



Published in final edited form as:

Ear Hear. 2012 May ; 33(3): 330–339. doi:10.1097/AUD.0b013e31823fb585.

Human Evoked Cortical Activity to Silent Gaps in Noise: Effects of Age, Attention, and Cortical Processing Speed

Kelly C. Harris, Ph.D., Sara Wilson, B.S., Mark A. Eckert, Ph.D., and Judy R. Dubno, Ph.D.
Department of Otolaryngology- Head & Neck Surgery, Medical University of South Carolina

Abstract

Objectives—The goal of this study was to examine the degree to which age-related differences in early or automatic levels of auditory processing and attention-related processes explain age-related differences in auditory temporal processing. We hypothesized that age-related differences in attention and cognition compound age-related differences at automatic levels of processing, contributing to the robust age effects observed during challenging listening tasks.

Design—We examined age-related and individual differences in cortical event-related potential (ERP) amplitudes and latencies, processing speed, and gap detection from twenty-five younger and twenty-five older adults with normal hearing. ERPs were elicited by brief silent periods (gaps) in an otherwise continuous broadband noise and were measured under two listening conditions, passive and active. During passive listening, participants ignored the stimulus and read quietly. During active listening, participants button pressed each time they detected a gap. Gap detection (percent detected) was calculated for each gap duration during active listening (3, 6, 9, 12 and 15 ms). Processing speed was assessed using the Purdue Pegboard test and the Connections Test. Repeated measures ANOVAs assessed effects of age on gap detection, processing speed, and ERP amplitudes and latencies. An “attention modulation” construct was created using linear regression to examine the effects of attention while controlling for age-related differences in auditory processing. Pearson correlation analyses assessed the extent to which attention modulation, ERPs, and processing speed predicted behavioral gap detection. Results: Older adults had significantly poorer gap detection and slower processing speed than younger adults. Even after adjusting for poorer gap detection, the neurophysiological response to gap onset was atypical in older adults with reduced P2 amplitudes and virtually absent N2 responses. Moreover, individual differences in attention modulation of P2 response latencies and N2 amplitudes predicted gap detection and processing speed in older adults. That is, older adults with P2 latencies that decreased and N2 amplitudes that increased with active listening had faster processing speed and better gap detection than those older adults whose P2 latencies increased and N2 amplitudes decreased with attention

Conclusions—Results from the current study are broadly consistent with previous findings that older adults exhibit significantly poorer gap detection than younger adults in challenging tasks. Even after adjusting for poorer gap detection, older and younger adults showed robust differences in their electrophysiological responses to sound offset. Furthermore, the degree to which attention modulated the ERP was associated with individual variation in measures of processing speed and gap detection. Taken together, these results suggests an age-related deficit in early or automatic levels of auditory temporal processing and that some older adults may be less able to compensate for declines in processing by attending to the stimulus. These results extend our previous findings and support the hypothesis that age-related differences in cognitive or attention-related processing, including processing speed, contribute to an age-related decrease in gap detection.

1. Introduction

Processing information in a timely manner is essential for communication. Age-related slowing is well documented across both cognitive and sensory domains (e.g., Cerella 1985;

Craik 1990; Salthouse et al. 2003) and has led to the hypothesis that age-related slowing of information processing is the result of a global dysfunction in the aging brain. When assessed in the same population, perceptual and psychomotor speed has been shown to share a common variance, supporting the notion of a general slowing of perceptual, motor, attentional, and cognitive processes (Cerella 1985; Craik 1990; Salthouse and Ferrer-Caja 2003). Age-related slowing of processing speed has been defined as a reduction in the speed with which cognitive operations can be executed and is measured using speeded tests of attention, sequencing, mental flexibility, visual search, and motor function (Salthouse et al., 2003). Moreover, age-related differences in processing speed, have been associated with age-related differences in auditory temporal processing (Harris et al., 2010). However, age-related differences in gap detection are often attributed to changes in earlier or automatic levels of processing. Indeed, Humes et al. (2009) found limited associations in older adults between measures of cognitive function and auditory temporal processing. The goal of the current study was to examine the degree to which age-related differences in early or automatic levels of auditory processing and attention-related processes explain age-related differences in auditory temporal processing. Understanding how aging affects the interaction between automatic and attention-related processing will provide better explanations of the extent to which older adults are able to compensate for processing declines.

