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Continued maturation of auditory brainstem function during adolescence: A longitudinal approach

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HIGHLIGHTS

- We longitudinally tracked subcortical speech encoding in adolescents from ages 14–17.
- Spectral representation, response consistency, and envelope tracking decreased. Peak latencies were stable.
- Subcortical auditory development continues through adolescence.

ABSTRACT

Objective: Considerable attention has been devoted to understanding development of the auditory system during the first few years of life, yet comparatively little is known about maturation during adolescence. Moreover, the few studies investigating auditory system maturation in late childhood have employed a cross-sectional approach.

Methods: To better understand auditory development in adolescence, we used a longitudinal design to measure the subcortical encoding of speech syllables in 74 adolescents at four time points from ages 14 through 17.

Results: We find a developmental decrease in the spectral representation of the evoking syllable, trial-by-trial response consistency, and tracking of the amplitude envelope, while timing of the evoked response appears to be stable over this age range.

Conclusions: Subcortical auditory development is a protracted process that continues throughout the first two decades of life. Specifically, our data suggest that adolescence represents a transitional point between the enhanced response during childhood and the mature, though smaller, response of adults. *Significance:* That the auditory brainstem has not fully matured by the end of adolescence suggests that auditory enrichment begun later in childhood could lead to enhancements in auditory processing and alter developmental profiles.

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Early studies on maturation of the auditory system found that

cortical evoked activity changes throughout childhood and adoles-

cence (Sharma et al., 1997; Cunningham et al., 2000; Ceponiene

et al., 2002; Sussman et al., 2008; Mahajan and McArthur, 2012)

whereas subcortical evoked responses approximate the response of

young adults by age two (Hecox and Galambos, 1974). These results

provided the basis for the widely held belief that auditory cortex

1. Introduction

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maturation follows a protracted time course while auditory brainstem maturation occurs rapidly up to age two and then plateaus until senescence (Schulman-Galambos and Galambos, 1979; Salamy, 1984). Recent cross-sectional evidence, however, has challenged this view by showing that changes in auditory brainstem function continue throughout childhood and adolescence (Lauter and Oyler, 1992; Johnson et al., 2008; Skoe et al., 2013b; Spitzer et al., 2015). These cross-sectional investigations indicated that while responses at age 2–3 are comparable to the young adult response, between 3 and 18 years of age responses demonstrate continued maturational plasticity (Johnson et al., 2008; Skoe et al., 2013b).

In particular, brainstem responses during the ages 5-11 years are characterized by earlier latencies, heightened intertrial response consistency, and more robust spectral encoding relative to younger children or adults. Based on this difference between children aged 5–11 years and adults we hypothesize that auditory brainstem function continues to mature through adolescence. In support of this, cross-sectional evidence suggests that after responses reach their developmental apex, spectral encoding, stimulus envelope tracking, and neural response consistency decline and response timing slows as the response continues to take on more adult-like characteristics. However, conclusive evidence of these changes occurring during adolescence requires a longitudinal analysis of this age range. Thus, to understand the maturational time course of subcortical auditory function in adolescence, we longitudinally tracked within-subject changes in auditory brainstem processing from age 14 years to 17 years by examining the subcortical evoked response to a synthesized speech syllable.

2. Methods

2.1. Participants

Four years of longitudinal data were collected on 74 adolescents (40 female). Participants were recruited from three Chicago-area public high schools. Participants were enrolled in the study during the summer before their freshman year of high school (average age at first test = 14.6 ± 0.4 years) and returned once a year over the next 3 years (average test-retest interval 344 days). Parental/guardian informed consent and adolescent informed assent were obtained prior to testing. All protocols and procedures were approved by the Northwestern University Institutional Review Board, and the participants were compensated for their participation.

At each test point, participants were screened to ensure that they met the inclusionary criteria, which included having no diagnosis of a reading, learning or neurological disorder, normal IQ (defined as a standard score ≥ 85 on the Wechsler Abbreviated Scale of Intelligence (WASI; Wechsler, 1999)), normal hearing as defined by air conduction thresholds <20 dB nHL for octaves between 125 Hz and 8000 Hz (ANSI, 2009) and an 80 dB SPL click-evoked wave V auditory brainstem response latency within lab-internal normal limits (5.24–5.99 ms). Year 1 test data were collected on an additional 14 participants, but these data were not included because of hearing loss (3 participants), failed IQ screening (1 participant), external diagnosis of a reading (2 participants) or learning (4 participants) disorder, and failure to return for testing in any or all of the subsequent years (4 participants).

