correlations were only calculated within an age-by-frequency condition, the fact that measures were repeated for adults but not for infants was irrelevant for the correlational analysis.

Behavioral thresholds

Average behavioral thresholds for infants and adults are shown in Fig. 2. Both 3-month-olds and 6-month-olds had higher thresholds than adults, consistent with many other studies of behavioral sensitivity in infants. Furthermore, the dependence of threshold on frequency appeared to change with age. Adults' and 3-month-olds' thresholds increased with increasing frequency, but the effect of frequency was more pronounced for 3-month-olds. As a result, the threshold difference between 3-month-olds and adults was great-

est at higher frequencies, averaging about 25 dB at 1 kHz, but almost 40 dB at 8 kHz. The pattern of results was quite different for 6-month-olds: Their thresholds were no better than those of 3-month-olds at 4 kHz, but decreased at 8 kHz. Consequently, 6-month-olds had more adultlike thresholds at 8 kHz than they did at 4 kHz; the difference between adults and 6-month-olds was about 35 dB at 4 kHz and only 20 dB at 8 kHz.

Analysis of variance showed that the trends evident in Fig. 2 were statistically significant. The effect of frequency was significant in each age group. For adults and 3-month-olds, 1-kHz thresholds were significantly lower than 4 kHz thresholds which were significantly lower than 8 kHz thresholds (all $P_s < 0.02$). For 6-month-olds, 8 kHz thresholds were significantly lower than 4 kHz thresholds ($P < 0.01$). The effect of age was also significant at all three frequencies. At 1 kHz, 3-month-olds had significantly higher thresholds than adults ($P < 0.001$); at 4 kHz, 3- and 6-month-olds had significantly higher thresholds than adults ($P_s < 0.001$), but 3- and 6-month-olds did not differ ($P > 0.6$); at 8 kHz, 3-month-olds had higher thresholds than 6-month-olds ($P < 0.001$), and 6-month-olds had higher thresholds than adults ($P < 0.001$).

ABR thresholds

In contrast to previous reports (e.g., Klein, 1984), 3-month-olds and 6-month-olds had adultlike ABR thresholds at all three frequencies. Average ABR thresholds are shown in Fig. 3. For each age group, threshold decreased slightly between 1 kHz and 4 kHz, then increased slightly at 8 kHz, with little apparent difference among age groups. Analysis of variance indicated that the effects of frequency were not significant for any group (3-month-olds, $P > 0.10$; 6-month-olds,

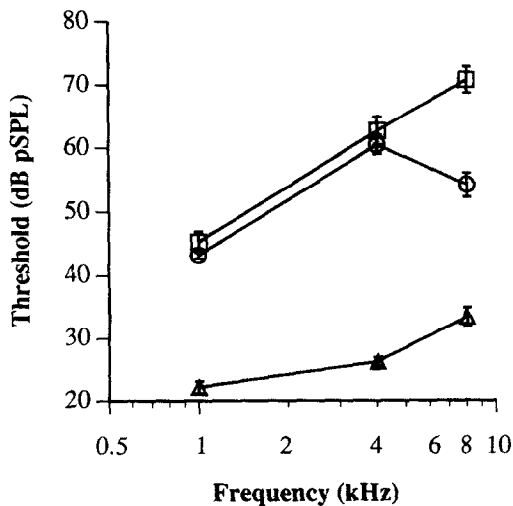


Fig. 2. Average behavioral tone pip threshold (± 1 standard error) as a function of frequency. Squares, 3-month-olds; circles, 6-month-olds; triangles, adults.

