FEATURE ARTICLE
Sequential Auditory Scene Analysis Is Preserved in Normal Aging Adults

Joel S. Snyder[1] and Claude Alain[1,2]

[1]The Rotman Research Institute, Baycrest Centre for Geriatric Care, Toronto, Ontario, Canada and [2]Department of Psychology, University of Toronto, Toronto, Ontario, Canada

Normal aging is accompanied by speech perception difficulties, especially in adverse listening situations such as a cocktail party. To assess whether such difficulties might be related to impairments in sequential auditory scene analysis, event-related brain potentials were recorded from normal-hearing young, middle-aged, and older adults during presentation of low (A) tones, high (B) tones, and silences (—) in repeating 3 tone triplets (ABA—). The likelihood of reporting hearing 2 streams increased as a function of the frequency difference between A and B tones (Δf) to the same extent for all 3 age groups and was paralleled by enhanced sensory-evoked responses over the frontocentral scalp regions. In all 3 age groups, there was also a progressive buildup in brain activity from the beginning to the end of the sequence of triplets, which was characterized by an enhanced positivity that peaked at about 200 ms after the onset of each ABA— triplet. Similar Δf- and buildup-related activity also occurred over the right temporal cortex, but only for young adults. We conclude that age-related difficulties in separating competing speakers are unlikely to arise from deficits in streaming and might instead reflect less efficient concurrent sound segregation.

Introduction

The ability to understand speech in adverse listening situations, such as a cocktail party, declines with age (Committee on Hearing, Bioacoustics, and Biomechanics 1988). Several factors likely contribute to speech processing difficulties in older adults including changes in peripheral and central auditory processing, as well as changes in brain areas responsible for more general cognitive functions such as attention and memory (Committee on Hearing, Bioacoustics, and Biomechanics 1988; Humes 1996; Schneider and others 2002). Evidence from recent studies suggests that age-related changes in listeners' abilities to perceptually organize incoming acoustic information, referred to as auditory scene analysis (Bregman 1990), may also play an important role in age-related difficulties in speech comprehension (Alain and others 2006).

Auditory scene analysis problems can be divided into 2 main categories: those that require segregation of multiple "concurrent" sounds (e.g., 2 discrete speech events spoken simultaneously) and those that require segregation of multiple "sequential" patterns of sound (e.g., 2 melodies with notes that alternate between 2 musical instruments). In the laboratory, it is useful to distinguish these 2 types of sound segregation because they present different problems to the auditory system and may thus rely on different neural mechanisms (Alain and Izenberg 2003). In real-world situations, however, both types

of sound segregation are likely to play a role in solving the cocktail party problem. Thus, an important question related to the hypothesis that difficulties in sound segregation contribute to age-related problems in speech comprehension (Alain and others 2006) is the extent to which aging affects concurrent and sequential sound segregation, respectively.

With respect to concurrent sound segregation, psychophysical research has clearly shown that older adults have higher thresholds for detecting a mistuned harmonic than do young or middle-aged adults even after statistically controlling for audiometric thresholds (Alain and others 2001). Listeners who find it difficult to detect mistuning may assimilate one or more frequency components coming from secondary sound sources into the target signal (cf., Roberts and Moore 1990). The inclusion of extraneous frequency components into the target signal would then lead to concomitant errors in perception, given the blend of acoustic energy incorrectly conjoined at an earlier stage of processing. Therefore, age-related increases in mistuning detection thresholds may relate to speech perception problems of older adults because the perception of a mistuned harmonic, like speech signals embedded in babble or noise, depends on the ability to parse auditory events based on their spectral pattern. Older adults also have greater difficulty than young adults in parsing 2 concurrently presented vowels based on fundamental frequency (f_0) and show decreased neural activity associated with this task (Snyder and Alain 2005).

Although these results suggest an age-related decline in concurrent sound segregation, the effects of age on sequential sound segregation (or "streaming") remain equivocal. Previous studies that used indirect objective measures of sequential sound segregation (e.g., detecting a change to a stimulus that is difficult without perceptual segregation) have shown no evidence for an effect of aging on streaming (Trainor and Trehub 1989; Alain and others 1996). Although such objective measures of sound segregation are desirable because they do not rely on self-reported measures, it is not always clear how they relate to more traditional conceptions of streaming that are based on subjectively perceiving 2 streams of sounds. In a study that used both indirect and direct measures of streaming, older hearing-impaired listeners showed an ability to segregate sequential sound patterns (Stainsby and others 2004). Performance was not compared with a control group, however, making it unclear whether these participants showed impairments related to age, hearing loss, or neither.

Using an objective method to estimate the frequency separation at which listeners could no longer hear 2 streams (fusion threshold), Mackersie and others (2001) observed only a weak (nonsignificant) relationship between listener age with hearing loss and fusion threshold. However, they found a

significant correlation between fusion threshold and simultaneous sentence perception, suggesting that sequential sound segregation processes may play an important role in solving the cocktail party problem. Rose and Moore (1997) showed that some (but not all) bilaterally hearing-impaired listeners required greater frequency separation than normal-hearing listeners for stream segregation to occur. In a study of subjective perception of streaming with harmonically complex tones, young adults perceived more streaming than older adults but only for tones with resolved harmonics (Grimault and others 2001). When the older adults were separated into 2 groups, those with hearing impairment surprisingly perceived more streaming than those without hearing impairment for the resolved tones. For tones with unresolved harmonics, however, robust streaming was observed for all groups of participants. The above studies thus show inconsistencies in terms of whether aging and hearing loss have a significant detrimental impact on segregation of sequential sound patterns.

The purpose of the present study was therefore to assess the effects of age on sequential stream segregation in normal-hearing adults. One paradigm that has been used extensively to study auditory stream segregation presents repeating ABA—triplets in which "A" (low) and "B" (high) are sinusoidal tones and "—" is a silent interval (van Noorden 1975), as shown in Figure 1. When the difference in frequency (Δf) between the A and B tones is small and the repetition rate of the sequence is slow, listeners hear a single stream of tones in a galloping rhythm (ABA—ABA—). When the frequency difference is large and the repetition rate is fast, listeners report hearing 2 streams of tones (A—A—A—A— and B——B——), each in a metronome-like rhythm (for a review on other factors affecting streaming, see Moore and Gockel 2002).

To determine the extent to which aging affects subjective perception of stream segregation with pure tones differing in frequency, the current study tested 3 groups of normal-hearing participants: young, middle-aged, and older adults. While participants were performing the streaming task, we recorded event-related brain potentials (ERP) to determine what aspects of stream segregation, if any, were affected by aging. In a recent ERP study, we found increases of the P1, N1, and P2 peak amplitudes of the auditory evoked response with increasing Δf between A and B tones during the streaming task (Snyder and others 2006; see also Gutschalk and others 2005). The Δf-related enhancement in P1, N1, and P2 waves at frontocentral sites was modeled with a bilaterally symmetrical pair of tangential dipoles in Heschl's gyrus. We also found a similar Δf-related increase in N1c over the right auditory cortex, consistent with radial sources on the lateral portions of auditory cortex (e.g., parabelt regions, Kaas and Hackett 2000). The Δf-related change in sensory-evoked responses at frontocentral and right temporal sites was not significantly affected by attention, suggesting that it indexes an attention-independent mechanism. The Δf-related ERP changes are similar to those observed following an abrupt change in acoustic parameters such as frequency, intensity, or location (Butler 1968; Picton and others 1978; Näätänen and others 1988; also see Jones and others 1998; Hung and others 2001) and likely indicate a release from suppressive mechanisms. Thus, it is possible that correlates of streaming in the P1–N1-P2 and N1c peaks (Gutschalk and others 2005; Snyder and others 2006) might not reflect perception of streaming directly but rather the action of more general neurophysiological mechanisms. On the other hand, modulation of these peaks depending on whether participants heard 1 stream or 2 streams suggests that the observed effects are at least partly related to perception (Gutschalk and others 2005).