Event-related potentials (ERPs) provide a powerful tool for examining the effects of age and attention on auditory temporal processing because they can be used to compare responses to the same stimuli when they are ignored (passive) or attended to (active). ERPs may also identify cortical levels at which differences in neuronal activity relate to age-related differences in auditory temporal processing. To date, most studies using ERPs to examine temporal processing and aging have focused on ERPs from the brainstem or cortex during passive listening (e.g, Humes 2005; Poth et al. 2001; Tremblay et al. 2004; Tremblay et al. 2002) and support the hypothesis that the perceptual difficulties of older adults may be attributed to age-related differences in early or automatic levels of processing of temporal information. Additional detrimental or compensatory effects of processing speed and attention on auditory temporal processing in older adults remain unknown.

The most consistent and robust effects of age on temporal processing are revealed when using complex tasks or stimuli. For example, robust age-related differences in gap detection are observed when the markers surrounding a silent gap are shorter than 10 ms (Schneider et al. 1999) and when the location of the gap falls near the onset or offset of the stimuli or is varied randomly (He et al. 1999). These results suggest that age-related differences in temporal processing may be more dependent on cognitive or attention-related factors than previously thought (He et al. 1999; Lister et al. 2002; Lister et al. 2005; Pichora-Fuller et al. 2006). Moreover, with relatively simple tasks, older adults may compensate for declines in early stages of auditory processing by exerting increased cognitive control or attention (Alain et al. 2004; Bertoli et al. 2001). Consistent with this hypothesis, Alain et al.(2004) observed age-related differences in ERP amplitudes during passive listening in a simple gap detection task, but not with active listening, which may reflect a decline in automatic processing of temporally modulated stimuli that can be compensated by attentional processes.

When faced with challenging listening tasks, older adults may be less able to compensate for age-related differences in auditory processing. Indeed, age-related declines in processing speed and attention may exaggerate deficits seen at automatic levels of processing. In support of this cognitive-driven hypothesis, Harris et al. (2010) reported that age-related differences in complex measures of gap detection were related to age-related differences in processing speed and attention and that older adults reported increased effort. These findings

are consistent with a large literature on age-related cognitive and neurobiologic changes in attention-related systems (e.g. Eckert 2011).

In the current study, we examined age-related differences in and associations among gap detection, processing speed, and cortical ERP latencies and amplitudes elicited by gaps in a continuous noise under passive and active listening. We hypothesized that age-related differences in attention and cognition compound age-related differences at automatic levels of processing, contributing to the robust age effects observed during challenging listening tasks. Consistent with our hypothesis, we predicted that (1) older adults would require longer gaps than younger adults to detect a gap and elicit an ERP, (2) age-related differences in ERP response latencies and amplitudes would occur during passive and active listening, and (3) older adults with slower processing speed would be less able to compensate for changes at automatic levels of processing by exerting increased attention.

2. Methods and Materials

2.1 Participants

Participants included two groups of adults: younger [n=25; mean age=24.19 (3.42) years; 17 females] and older [n=25; mean age=69.82 (7.11) years; 17 females]. All participants were right-handed monolingual native speakers of American English. Each participant completed the Mini Mental State Examination (Folstein et al. 1983) with three or fewer errors, indicating little or no cognitive impairment (as reviewed in Tombaugh et al. 1992). Pure-tone thresholds at conventional frequencies were measured with a Madsen OB922 clinical audiometer, calibrated to appropriate ANSI standards (ANSI 2004) and equipped with TDH-39 headphones. All participants had normal hearing (defined as thresholds ≤ 25 dB HL at 250, 500, 1000, 2000, 3000 and 4000 Hz); differences in thresholds between right and left ears did not exceed 15 dB at each frequency. Mean pure-tone audiometric thresholds for the test ear (right ear) (± 1 S.E.M.) are shown in Figure 1. Thresholds for younger and older subjects were significantly different at 3000, 4000, and 8000 Hz. Individual differences in pure-tone thresholds at each frequency were used to assess associations between tonal detection, gap detection, processing speed, and ERP latencies and amplitudes. Participants provided written informed consent before participating in this MUSC Institutional Review Board approved study.