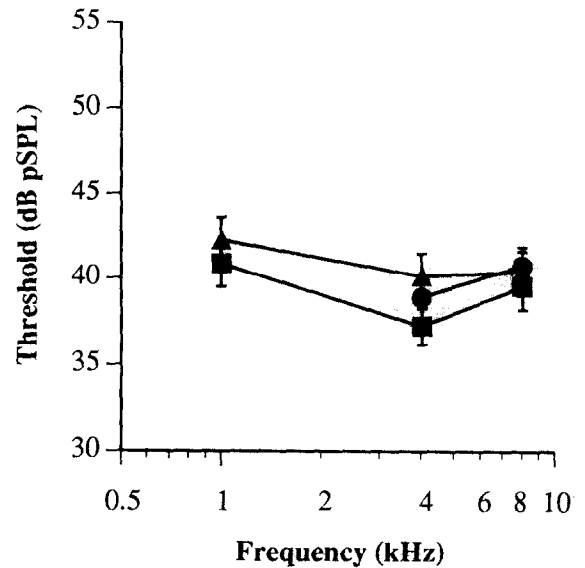


Fig. 3. Average ABR tone pip threshold (± 1 standard error) as a function of frequency. Squares, 3-month-olds; circles, 6-month-olds; triangles, adults.

$P > 0.48$; adults, $P > 0.46$). The age effect was far from significant at each frequency (lowest $P = 0.20$).

Relationship between behavioral and ABR thresholds

Three potential relationships between behavioral and ABR thresholds were outlined above. The first of these was that the absolute values of thresholds measured by the two methods would be equal; that is, $\theta_{ABR} = \theta_{BEH}$. The data from Figs. 2 and 3 have been replotted in Fig. 4 to make it easier to evaluate the absolute values of θ_{ABR} and θ_{BEH} in each age group. The bottom panel of Fig. 4 shows the thresholds obtained from adult subjects. As expected, θ_{ABR} does not equal θ_{BEH} at any frequency for adults; rather, $\theta_{ABR} > \theta_{BEH}$. This result is consistent with the literature on the relationship between frequency-specific ABR threshold and audiometric threshold in adult listeners (Gorga et al., 1988). It is interesting that the same difference between thresholds, 10–20 dB, was seen in the case where the same short-duration, frequency-specific stimuli were used to generate the evoked potential and the behavioral response. The difference between adult behavioral and ABR threshold was dependent on stimulus frequency, however: Behavioral thresholds grew progressively closer to ABR thresholds as frequency increased. A likely explanation is that the ABR is most readily recorded in response to stimulation in the higher frequency regions (Folsom, 1984), because higher traveling wave velocity near the base of the cochlea promotes greater neural synchrony. Thus, the ABR threshold at lower frequencies, such as 1 kHz, tends to underestimate sensitivity at those frequencies.

The relationship between the absolute values of behavioral and ABR thresholds is quite different in infants, as the upper panels of Fig. 4 show. In fact, for infants the relationship is the reverse of that seen for adults; that is, $\theta_{\text{ABR}} < \theta_{\text{BEH}}$. This result is also consis-