In addition to Δf-related changes in ERP amplitude, we found a slow positive wave that increased in amplitude as the sequence progressed and was interpreted as an index of the
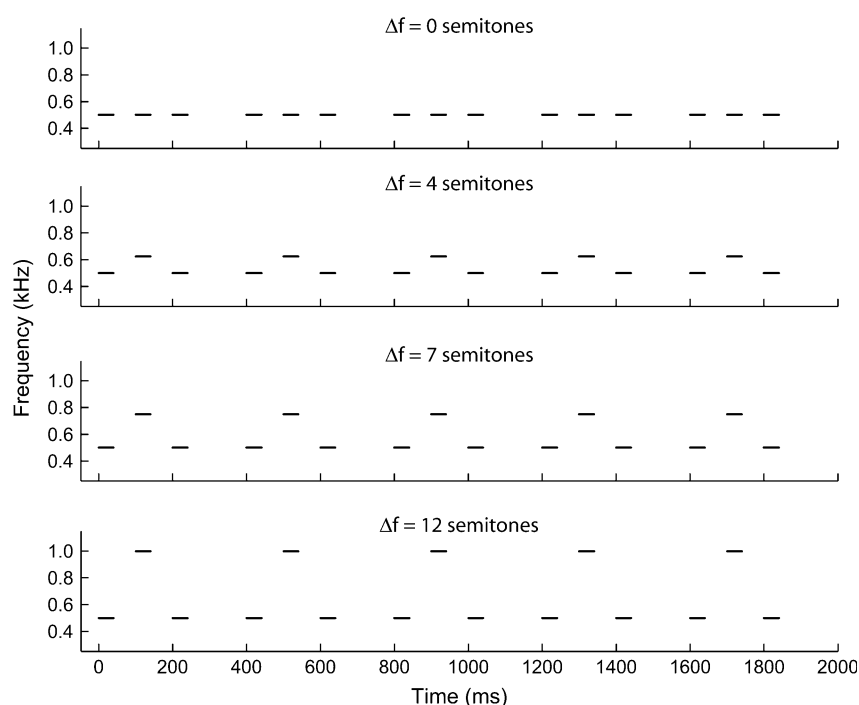
Figure 1. Five cycles of pure-tone stimuli in a repeating triplet pattern with low tones, high tones, and silences, with 4 different frequency separations between low and high tones (Δf = 0, 4, 7, and 12 semitones). Each bar represents a pure tone in a galloping rhythm. Actual trials were composed of 27 cycles.

buildup of stream segregation. Unlike the Δf-related increase in ERP amplitude, this buildup-related activity was strongly diminished at frontocentral and right temporal electrodes when participants were asked to ignore the auditory stimuli, mirroring the effects of attention on the perceptual buildup of streaming (Carlyon and others 2001). In the current study, participants were presented with ABA—triplets for 10.8 s and were asked to indicate at the end of the sequence whether it had a gallop-like rhythm or whether it split into 2 parallel streams of sounds. As in our original study (Snyder and others 2006), Δf was varied from trial to trial. We examined whether aging affects listeners' likelihood of reporting 2 auditory streams and whether aging has differential effects on ERP correlates of Δf- and buildup-related aspects of streaming at frontocentral and temporal electrode sites. The data from the young participants were the same as in our previous report (Snyder and others 2006), but new data sets were collected from normal-hearing middle-aged and older adults.

Materials and Methods

Participants

Ten young adults (6 men and 4 women, age range = 23–38 years, mean age = 29.5 years), 10 middle-aged adults (3 men and 7 women, age range = 41–54 years, mean age = 46.6 years), and 10 older adults (3 men and 7 women, age range = 62–79 years, mean age = 72.7 years) participated after giving written informed consent according to the guidelines of the Baycrest Centre for Geriatric Care and the University of Toronto. All participants were right handed except 1 young adult and 2 older adults. All had subclinical pure-tone thresholds (<30 dB hearing level) in both ears from 500–1000 Hz, corresponding to the frequency range of the experimental stimuli (see Table 1). In the broader range 250–8000 Hz, there were no significant differences between the 2 ears, $F_{1,27} < 1$, $P = 0.61$. However, there was a significant age-related increase in hearing thresholds, $F_{2,27} = 47.64$, $P < 0.001$, which is considered a normal aspect of aging (Committee on Hearing, Bioacoustics, and Biomechanics 1988). A planned contrast showed that this was due to elevated thresholds in older adults compared with middle-aged adults ($P < 0.001$) but no difference occurred between young and middle-aged adults ($P = 0.78$). There was also a significant age by frequency interaction, $F_{12,162} = 24.85$, $P < 0.001$, due to greater age difference in hearing thresholds at frequencies above 2000 Hz.

Stimuli and Procedure

As shown in Figure 1, sound sequences consisted of alternating A and B tones with every other B tone omitted (taking the form ABA—ABA—ABA—. . .). Tone duration was 20 ms including 5 ms rise and fall times. The stimulus onset asynchrony was 100 ms between adjacent A and B tones within each ABA—cycle. The silent duration (—) between ABA triplets was 100 ms. The A tones repeated every 200 ms, and the B tones repeated every 400 ms. Within each trial, the A tone frequency was always 500 Hz and the B tone frequency was 500, 625,

Table 1

Young, middle-aged, and older adults' mean (standard deviation) pure-tone hearing thresholds (dB hearing level)

Frequency (Hz)	Young		Middle aged		Older	
	Right ear	Left ear	Right ear	Left ear	Right ear	Left ear
250	21.0 (8.8)	21.0 (6.6)	5.0 (7.1)	4.5 (5.0)	13.0 (9.2)	15.5 (10.7)
500	16.5 (5.8)	17.5 (5.4)	9.0 (3.9)	8.5 (6.3)	16.5 (8.2)	18.5 (9.7)
1000	−2.5 (8.2)	−3.0 (8.6)	9.0 (3.9)	7.5 (4.2)	14.5 (7.2)	15.0 (8.2)
2000	−0.5 (8.0)	0.5 (5.0)	5.0 (7.5)	5.0 (9.7)	20.0 (11.3)	18.0 (12.5)
4000	3.5 (8.8)	1.0 (8.4)	1.0 (5.2)	0.0 (4.7)	28.5 (12.0)	31.5 (13.3)
6000	11.0 (12.9)	9.0 (9.1)	13.0 (6.7)	11.0 (7.4)	50.0 (15.5)	47.5 (17.2)
8000	9.0 (14.5)	5.0 (7.5)	21.0 (11.5)	25.0 (10.8)	66.5 (19.9)	66.0 (20.5)

750, or 1000 Hz. This corresponds to Δf levels of 0, 4, 7, and 12 semitones. Stimuli were converted to analog form using a Tucker Davis Technologies (TDT) RP-2 real-time processor (24 bit, 90-kHz bandwidth) under the control of MATLAB running on a Dell computer with a Pentium 4 processor. The analog outputs were fed into a Headphone driver (TDT HB-7). Stimuli were then transduced and presented binaurally through Sennheiser HD 265 headphones (Sennheiser Electronic Corporation, Old Lyme, CT) at about 85 dB sound pressure level.

On each trial, participants were presented with 10.8 s of the ABA—triplet (27 ABA—repetitions). Within a block of trials, 80 trials were presented in which Δf varied pseudorandomly from trial to trial during electrophysiological recording (20 per Δf level). Participants pressed a button at the end of the sequence to indicate if they heard the pattern as 1 stream for the entire trial and another button if they heard the pattern as splitting into 2 streams at any point during the trial. The next trial began 2000 ms after the response. Participants were instructed to focus on the rhythm as a cue (i.e., not galloping or galloping) to determine whether the pattern had split into 2 streams. They were also instructed to let their perception take a natural time course rather than biasing themselves toward hearing the patterns in one way or another. Each participant performed 4 blocks for a total of 320 trials (80 per Δf level). Prior to the experiment, participants completed 8 practice trials with 2 examples of each Δf level. The experimental session lasted around 75 min.

Electrophysiological Recording and Analysis

The electrophysiological responses were continuously collected and digitized (250 Hz sampling rate; band-pass filtered 0.05–50 Hz) from an array of 64 electrodes using NeuroScan SynAmps (Compumedics USA, El Paso, TX) and stored for off-line analysis. Eye movements were monitored with electrodes placed at the outer canthi and at the superior and inferior orbit. During recording, all electrodes were referenced to Cz, but they were re-referenced to an average reference for off-line analysis.

Trials contaminated by excessive peak-to-peak deflection at the sites not adjacent to the eyes were automatically rejected before averaging. The rejection threshold was ±100–150 μV, determined individually for each participant, excluding about 15% of trials. ERPs were averaged separately for each level of Δf and for each electrode site. For each individual average, ocular artifacts (e.g., blinks, saccades, and smooth movements) were corrected by means of ocular source principal components using the brain electrical source analysis (BESA 3.0) software (Berg and Scherg 1994; Picton and others 2000). ERPs were also digitally filtered using BESA 3.0 to attenuate frequencies outside 1–20 Hz.

The first off-line ERP analysis used epochs that included a baseline of 200 ms and the first 2000 ms after the beginning of the trial. There were 80 such 2200-ms epochs for each Δf level for each participant. Another set of analyses used epochs that included 48 ms before and 400 ms after the onset of each ABA—triplet, excluding the first and last ABA—triplet of each trial. These 448-ms epochs were sorted into 5 time bins taken from successive 2 s periods within the 10.8-s trial, with each time bin containing 5 repetitions of the ABA—cycle. For each time bin, there were thus 400 epochs (80 trials × 5 ABA—cycles) for each Δf level for each participant.

We examined the effects of Δf in each time bin by subtracting the 0 semitone condition from the non-0 semitone conditions at each time bin. Δf-related modulations throughout the trial were quantified relative to a baseline of 48 ms prior to the B tone because this tone was the one varying in frequency. To test for effects of time, we measured the mean amplitude of brain responses across 5 consecutive triplets (i.e., 2-s segment) and compared ERP amplitude obtained during the 2nd, 3rd, 4th, and 5th segment relative to the 1st 2-s segment. Because of the ongoing nature of the ABA—triplets, ERP amplitude related to buildup over time was measured relative to the mean activity across the entire 448-ms epoch because it was unclear whether buildup was time locked to any specific event in the ABA—triplet.