2.2. Recording parameters

During data collection, the participant sat in a comfortable reclining chair in a soundproof, electromagnetically-shielded booth. Ag–AgCl electrodes were applied to the participant in an ipsilateral vertical montage (active electrode at Cz, reference electrode on the right ear, and ground placed on the forehead).

Individual electrode impedance was kept at $\leq 5 \text{ k}\Omega$ and inter-electrode impedance differences were maintained below $< 3 \text{ k}\Omega$. Stimuli included two variants of a consonant vowel stimulus (referred to as "long-da" and "short-da", collected separately using NeuroScan and Bio-logic systems, respectively, described below) presented in alternating polarity at 80 ± 1 dB SPL to the participant's right ear at a rate of 3.9 Hz (long-da) and 10.9 Hz (short-da). During the recording sessions, the participant watched a self-selected movie with the movie's soundtrack presented in free field at <40 dB SPL. The left ear remained unoccluded so that the participant could hear the movie's soundtrack (see Skoe and Kraus, 2010 and Kraus, 2011 for details about the auditory brain-stem response to complex sounds (cABR)).

2.3. Stimulus characteristics and response processing

2.3.1. Long-da

The long-da is a 170 ms speech sound. This stimulus is a six-formant syllable stimulus synthesized with a Klatt synthesizer (Klatt, 1980) at a 20 kHz sampling rate. During the first 5 ms the onset of the sound is marked by a short burst of broadband energy. The consonant–vowel formant transition begins at 5 ms and continues for 45 ms, during which the fundamental frequency (F_0) remains at 100 Hz, while the first formant increases from 400 Hz to 720 Hz, and the second and third formants decline from 1700 Hz and 2580 Hz to 1240 Hz and 2500 Hz, respectively. The steady state vowel lasts from 50 ms to 170 ms, during which the first three formants (F_1 - F_3) are steady at 720, 1240, and 2500 Hz. From 5 ms to 170 ms the fourth, fifth, and sixth formants are constant at 3330, 3750, and 4900 Hz, respectively. The long-da was presented in NeuroScan Stim² software (Compumedics; Charlotte, NC).

Responses to the long-da were processed off-line. First, the responses were bandpass filtered in Neuroscan Edit from 70 Hz to 2000 Hz (12 dB/octave, zero phase-shift), which captures the limits of brainstem phase-locking (Liu et al., 2006; Chandrasekaran and Kraus, 2010). Responses were segmented into epochs -40 to 190 ms referenced to stimulus onset and baselined to average prestimulus amplitude. Epochs with amplitude exceeding $\pm 35 \,\mu$ V were rejected as artifact, and 6000 of the remaining artifact free trials were averaged to create the final responses. Fig. 1(A) displays the stimulus and response waveforms, with labels for the formant transition and steady-state regions.

2.3.2. Short-da

To demonstrate the generalizability of the change in the auditory brainstem response as a function of age and to replicate previous cross-sectional results (Skoe et al., 2013b), a 40 ms speech sound, 'da' (short-da) was also presented to seventy-one of the seventy-four participants (Fig. 1B). The short-da is a five-formant synthesized speech sound (Klatt, 1980) beginning with a noise burst that is followed by a formant transition between the consonant 'd' and the vowel 'a'. Although the stimulus does not contain a steady-state vowel, it is still perceived as the syllable 'da'. Over the 40-ms duration of the stimulus, there is a linear change in the F_0 and the first three formants (F₁, F₂, F₃): F₀ from 103 to 125, F₁ from 220 to 720, F_2 from 1700 to 1240, and F_3 from 2580 to 2500 Hz. F_4 and F₅ remain constant at 3600 and 4500 Hz, respectively. For the short-da, stimuli were presented and responses were collected with the Bio-logic Navigator Pro System (Natus Medical Incorporated, Mundelein, IL).

Responses to this stimulus were processed online. The responses were bandpass filtered from 100 to 2000 Hz. The recording window spanned -15 to 70 ms. Trials beyond $\pm 23.8 \,\mu$ V were considered artifact and so were excluded from the running average. Two sub-averages of 3000 trials were collected. Because the effects of maturation on the response to short-da were similar to

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