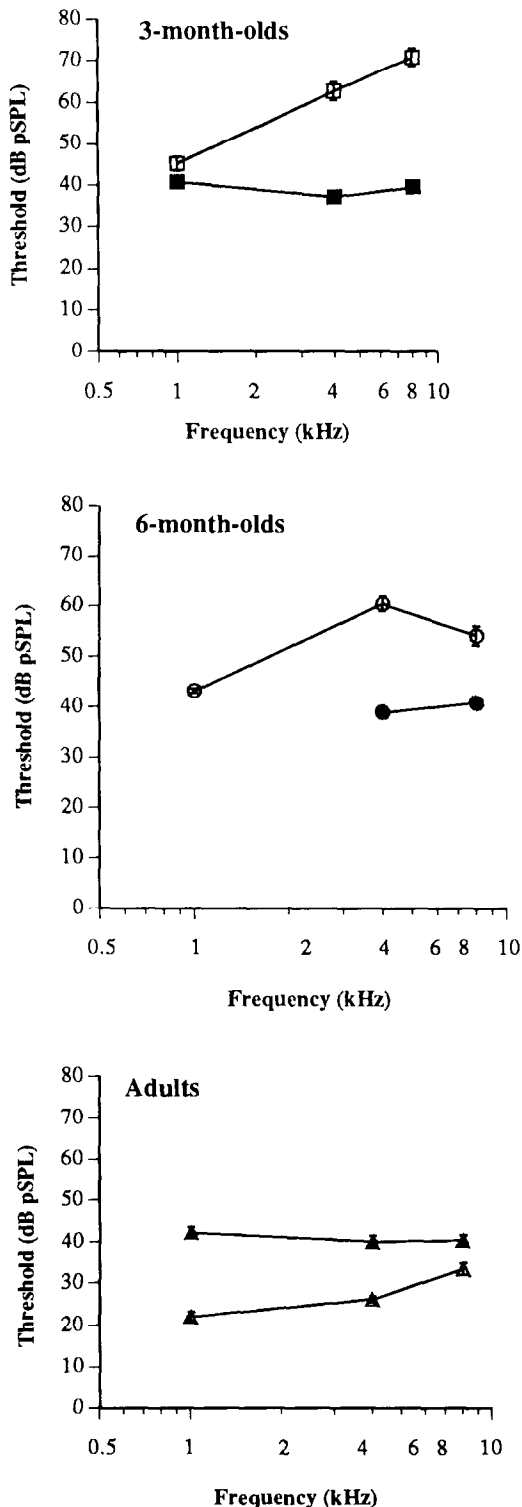


Fig. 4. A comparison between average behavioral and ABR tone pip thresholds as a function of frequency in three age groups. Filled symbols, ABR; open symbols, behavior.

tent with previous studies that have compared click-evoked ABR and audiometric thresholds in infants (Kaga and Tanaka, 1980; Ruth et al., 1983). As was the case for adults, the difference between infant behavioral and ABR threshold was frequency dependent; however, 3-month-olds differed from 6-month-olds in the nature of this dependence. Six-month-olds were similar to adults in that their behavioral and ABR thresholds were more similar at 8 kHz than at 4 kHz. Three-month-olds, in contrast, have behavioral thresholds that increasingly diverge from ABR threshold with increasing frequency: At 1 kHz, the two thresholds are quite similar in 3-month-olds, but at 8 kHz behavioral thresholds are about 30 dB higher than ABR thresholds. These results for infants strongly suggest that ν_{BEH} makes a large contribution to the behavioral threshold; however, it is not clear whether that contribution is in the form of primary auditory immaturities central to the brainstem or of factors not specific to the auditory modality, such as attention and motivation.

The second potential relationship between θ_{ABR} and θ_{BEH} is that these measures would vary with age in a similar way. It should be evident from Figs. 2 and 3 that they do not, at least between 3 months and adulthood. On the contrary, ABR thresholds appear to have achieved adult values by 3 months, while behavioral thresholds remain immature, particularly at 4 kHz, at 6 months. These results are consistent with those of other studies in that behavioral thresholds appear to take longer to mature than do ABR thresholds (Kaga and Tanaka, 1980; Ruth et al., 1983). This suggests that the factors governing maturation of the behavioral response are at least partially independent of those governing maturation of the ABR during this period of development.

The third potential relationship between θ_{ABR} and θ_{BEH} is that the two measures would be positively correlated. Pearson product-moment correlations were calculated for subjects who provided both behavioral and ABR thresholds, with separate correlations computed for each age group at each frequency. Scatterplots of ABR threshold v. behavioral threshold and the correlations between measures are shown in Fig. 5. At 3 months, the only frequency at which a significant positive correlation was found was at 4 kHz. At 6 months, neither the correlation at 4 kHz nor the correlation at 8 kHz was significant. For the adults, the correlations were not significant at 1 or 4 kHz, but a significant correlation was found at 8 kHz. Both of the significant correlations were modest in magnitude, suggesting that only about 25% of the variance is common to the two measures.