ERPs were quantified as the mean amplitudes across 9 frontocentral electrodes (Fz, F1/2, FCz, FC1/2, Cz, C1/2) and separately for the left and right temporal electrodes (T7 and T8). The frontocentral and the temporal electrodes were chosen for separate analyses because they

reflect auditory cortical areas with tangential and radial sources, respectively. Previously, we found that activity at frontocentral sites and at T8 (but not T7) showed Δf-related activity that correlated significantly with participants' perception of streaming (Snyder and others 2006). We therefore examined these electrodes again to test for main effects of Δf and buildup over time and also interactions between these factors and age group. Such interactions would indicate age-related changes in Δf- and buildup-related mechanisms of stream segregation.

Statistical Analysis

The proportions of trials in which participants reported hearing 2 streams were analyzed using a mixed design analysis of variance (ANOVA) with age (young, middle aged, older) as the between-subject factor and Δf (0, 4, 7, and 12 semitones) as the within-subject factor. ERP amplitudes averaged across 9 frontocentral electrodes were analyzed using a 3-factor ANOVA with age, Δf, and time bin ($t1$-$t5$). ERP amplitudes at temporal electrodes (T7 and T8) were analyzed using a 4-factor ANOVA with hemisphere (left and right), age, Δf, and time bin. When appropriate, the degrees of freedom were adjusted with the Greenhouse-Geisser epsilon (ε). All reported probability estimates are based on the reduced degrees of freedom, although the original degrees of freedom are reported. ERP peak amplitudes were related to behavioral judgments of streaming by simple correlations for each participant. These simple correlations were submitted to 1-sample t-tests, assessing the hypothesis that the correlations were different than 0, with Bonferroni corrections for multiple tests.

Results

Behavioral Data

Figure 2 shows the group mean proportion of trials heard as streaming at each of the Δf levels for young, middle-aged, and older participants. As expected, the likelihood of reporting perception of 2 streams increased with Δf in all 3 age groups (main effect of Δf, $F_{3,81} = 248.75$, $P < 0.001$), with all adjacent levels of Δf differing from each other ($P < 0.001$). At 0 semitones, participants rarely reported hearing streaming, whereas at 12 semitones, participants almost always reported hearing 2 streams of sounds. At intermediate levels (4 and 7 semitones), participants sometimes heard streaming and sometimes heard galloping for the whole trial. There was no main effect of age, $F_{1,27} = 2.27$, $P = 0.12$, and also there was no significant interaction between age and Δf, $F_{6,81} = 1.25$, $P = 0.31$, suggesting
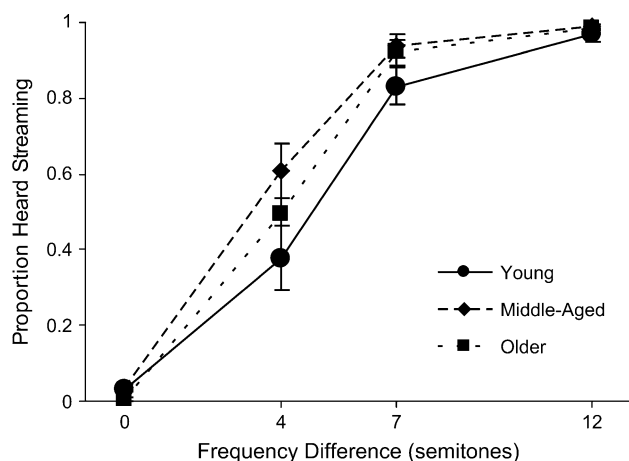

Figure 2. Group mean (±standard error) proportion of trials heard as streaming for young ($n = 10$), middle-aged ($n = 10$), and older ($n = 10$) participants for the 4 Δf levels.

that the 3 age groups perceived streaming to the same extent across all levels of Δf.

Transient and Sustained Neural Activity after Trial Onset

Figure 3A shows ERPs at the frontocentral midline electrode (FCz) and at the left and right temporal electrodes (T7 and T8) elicited by the onset of the 10.8-s trial collapsed across Δf for young, middle-aged, and older adults. One older adult was excluded from the analyses of these responses because of excessive artifacts at the frontocentral electrodes. In all 3 age groups, these ERPs included P1, N1, P2, and N2 waves that were maximal at FCz peaking around 60, 120, 160, and 200 ms, respectively. The N1 showed a significant effect of age group, with larger amplitude for young adults, $F_{2,26} = 3.89$, $P < 0.05$. The P2 also showed a significant age effect, but in this case older adults showed the largest response, $F_{2,26} = 3.81$, $P < 0.05$. As shown in Figures 3B and 4, the N2 showed a significant effect of Δf, $F_{3,78} = 17.99$, $P < 0.001$. All 3 age groups showed this N2 effect, as indicated by a lack of interaction between age and Δf, $F_{3,78} = 0.75$, $P = 0.60$. No other significant effects of age, Δf, or their interaction were observed on the transient peaks at the frontocentral electrodes. Following the transient responses, there was a sustained potential (SP) that was negative and maximal over the frontal scalp regions. A large influence of age was observed on the SP, with substantial age-related decreases in amplitude, $F_{2,26} = 6.60$, $P < 0.005$. The SP showed a nonsignificant trend for larger amplitude with increasing Δf, $F_{3,78} = 2.44$, $P = 0.08$, and a nonsignificant interaction between Δf and age, $F_{6,78} = 2.11$, $P = 0.07$.

At T7 and T8, transient peaks were observed following the trial onset, including P1t, N1t, P2t, and N2t waves peaking around 100, 150, 200, and 270 ms, respectively (Fig. 3A). The small P1t and N1t are likely transient responses to the first A tone of the trial from regions of auditory cortex with a radial orientation (Wolpaw and Penry 1975). The larger P2t and N2t peaks that follow likely reflect responses to the B tone. Following these transient peaks was a sustained positive response (SPt) that lasted until around 600 ms following trial onset. P2t, N2t, and SPt responses were larger on the right side of the head, $F_{1,26} = 6.08$, 13.69, 8.94, $P < 0.025$, and the P2t and SPt waves were largest in young adults, $F_{1,26} = 4.33$, 5.00, $P < 0.025$. No significant main effects of Δf or interactions involving hemisphere and age were observed on ERP activity recorded at T7 and T8. These results, therefore, indicate rightward hemispheric asymmetry and significant age effects for activity following the onset of the second tone of the trial (i.e., P2t, N2t, SPt). The lack of significant effects for the earlier P1t and N1t responses indicates that presentation of at least 2 tones was necessary to observe an effect of age on ERP amplitude at temporal electrodes.

Neural Activity Reflecting Frequency-Based Segregation

To visualize neural activity reflecting increases in Δf, we subtracted mean ERPs corresponding to a single cycle of the ABA— triplet during the 0 semitone condition from mean ERPs during the 4, 7, and 12 semitone conditions, yielding 3 difference waves (4-0, 7-0, 12-0 semitones) for each of the 3 age groups (Fig. 5A). In all 3 age groups, Δf-related activity was characterized by P1, N1, and P2 waves at frontocentral sites (e.g., FCz). The P1, N1, and P2 waves were inverted in polarity at
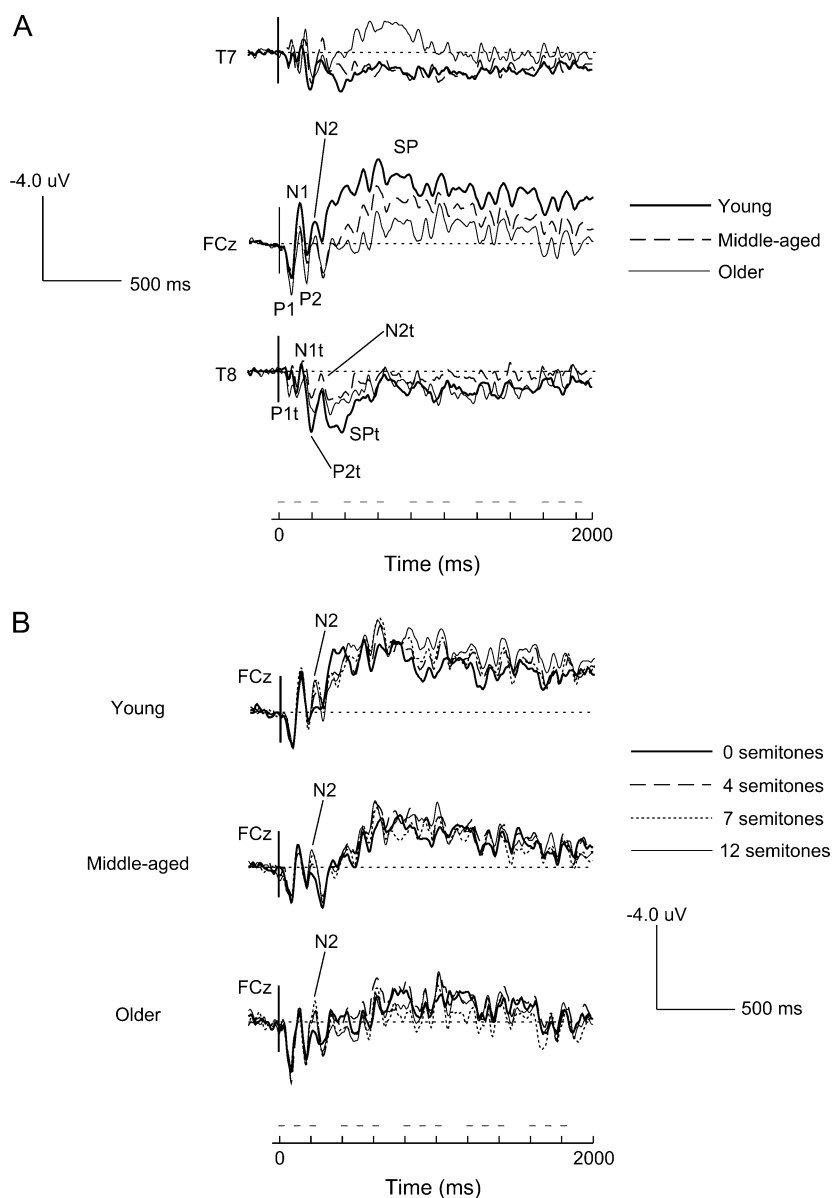
Figure 3. Group mean ERPs at the beginning of the trial. (*A*) ERP response to the first 2 s of each trial for young, middle-aged, and older participants collapsed across Δ*f* at the frontocentral midline (FCz) and left and right temporal (T7 and T8) electrodes. Horizontal bars above the timescale represent pure tones in the stimulus pattern. (*B*) Same as Figure 3*A* separately for the 4 Δ*f* levels from young, middle-aged, and older adults at FCz.

inferior temporal–occipital sites (Fig. 5*B*), consistent with a tangential source in the superior temporal plane. The amplitude of the P1 and N1 could not be quantified because these responses were partially contaminated by enhanced slow-wave activity in middle-aged and older adults. Hence, the effects of age on the Δ*f*-related activity at frontocentral sites were examined solely on the P2 amplitude. The ANOVA yielded a main effect of Δ*f* on the P2 mean amplitude (150–200 ms relative to the B tone onset), $F_{3,81} = 46.06$, $P < 0.001$ (see Fig. 6). Neither was the main effect of age significant nor was the interaction between age and Δ*f* significant, $F_{6,81} = 1.92$, NS, suggesting comparable sized Δ*f*-related increases in sensory-evoked responses in all 3 age groups.

These Δ*f*-related increases in sensory-evoked responses over the frontocentral scalp region were accompanied by an N1c component at right temporal sites, which also depended on Δ*f*

but occurred only in young adults (Fig. 5*A,B*). An ANOVA on the mean ERP amplitude (120–190 ms relative to the B tone onset) recorded over the left and right temporal cortex yielded a main effect of Δ*f*, $F_{3,81} = 5.41$, $P < 0.025$, a significant Δ*f* by age interaction, $F_{6,81} = 3.71$, $P < 0.025$, a significant hemisphere by Δ*f* interaction, $F_{3,81} = 12.69$, $P < 0.001$, and a significant hemisphere by Δ*f* by age interaction, $F_{6,81} = 5.47$, $P < 0.05$ (see Fig. 6). These results indicate that aging had a greater impact on neural activity recorded over the right than the left auditory cortex.

To test for relationships between the Δ*f*-related increase in P2 (at frontocentral sites) and N1c (at the right temporal electrode) and perception, we correlated mean amplitudes of these responses with the proportion of trials heard as streaming, for each participant. We then submitted these correlations to 2-tailed 1-sample *t*-tests, separately for each age group, to test for
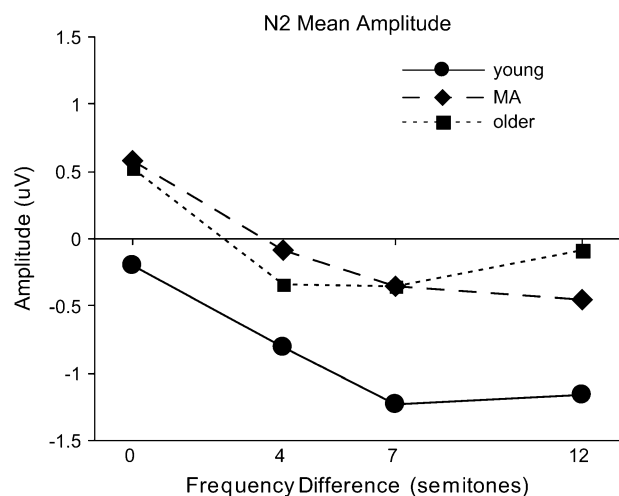
Figure 4. Average ERP amplitude as a function of Δf in the N2 time region (196–252 ms after the beginning of the trial) across 9 frontocentral sites for young, middle-aged, (MA) and older adults.

correlations significantly different than 0. The P2 amplitude correlated significantly with streaming judgments for all 3 age groups, $r_2 = 0.91, 0.81, 0.58, t_9 = 22.61, 5.59, 4.15, P < 0.005$. In contrast, the N1c amplitude correlated significantly with streaming judgments for young participants only, $r_2 = -0.83, t_9 = 6.74, P < 0.001$, with nonsignificant correlations for middle-aged and older adults, $r_2 = -0.40, -0.04, t_9 = 1.77, 0.18$, NS. This is consistent with the lack of robust N1c response in middle-aged and older adults.

Neural Activity Reflecting Buildup of Streaming

To visualize neural activity reflecting temporal buildup of stream segregation, we subtracted ERPs corresponding to an average of the first 5 ABA—triplets during the first 2 s of the trial (t1) from similar averages of 5 consecutive ABA—triplets during the 4 subsequent 2-s time bins (t2–t5). This yielded 4 difference waves (t2–t1, t3–t1, t4–t1, t5–t1) for each level of Δf for each participant. Previously, we found that activity at FCz and T8 (but not T7) increased as a function of time throughout the 10.8-s trial (Snyder and others 2006), possibly reflecting
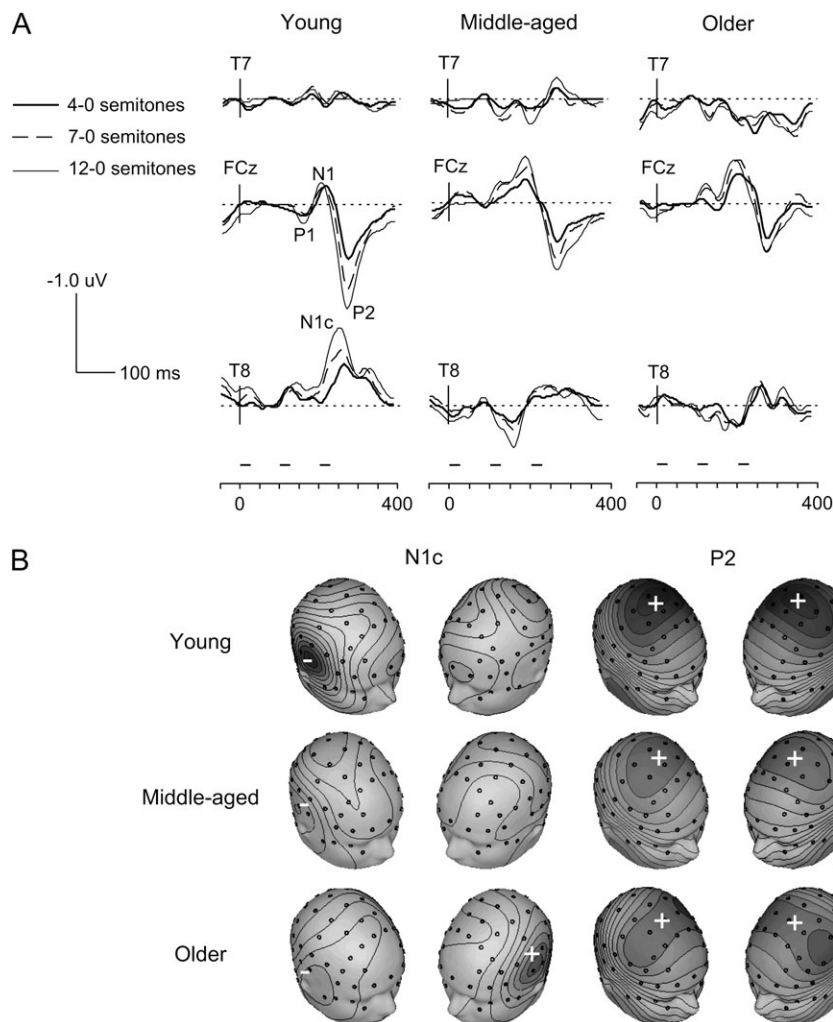

Figure 5. Difference waves between ERPs elicited by 0 semitone and those elicited by 4, 7, and 12 semitone Δf for young, middle-aged, and older adults, respectively. (A) Difference waves to the 0.4 s ABA—triplet averaged at T7 (left temporal), FCz (midline frontocentral), and T8 (right temporal) for the 3 age groups. Horizontal bars above the timescale represent pure tones in the stimulus pattern. (B) Scalp distribution of voltage of the difference waves during the N1c and P2 waves for the 3 age groups collapsed across the 3 levels of non-0 Δf. Darker regions indicate more activity, with polarity labeled by + and – signs. Isocontour lines represent 0.14 μV/step for P2 and 0.05 μV/step for N1c.

perceptual buildup of streaming (Bregman 1978; Anstis and Saida 1985). We therefore examined these electrodes again to test for effects of time and interactions between time and age group. Such interactions would indicate age-related changes in neural mechanisms for the temporal buildup of streaming.