Two aspects of the results shown in Fig. 5 may deserve further comment. First, behavioral thresholds of both infants and adults can be quite variable. Clearly, much of this variance is unrelated to peripheral sen-

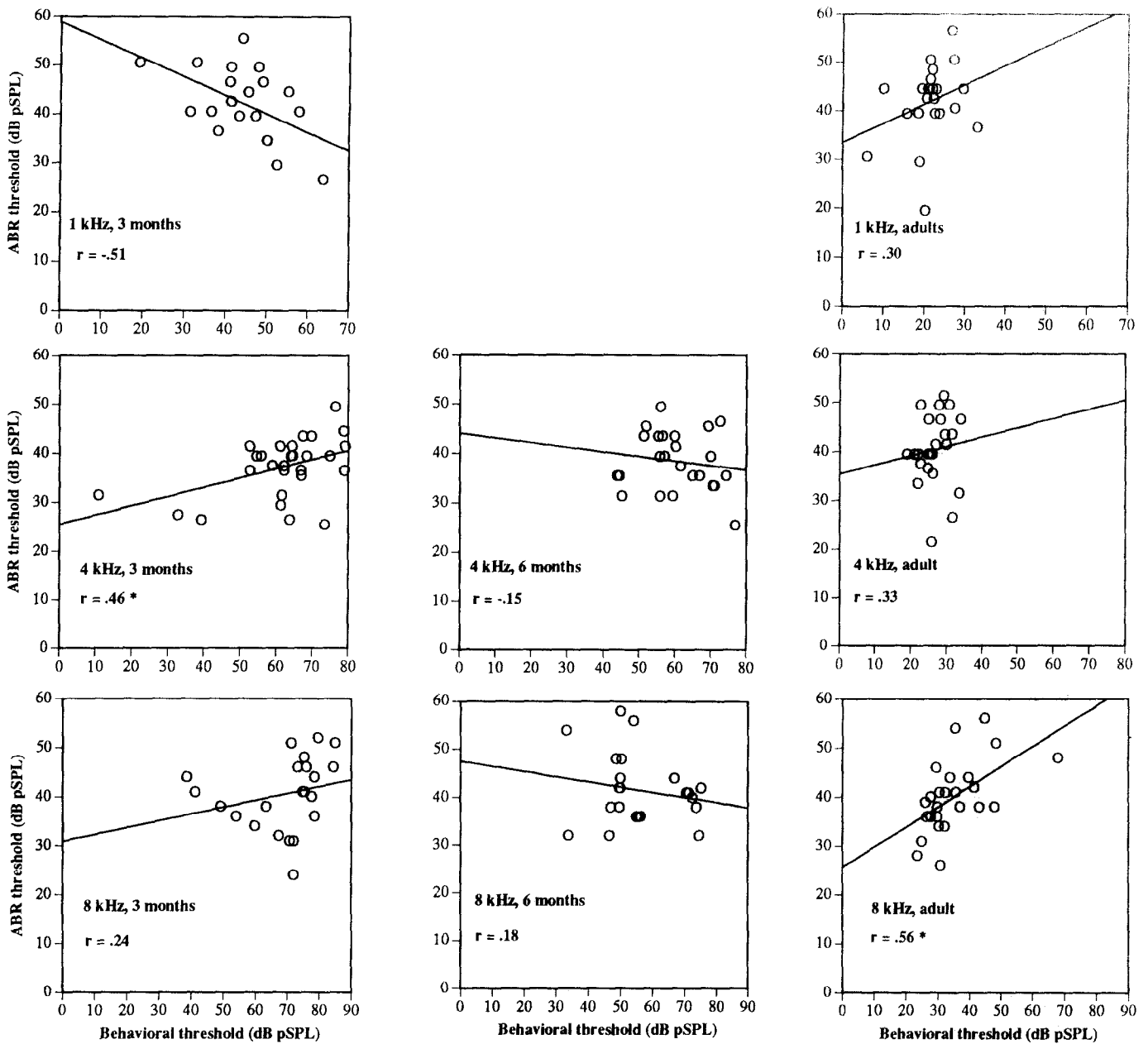


Fig. 5. Scatterplots of ABR threshold against behavioral threshold for three ages and three frequencies. * indicates a significant ($P < 0.05$, one-tailed) correlation.

sory function, particularly among adults. While other procedures could produce less variable results for adults (e.g., two-alternative, forced-choice with defined observation intervals), those other procedures cannot be applied to infants. We chose to apply the same procedure to both infants and adults to try to equate procedural effects, but certainly the resulting variability could have reduced our chances of finding correlations. Second, the correlations described above and illustrated in Fig. 5 were not strongly affected by the inclusion of outliers. Influence analysis, in which the contribution of each data point to the correlation is assessed, indicated approximately equivalent contribu-

tions of each individual in these plots. Furthermore, excluding certain obvious outliers (e.g., the 3-month-old with very low thresholds at 4 kHz or the adult with very high thresholds at 8 kHz) reduced the significant correlations somewhat, but left the correlations significant.

Discussion

Three major conclusions can be drawn from the results of this study. First, frequency specific auditory brainstem response measures of sensitivity approach maturity by the time an infant is 3 months old. Second,

behavioral thresholds for the same stimuli are immature at this age, and thresholds are more immature at high frequencies than they are at low frequencies. Behavioral thresholds improve at the highest frequencies between 3 and 6 months. Third, the relationship between behavioral and evoked potential measures of sensitivity suggests that part of the immaturity in behavioral thresholds at 3 months can be accounted for by immaturity of the sensory system at or peripheral to the auditory brainstem. The remaining immaturity must be due to immaturity central to the brainstem, either in the primary auditory pathway or in central processing not specific to the auditory modality.

The ABR thresholds reported here are similar in magnitude to those reported by Klein (1984). Klein found that while 21- to 28-week-old infants' ABR thresholds for 4 and 10 kHz tone pips did not differ from those of adults, 13- to 20-week-old infants had significantly higher thresholds at 4, but not 10, kHz. In contrast, we do not find a difference between 3-month-olds and adults at any frequency. The most likely explanation for this discrepancy is the type of earphone used. Klein presented his stimuli using a headphone in an MX41/AR cushion, while in the present study we used an insert earphone. As Klein notes, differences between infants and adults in the frequency response of the external ear could have contributed to the threshold differences he observed at 4 kHz. The insert earphone, on the other hand, completely eliminates the resonance of the concha as a factor and shifts the resonance frequency of the ear canal beyond the sound delivery tube to a very high value for both infants and adults. Thus, Klein's thresholds include the contributions of the external ear to sensitivity, while the present thresholds minimize those contributions.

As would be expected, the behavioral thresholds reported here are higher than those reported for 3- and 6-month-olds in studies (summarized by Olsho et al., 1988) where long duration stimuli were presented in sound field or over headphones. In fact, the difference between tone-pip and long-duration tone thresholds is greater for infants than for adults. A similar 'steep temporal integration function' has been previously reported for infants (Berg, 1991; Berg, 1993; Gray, 1990; Thorpe and Schneider, 1987; Werner and Marean, 1991), and is consistent with the idea that infants are relatively inefficient at processing short-duration stimuli. It is noteworthy that published infant thresholds for long-duration sounds are generally lower than the ABR thresholds reported here (e.g., Olsho et al., 1988; Sinnott et al., 1983; Trehub et al., 1980). Thus, the relationship between infant ABR and long-duration behavioral thresholds may be more adultlike than that between infant ABR and short-duration behavioral thresholds.