As shown in Figure 7A,B, the activity in all 3 age groups at FCz indicated a slow positive wave whose amplitude increased as a function of time, $F_{4,81} = 35.06$, $P < 0.001$. The interaction between age and time was not significant, $F_{8,81} = 1.66$, NS, suggesting comparable buildup-related activity over the fronto-central scalp region (see Fig. 8). The interaction between time and Δf was not significant, $F_{8,81} = 1.63$, $P = 0.13$, although all 3 age groups showed a tendency to have less buildup for the 0 semitone condition.

As was the case for the Δf-related activity measured over the right temporal electrodes, the buildup-related activity measured over this region was observed only for young adults (Fig. 7A,B). This was confirmed by a main effect of time, $F_{4,81} = 16.96$, $P < 0.001$, a significant hemisphere by time interaction, $F_{4,81} = 3.93$, $P < 0.01$, and a significant hemisphere by time by age interaction, $F_{8,81} = 2.51$, $P < 0.05$ (Fig. 8). As with the Δf-related activity, these findings revealed age-related changes in brain responses over the right temporal cortex. There was an additional time by Δf interaction, $F_{12,324} = 2.85$, $P < 0.005$, due to a smaller effect of time when Δf was 0 semitones compared with when Δf was larger than 0 semitones.

Brain Electrical Source Analysis
We used BESA (5.0) to determine how well sources in auditory cortex (i.e., Heschl's gyrus) could account for effects of age on Δf-based segregation and buildup activity measured at the scalp. For the group averaged Δf- and buildup-related activity, we
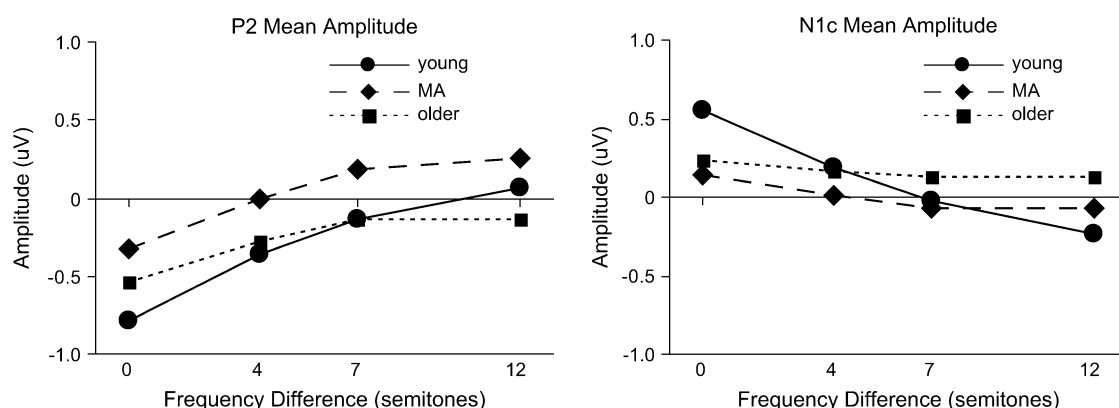

Figure 6. Average ERP amplitude as a function of Δf in the P2 time region (252–296 ms) across 9 frontocentral sites (left) and the N1c time region (224–292 ms) at T8 (right) for young, middle-aged (MA), and older adults.
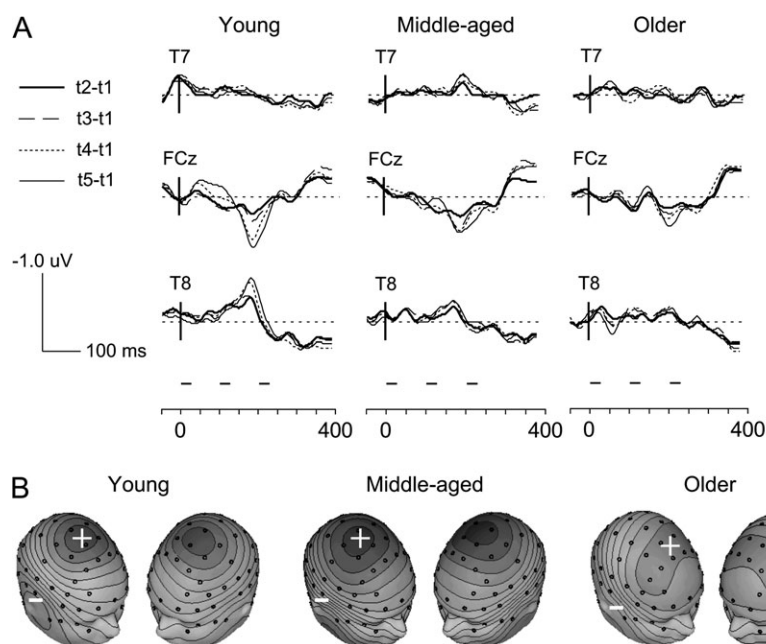

Figure 7. Difference waves between ERPs elicited by the first time bin ($t1$) and those elicited by the following time bins ($t2–t5$) for young, middle-aged, and older adults. (A) Difference waves to the 0.4 s ABA—triplet averaged at T7, FCz, and T8 for the 3 age groups. Horizontal bars above the timescale represent pure tones in the stimulus pattern. (B) Scalp distribution of voltage during the peak of the buildup difference waves, respectively, for the 3 age groups collapsed across the 4 time bins. Darker regions indicate more activity, with polarity labeled by + and − signs. Isocontour lines represent 0.07 μV/step.
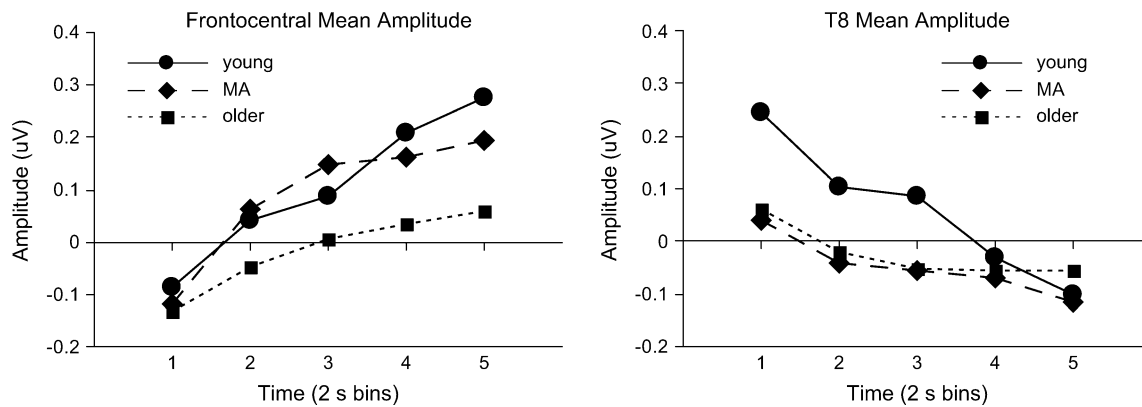
Figure 8. Average ERP amplitude as a function of time bin ($t1$–$t5$) from 160–232 ms across 9 frontocentral sites (left) and at T8 (right) for young, middle-aged (MA), and older adults.

modeled the difference waves at all electrodes collapsed across Δf and time bins, respectively. Collapsing across participants, Δf, and time bin served to enhance the signal-to-noise ratios of the modeled waveforms. The analysis assumed a 4-shell ellipsoidal head model with relative conductivities of 0.33, 0.33, 0.0042, and 1 for the head, scalp, bone, and cerebrospinal fluid, respectively, and sizes of 85 mm (radius), 6 mm (thickness), 7 mm (thickness), and 1 mm (thickness).

As an initial step, 2 symmetrical regional sources were placed at the Talairach coordinates of Heschl's gyrus in the right hemisphere (RH) and left hemisphere (LH) ($x = \pm 47$, $y = -26$, $z = 11$). Each source contained 3 orthogonal dipoles representing 3 directions of current flow in auditory cortex relative to the temporal scalp (tangential, radial, and anterior/posterior). Maintaining the locations and orthogonality of the 3 dipoles in each regional source, the dipoles were rotated such that the orientation of the first dipole was aligned with the maximum direction of activity. This optimization of the orientations was performed using the 140–400 ms interval in the Δf activity for the young adults because it contained the clearest examples of tangential and radial activity. The resulting model, shown in Figure 9A, was then used as a spatial filter to derive time courses of source activity in the 3 spatial orientations for Δf and buildup activity in each age group. The orientations of the dipoles are consistent with previous models of the auditory evoked response (Scherg and von Cramon 1985; Ponton and others 2002). It should be noted that we do not make any strong claims about the precise location or number of sources in auditory cortex. For example, it is likely that multiple source locations in auditory cortex contribute to the ERPs observed here (Yvert and others 2005), and there is evidence that activity in the parietal lobe might specifically contribute to perception of streaming (Cusack 2005).