There is evidence here that sensory factors do contribute to variability in thresholds in infants, at least at 4 kHz in 3-month-olds. According to the model outlined in the introduction, that a correlation exists between behavioral and ABR thresholds in this condition at 3 months and that this correlation is not present in either 6-month-olds or adults, suggests that characteristics of the primary auditory system at or peripheral to the auditory brainstem contribute significant variability to sensitivity measures at 3 months. These auditory system characteristics apparently no longer contribute to sensitivity at later ages. That the average ABR threshold is nearly adultlike at this age suggests that we are catching the tail end of the developmental process: Although threshold is approaching adult values, there remains enough variability in sensory maturity among infants to support a significant correlation between ABR and behavioral thresholds. The proportion of variance common to these two measures is modest at 3 months, amounting to only 25% of the total. Thus other factors, such as nonsensory effects or characteristics of the primary auditory system central to the brainstem, must account for the remaining variance in behavioral threshold, just as other factors, such as neural synchrony and head size, must account for the remaining variance in ABR threshold. The differential frequency dependence exhibited by ABR and behavioral measures and the interaction of age and frequency in their effects on behavioral threshold support the contention that these additional factors are qualitatively different for the two measures.

A puzzling aspect of the correlational analyses is the pattern of results at 8 kHz. Behavioral thresholds improved dramatically between 3 and 6 months at this frequency; however, the correlation between behavioral and ABR thresholds was not significant for the infants. This suggests that the improvement seen between 3 and 6 months cannot result from maturation of the primary auditory system at or peripheral to the auditory brainstem. That sensitivity at 8 kHz would be mature, at least for more peripheral structures, prior to sensitivity at 4 kHz suggests that sensitivity in the mid-frequency range matures later than sensitivity at both lower and higher frequencies. Such a pattern is, in fact, evident in Klein's (1984) developmental study of frequency-specific ABR thresholds during infancy. However, there are also reports that low-frequency sensitivity matures before high (e.g., Folsom and Wynne, 1986; Folsom and Wynne, 1987; Olsho et al., 1988; Teas et al., 1982) and that high-frequency sensitivity matures before low (e.g., Schneider et al., 1989) in humans. In fact, Eggermont et al. (1991) and Ponton et al. (1992) report that the delay between waves I and V of the ABR matures first in the midfrequency range in humans. Thus, we are unable at this point to draw any strong conclusions about the frequency depen-

dence of sensitivity development in humans. It is clear, however, that the factors that contribute to infant behavioral threshold elevation at 8 kHz, and that account for the improvement in threshold at this frequency between 3 and 6 months depend on frequency in a different way from the factors that are common to the ABR and behavioral thresholds.

The finding that a correlation between behavioral and ABR threshold is present for apparently normal-hearing young adults suggests that there is more variability in performance at 8 kHz than at lower frequencies. Such variability could be explained in one of two ways. First, it is possible that age-related hearing loss, which tends to occur first at high frequencies, has already occurred to some extent in this group of young adults. By the same model of correlation that we have used throughout this paper, during the aging process variability among individuals would be increased relative to the prior period of maturity. Second, it is possible that high-frequency hearing, by the nature of the mechanisms which subserve it, is simply more variable, even in the absence of presbycusis or other types of hearing loss. For example, high-frequency regions of the cochlea receive more efferent innervation and may be more dependent on the so-called active mechanism which is thought to sharpen tuning and increase sensitivity in the cochlea (Dallos, 1988). Clearly, other experimental approaches would be necessary to decide between these alternatives. The lack of correlations at 8 kHz among infants, however, would argue against the position that variability in high-frequency hearing is higher in normal function.

In conclusion, the major finding of this study is that both sensory function and nonsensory factors contribute to variability in both behavioral and ABR measures of sensitivity during development. The correlational approach described here represents one way that we can estimate the relative contributions of these factors, and may be the only way that they can be approached in humans. It would be interesting to use this approach to address the same general issues in other ways. For example, if neural synchrony is an important variable for the ABR during development, then one would predict that ABR measures should be more strongly related to behavioral measures that also depend on neural synchrony, such as discrimination of repetition rate.

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