Figure 9B shows the tangential, radial, and anterior/posterior source waveforms of Δf-related activity in the LH and RH for the young, middle-aged, and older adults. The model accounted for most of the neuroelectric scalp patterns in the 140–400 ms interval in all 3 age groups with residual variances of 3.58%, 5.43%, and 4.30% for young, middle-aged, and older adults, respectively. The bilateral tangential sources accounted for the P1–N1–P2 waves and reproduced the differences in morphologies between the 3 groups. In particular, there was a sustained negativity leading up to the N1 in middle-aged and older adults but not in young adults. The radial source in the RH accounted for the larger N1c response in young adults compared with

middle-aged and older adults, with little or no N1c appearing in the LH. Finally, the bilateral anterior/posterior sources contributed to the P1 wave in all 3 age groups, and the left anterior/posterior source contributed to the sustained negativity leading up to the N1 in middle-aged and older adults.

Figure 10 shows the 3 source waveforms of buildup-related activity in both hemispheres for the 3 age groups. The dipole model accounted for most of the neuroelectric scalp patterns in the 160–232 ms interval in all 3 age groups with residual variances of 7.01%, 4.59%, and 4.86% for young, middle-aged, and older adults, respectively. The bilateral tangential sources accounted for most of the buildup-related activity and showed similar sized responses across the 3 age groups. The radial source in the RH showed age effects with larger amplitude in young adults compared with middle-aged and older adults, but little or no activity in the LH. Finally, the anterior/posterior sources did not show much recognizable activity related to scalp-recorded waveforms. Thus, the source analysis of Δf- and buildup-related activity is consistent with the interpretation that auditory cortical areas contributing to stream segregation with radial orientations are more affected by age than areas with tangential orientations.

Discussion

Young, middle-aged, and older adults showed similar perception of streaming, as measured using self-reported judgments made at the end of 10.8-s trials. This lack of age-related change in sequential sound segregation is consistent with previous behavioral studies using objective measures of stream segregation such as temporal order judgments (Trainor and Trehub 1989) and response time to infrequent targets (Alain and others 1996). It is unlikely that the absence of an age effect on perception in the current study was due to lack of power because there was no trend in the expected direction. These data, therefore, provide support for a relative sparing of sequential sound segregation, suggesting that age-related impairments in speech comprehension related to deficits in auditory scene analysis (Alain and others 2006) are more likely explained by difficulties with concurrent sound segregation (Alain and others 2001; Grube and others 2003; Snyder and Alain 2005).

In all 3 age groups, the perception of stream segregation was paralleled by enhanced ERP amplitude over the frontocentral scalp region. More importantly, Δf- and buildup-related
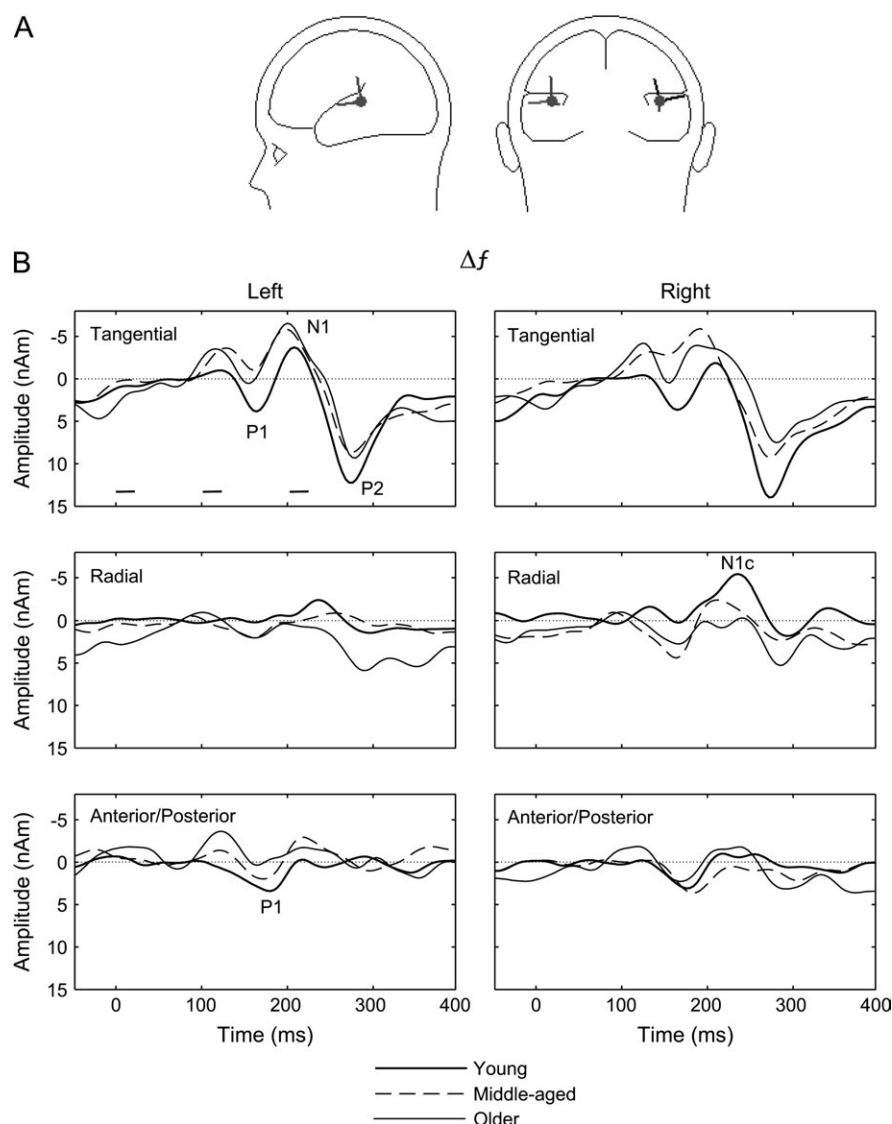
Figure 9. BESA. (*A*) Left and back views of the head showing symmetrical source locations in Heschl's gyrus containing orthogonal dipoles with tangential, radial, and anterior/posterior orientations relative to the temporal portion of the scalp. This dipole model was used as a spatial filter for the Δf- and buildup-related activity in young, middle-aged, and older adults. (*B*) Source amplitude time courses of the tangential (top), radial (middle), and anterior/posterior (bottom) dipoles for Δf-related activity (12–0 semitone difference wave) in the LH (left) and RH (right) for young, middle-aged, and older adults. Horizontal bars above the timescale in the left tangential panel represent pure tones in the stimulus pattern.

activities were present to the same extent in all 3 age groups. This result extends previous findings in young adults (Snyder and others 2006) to middle-aged and older adults and provides convergent evidence that sequential auditory scene analysis is preserved in normal aging adults. At right temporal sites, substantial changes were found for neuroelectric correlates of Δf and buildup in middle-aged and older adults. In young adults, symmetrical regional sources accounting for 3 dimensions of current flow in auditory cortex provided a good model for the activity observed across the array of scalp electrodes. The residual variances for this model were also low for the middle-aged and older adults suggesting a good fit of the scalp-recorded data. More importantly, the scalp-recorded data of middle-aged and older adults were best represented by dipoles with tangential and anterior/posterior orientation, whereas brain responses represented along the radial components over the right temporal cortex showed a marked age-related decrement

in amplitude. This age-related difference in the neural generators of the Δf- and buildup-related activity may be indicative of physiological or structural changes in the brain that occur with normal aging.

In addition to changes at right temporal sites, sustained activity during the first 5 repetitions of the ABA—triplets at the beginning of each trial showed dramatic age-related decrements. A similar age-related decrement was previously found in sustained activity that occurred for the duration of long sounds (Chao and Knight 1997) and for slow-wave activity in auditory oddball paradigms (Pfefferbaum and others 1980; Iragui and others 1993). Recent evidence suggests that activity lasting throughout the duration of a sound pattern arises from different auditory cortical areas (Seifritz and others 2002) and may indicate responses to preferred stimuli than more transient activity that occurs only at the onset of sounds (Wang and others 2005). Thus, it is possible that older adults have a deficit
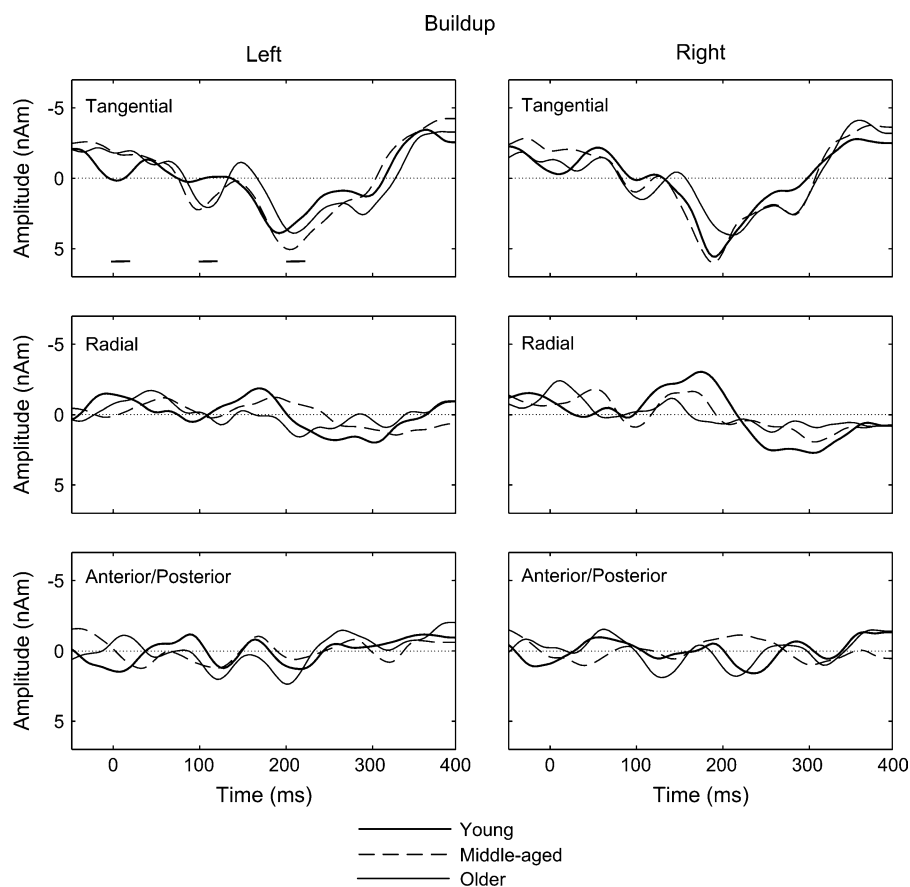
Figure 10. Same as Figure 9*B* but for buildup-related activity (*t*5–*t*1 difference wave).

in neural populations that are active throughout the duration of a stimulus pattern. It is also possible that deficits in higher-level functions such as sustained attention could account for the smaller activity observed in the present study and in previous studies.

The current study showed no age-related changes in stream segregation. This finding suggests that previous reports of impairment in stream segregation among older adults with supraclinical levels of hearing impairment were due to their abnormal audiometric status rather than their age (Rose and Moore 1997; Mackersie and others 2001). However, this conclusion conflicts with one study in which both normal-hearing and hearing-impaired older adults showed less streaming than young adults for resolved harmonic complexes (Grimault and others 2001). This discrepancy with the current results could be explained by the use of different types of stimuli, a possibility that should be tested in future studies. The lack of a genuine age effect on perception of streaming in the current study suggests that sequential sound segregation is spared in normally aging adults with good hearing, in contrast to concurrent sound segregation in which older adults show substantial impairments compared with young adults (Alain and others 2001; Grube and others 2003; Snyder and Alain 2005). The apparent dissociation between the effects of age on concurrent and sequential sound segregation might be attributable to the presence of different neural mechanisms for these 2 types of sound segregation, a possibility that should be addressed further in future studies.

In the present study, we modeled the Δf- and buildup-related activity with sources in the superior temporal plane. In agreement with animal studies (e.g., Fishman and others 2001; Kanwal and others 2003; Bee and Klump 2004; Micheyl and others 2005), our results suggest that processes involved in auditory stream segregation are located in auditory cortex. Interestingly, our model adequately accounted for the ERP response to ABA—triplets in the 3 age groups. In particular, the observed age difference over the right temporal lobe could be accounted for by changes in a generator on the right superior temporal plane with radial orientation to the temporal scalp.

The N1c response that increased as a function of Δf in young adults has a large dependence on musical experience (Shahin and others 2003) and frequency discrimination training (Bosnyak and others 2004). This suggests the N1c as being particularly important for processing frequency content, which is consistent with the proposal that right auditory cortex is specialized for spectral representation (Zatorre and others 2002). It is therefore possible that age-related neural changes in these sources could have important consequences for other types of processes that rely on detecting frequency change such as melody perception (Lynch and Steffens 1994; Andrews and others 1998). The effects of aging on activity from radial sources could also reflect an age-related change in attention-dependent auditory processing (e.g., Bennett and others 2004). This appears unlikely, however, because the Δf- and buildup-related activity were similarly affected by aging in the current study despite the fact that the buildup-related activity was more

dependent on attention than the Δf-related activity in our previous study (Snyder and others 2006).

Although the effects of age on radial activity appeared to be uncoupled to perception of streaming in middle-aged and older adults, it is unclear whether or not the neural generator of this source contributes to perception of streaming in young adults in whom it was strongly expressed and correlated significantly with perception. One possibility is that in young adults there are multiple representations of Δf-based segregation, some with tangential and some with radial orientations. It is possible that in middle-aged and older adults some of these representations may begin to undergo age-related degradation, but there is enough redundancy in the auditory cortex to support robust coding of frequency. It is also possible that such age-related changes in auditory cortex might cause functional reorganization of neural networks involved in auditory perception (e.g., Cabeza and others 2002; Della-Maggiore and others 2002; Grady and others 2003), enabling comparable levels of stream segregation in middle-aged and older adults as compared with young adults. A final possibility is that the brain areas generating the radial sources in young adults exhibit a rotation in orientation due to structural changes in the temporal lobe without any substantial change in neurophysiology. Such a change in source orientation in middle-aged and older adults could result in the inability to detect the N1c at the scalp.

Given the lack of detailed information about anatomical changes in auditory cortex during normal aging, it is currently difficult to distinguish between structural and physiological explanations of age-related changes in scalp-recorded ERPs. Morphological studies have shown volume loss associated with a reduction in cell size in many auditory relays, auditory cortices, and posterior association cortices, for example, Wernickes' area (Olso and others 1985). Autopsy studies and structural magnetic resonance imaging studies show that the loss of axonal fibers and a decrease in the size of neuron somas contribute to a global reduction in the brain's volume with increasing age (Terry and others 1987). The thinning of gray matter is also characteristic of cortical degeneration in the elderly, although this occurs less in the temporal lobes than in other areas (Sowell and others 2003; Salat and others 2004). In the future, more detailed analyses of auditory cortical anatomy should be performed to identify different patterns of aging that are specific to individual areas within auditory cortex. Additionally, the effects of aging on auditory perception, anatomy, and physiology should be performed in the same participants to better determine function–structure–process relationships.

If the lack of radial activity in middle-aged and older adults related to Δf and buildup processes indicates a physiological impairment rather than an anatomical change in source orientation, it would be important to understand whether the deficits are specific to the streaming paradigm or whether they indicate a more general impairment of radial generators in auditory cortex. The lack of age-related decrement in response amplitude for early transient responses at the onset of the trials (P1t, N1t) at temporal electrodes argues against a general decline in radial sources of auditory cortex. An age-related impairment appeared, however, as early as 200 ms following the start of the trial with responses that were likely time locked to the second (B) tone of the trial (P2t, SPt). It is therefore possible that the impaired radial activity could be specific to tasks that require processing of sequences (i.e., at least 2 successive sound events), which has been shown to be impaired in older adults

(Trainor and Trehub 1989; Lynch and Steffens 1994; Andrews and others 1998).

Concluding Remarks

Despite the fact that aging has profoundly detrimental influences on many aspects of hearing (Committee on Hearing, Bioacoustics, and Biomechanics 1988; Humes 1996; Schneider and others 2002), we found that the ability to sequentially organize acoustic patterns into distinct perceptual streams is spared in middle-aged and older adults compared with young adults. No age-related change was found in the perception of auditory streaming, and ERP correlates of streaming at fronto-central electrodes were similar across the 3 age groups tested. Age-related decrements were found in streaming-related brain activity at right temporal electrodes and in sustained activity at frontocentral electrodes occurring during the first seconds of the sound patterns. Further research is needed to assess whether stream segregation based on other acoustic cues (e.g., location, timbre, etc.) is also preserved in older adults and to what extent the observed age-related ERP changes are related to streaming versus other aspects of auditory processing.

References

Alain C, Dyson BJ, Snyder JS. 2006. Aging and the perceptual organization of sounds: a change of scene? In: Conn PM, editor. Handbook of models for human aging. Oxford Elsevier, UK: p 759-770.

Alain C, Izenberg A. 2003. Effects of attentional load on auditory scene analysis. J Cogn Neurosci 15:1063–1073.

Alain C, McDonald KL, Ostroff JM, Schneider B. 2001. Age-related changes in detecting a mistuned harmonic. J Acoust Soc Am 109:2211–2216.

Alain C, Ogawa KH, Woods DL. 1996. Aging and the segregation of auditory stimulus sequences. J Gerontol Ser B Psychol Sci Soc Sci 51:P91–P93.

Andrews MW, Dowling WJ, Halpern AR, Bartlett JC. 1998. Identification of speeded and slowed familiar melodies by younger, middle-aged, and older musicians and nonmusicians. Psychol Aging 13:462–471.

Anstis S, Saida S. 1985. Adaptation to auditory streaming of frequency-modulated tones. J Exp Psychol Hum Percept Perform 11:257–271.

Bee MA, Klump GM. 2004. Primitive auditory stream segregation: a neurophysiological study in the songbird forebrain. J Neurophysiol 92:1088–1104.

Bennett IJ, Golob EJ, Starr A. 2004. Age-related differences in auditory event-related potentials during a cued attention task. Clin Neurophysiol 115:2602–2615.

Berg P, Scherg M. 1994. A multiple source approach to the correction of eye artifacts. Electroencephalogr Clin Neurophysiol 90:229-241.

Bosnyak DJ, Eaton RA, Roberts LE. 2004. Distributed auditory cortical representations are modified when non-musicians are trained at pitch discrimination with 40 Hz amplitude modulated tones. Cereb Cortex 14:1088–1099.

Bregman AS. 1978. Auditory streaming is cumulative. J Exp Psychol Hum Percept Perform 4:380–387.

Bregman AS. 1990. Auditory scene analysis: the perceptual organization of sound. Cambridge, MA: MIT Press.

Butler RA. 1968. Effect of changes in stimulus frequency and intensity on habituation of human vertex potential. J Acoust Soc Am 44:945-950.

Cabeza R, Anderson ND, Locantore JK, McIntosh AR. 2002. Aging gracefully: compensatory brain activity in high-performing older adults. Neuroimage 17:1394-1402.

Carlyon RP, Cusack R, Foxton JM, Robertson IH. 2001. Effects of attention and unilateral neglect on auditory stream segregation. J Exp Psychol Hum Percept Perform 27:115-127.

Chao LL, Knight RT. 1997. Prefrontal deficits in attention and inhibitory control with aging. Cereb Cortex 7:63-69.

Committee on Hearing, Bioacoustics, and Biomechanics. 1988. Speech understanding and aging. J Acoust Soc Am 83:859-895.

Cusack R. 2005. The intraparietal sulcus and perceptual organization. J Cogn Neurosci 17:641-651.

Della-Maggiore V, Grady CL, McIntosh AR. 2002. Dissecting the effect of aging on the neural substrates of memory: deterioration, preservation or functional reorganization? Rev Neurosci 13:167-181.

Fishman YI, Reser DH, Arezzo JC, Steinschneider M. 2001. Neural correlates of auditory stream segregation in primary auditory cortex of the awake monkey. Hear Res 151:167-187.

Grady CL, McIntosh AR, Beig S, Keightley ML, Burian H, Black SE. 2003. Evidence from functional neuroimaging of a compensatory prefrontal network in Alzheimer's disease. J Neurosci 23:986-993.

Grimault N, Micheyl C, Carlyon RP, Arthaud P, Collet L. 2001. Perceptual auditory stream segregation of sequences of complex sounds in subjects with normal and impaired hearing. Br J Audiol 35:173-182.

Grube M, von Cramon DY, Rubsamen R. 2003. Inharmonicity detection: effects of age and contralateral distractor sounds. Exp Brain Res 153:637-642.

Gutschalk A, Micheyl C, Melcher JR, Rupp A, Scherg M, Oxenham AJ. 2005. Neuromagnetic correlates of streaming in human auditory cortex. J Neurosci 25:5382-5388.

Humes LE. 1996. Speech understanding in the elderly. J Am Acad Audiol 7:161-167.

Hung J, Jones SJ, Vaz Pato M. 2001. Scalp potentials to pitch change in rapid tone sequences: a correlate of sequential stream segregation. Exp Brain Res 140:56-65.

Iragui VJ, Kutas M, Mitchiner MR, Hillyard SA. 1993. Effects of aging on event-related brain potentials and reaction times in an auditory oddball task. Psychophysiology 30:10-22.

Jones SJ, Longe O, Vaz Pato M. 1998. Auditory evoked potentials to abrupt pitch and timbre change of complex tones: electrophysiological evidence of 'streaming'? Electroencephalogr Clin Neurophysiol 108:131-142.

Kaas JH, Hackett TA. 2000. Subdivisions of auditory cortex and processing streams in primates. Proc Natl Acad Sci USA 97:11793-11799.

Kanwal JS, Medvedev AV, Micheyl C. 2003. Neurodynamics for auditory stream segregation: tracking sounds in the mustached bat's natural environment. Netw Comput Neural Syst 14:413-435.

Lynch MP, Steffens ML. 1994. Effects of aging on processing of novel musical structure. J Gerontol 49:P165-P172.

Mackersie CL, Prida TL, Stiles D. 2001. The role of sequential stream segregation and frequency selectivity in the perception of simultaneous sentences by listeners with sensorineural hearing loss. J Speech Lang Hear Res 44:19-28.

Micheyl C, Tian B, Carlyon RP, Rauschecker JP. 2005. Perceptual organization of tone sequences in the auditory cortex of awake macaques. Neuron 48:139-148.

Moore BCJ, Gockel H. 2002. Factors influencing sequential stream segregation. Acta Acustica United Acustica 88:320-333.

Näätänen R, Sams M, Alho K, Paavilainen P, Reinikainen K, Sokolov EN. 1988. Frequency and location specificity of the human vertex N1 wave. Electroencephalogr Clin Neurophysiol 69:523-531.

Olso LW, Harkins SW, Lenhardt ML. 1985. Aging and the auditory system. In: Birren JE, Schaie KW, editors. Handbook of the psychology of aging. New York: Van Nostrand Reinhold Company. p 332-377.

Pfefferbaum A, Ford JM, Roth WT, Kopell BS. 1980. Age-related changes in auditory event-related potentials. Electroencephalogr Clin Neurophysiol 49:266-276.

Picton TW, Campbell KB, Baribeau-Brown J, Proulx GB. 1978. The neurophysiology of human attention: a tutorial review. In: Requin J, editor. Attention and performance VII. Hillsdale, NJ: Lawrence Erlbaum. p 429-467

Picton TW, van Roon P, Armilio ML, Berg P, Ille N, Scherg M. 2000. The correction of ocular artifacts: a topographic perspective. Clin Neurophysiol 111:53-65.

Ponton C, Eggermont JJ, Khosla D, Kwong B, Don M. 2002. Maturation of human central auditory system activity: separating auditory evoked potentials by dipole source modeling. Clin Neurophysiol 113:407-420.

Roberts B, Moore BC. 1990. The influence of extraneous sounds on the perceptual estimation of first-formant frequency in vowels. J Acoust Soc Am 88:2571-2583.

Rose MM, Moore BCJ. 1997. Perceptual grouping of tone sequences by normally hearing and hearing-impaired listeners. J Acoust Soc Am 102:1768-1778.

Salat DH, Buckner RL, Snyder AZ, Greve DN, Desikan RS, Busa E, Morris JC, Dale AM, Fischl B. 2004. Thinning of the cerebral cortex in aging. Cereb Cortex 14:721-730.

Scherg M, von Cramon D. 1985. Two bilateral sources of the late AEP as identified by a spatio-temporal dipole model. Electroencephalogr Clin Neurophysiol 62:32-44.

Schneider BA, Daneman M, Pichora-Fuller MK. 2002. Listening in aging adults: from discourse comprehension to psychoacoustics. Can J Exp Psychol 56:139-152.

Seifritz E, Esposito F, Hennel F, Mustovic H, Neuhoff JG, Bilecen D, Tedeschi G, Scheffler K, Di Salle F. 2002. Spatiotemporal pattern of neural processing in the human auditory cortex. Science 297:1706-1708.

Shahin A, Bosnyak DJ, Trainor LJ, Roberts LE. 2003. Enhancement of neuroplastic P2 and N1c auditory evoked potentials in musicians. J Neurosci 23:5545-5552.

Snyder JS, Alain C. 2005. Age-related changes in segregating concurrent vowels: neural evidence for impairment and compensation. Brain Res Cogn Brain Res 24:492-499.

Snyder JS, Alain C, Picton TW. 2006. Effects of attention on neuroelectric correlates of auditory stream segregation. J Cogn Neurosci 18:1-13.

Sowell ER, Peterson BS, Thompson PM, Welcome SE, Henkenius AL, Toga AW. 2003. Mapping cortical change across the human life span. Nat Neurosci 6:309-315.

Stainsby TH, Moore BCJ, Glasberg BR. 2004. Auditory streaming based on temporal structure in hearing-impaired listeners. Hear Res 192:119-130.

Terry RD, DeTeresa R, Hansen LA. 1987. Neocortical cell counts in normal human adult aging. Ann Neurol 21:530-539.

Trainor LJ, Trehub SE. 1989. Aging and auditory temporal sequencing: ordering the elements of repeating tone patterns. Percept Psychophys 45:417-426.

van Noorden LPAS. 1975. Temporal coherence in the perception of tone sequences. Eindhoven: Eindhoven University of Technology.

Wang X, Lu T, Snider RK, Liang L. 2005. Sustained firing in auditory cortex evoked by preferred stimuli. Nature 435:341-346.

Wolpaw JR, Penry JK. 1975. A temporal component of the auditory evoked response. Electroencephalogr Clin Neurophysiol 39:609-620.

Yvert B, Fischer C, Bertrand O, Pernier J. 2005. Localization of human supratemporal auditory areas from intracerebral auditory evoked potentials using distributed source models. Neuroimage 28:140-153.

Zatorre RJ, Belin P, Penhune VB. 2002. Structure and function of auditory cortex: music and speech. Trends Cogn Sci 6:37-46.