2.2 Paradigm

The duration and type of leading and lagging markers in gap stimuli may affect the magnitude of age-related differences in gap detection. Gap detection is typically measured using short durations of noise or tones separated by a very short silent gap. With these stimuli, an ERP is generated in response to the onset of the leading marker and the onset of the gap. The response to the marker onset can overlap with the response to the gap onset, making it difficult to assess the response to the gap alone. Possible solutions are to: (1) compute difference waves, where the ERP to the stimulus with a gap is subtracted from the response to a similar stimulus without a gap, or (2) increase the duration of the leading marker to separate in time the response to marker onset from the response to the gap onset. To further reduce the effect of the response to the marker onset, we used a continuous noise that was interrupted every ~ 2 seconds (Figure 2); the responses to the onset of each gap are averaged (Michalewski et al. 2005; Pratt et al. 2005). The potentials generated by the gap onset differ in their morphology and neural generators from those to the marker onset (Michalewski et al. 2005; Pratt et al. 2005) and the effects of age are unknown. The current study examined age-related differences in ERPs to gap onset.

2.3 Stimuli

A broadband noise, low-pass filtered at 5 kHz, was presented continuously, with silent gaps of 3, 6, 9, 12, or 15 ms distributed every 2 to 2.2 s (Figure 2). Each gap duration was presented sequentially 250 times, followed by the next gap duration. The order of presentation was randomized across listening conditions and participants. Stimuli were digitally created using Tucker Davis Technologies (TDT) system 3 hardware. Stimuli were attenuated (TDT PA4), passed through a headphone buffer (TDT HB5), presented monaurally to the right ear through a TDH-39 headphone at an overall level of 80 dB SPL. Stimuli were monitored by oscilloscope at the input to the earphone and acoustically calibrated with the earphone placed in a NBS-9A coupler using a Larson-Davis Model 800B sound level meter equipped with a 1 in pressure microphone (Model 2575).

2.4 Data Acquisition and Analysis

Participants were seated in a comfortable reclining chair in a sound-treated room. During passive listening, participants were instructed to ignore the stimulus and read quietly. During active listening, participants were instructed to button press each time they detected a gap. The passive and active listening experiments were conducted during the same test session. Active listening followed passive listening after a short break to reduce the effects of attention during passive listening. Electrode impedances were examined prior to the start of each phase of data collection.

Percent detected and reaction time (RT) was measured during active listening. To quantify gap detection, percent detected was calculated for each gap duration (3, 6, 9, 12 and 15 ms). Percent detected was defined as the percentage of correct detections of gaps divided by the total number of gaps presented (Pratt et al. 2005). RT was calculated as the time post gap onset to button press. Behavioral responses that occurred less than 75 ms or more than 1500 ms after stimulus presentation were excluded. The intraindividual coefficient of variation (ICV) was calculated by dividing the SD across trials by the mean RT across trials for each participant to adjust for the relationship between intraindividual variability and mean RT (Stuss, et al., 2003).

Electrophysiological (EEG) signals were recorded with a 64-channel Neuroscan Quickcap™ based on the international 10-20 system and connected to a SynAmpsRT [A/D rate=1000 Hz, bandpass filtered 0.1 Hz to 200 Hz]. Bipolar electrodes were placed on the skin above and below the left eye for recording vertical electro-oculogram (VEOG) activity. SCAN version 4.4 acquisition software was used to record and analyze the EEG signal. Offline, raw EEG recordings were subjected to an automatic artifact rejection algorithm. Trials contaminated by excessive peak-to-peak deflections ($\pm 150 \mu\text{V}$) at the channels not adjacent to the eyes were automatically rejected. For each individual, ocular artifacts were corrected by means of ocular source components (Berg et al. 1994; Picton et al. 2000). Individual trials were then segmented into epochs surrounding the onset of the gap (-100 ms to 1000 ms). Epochs were baseline corrected and band-pass filtered from 1 to 30 Hz. For each subject, average waveforms (ERPs) were computed relative to gap onset for each gap duration. Group average waveforms were computed for both passive and active listening for younger and older subjects.

The effects of age and attention were examined in a cluster of electrodes where the ERP showed maximal activity (Fz, FCz, Cz, FC1, FC2) (e.g. Alain et al., 2004). Scalp topography maps for time periods surrounding peaks of interest are provided in Figure 4. As described in previous studies using a similar continuous noise paradigm, P1 is greatly reduced or absent in response to the gap onset (Michalewski et al. 2005; Pratt et al. 2005). Accordingly, P1 will not be discussed further. The mean global field power (mGFP) has a

local maximum when the amplitude difference between electrodes is strongest; its maxima reflect components, such as N1, P2, and N2, in the ERP (Lehmann et al. 1980) and were used to determine peak latency windows for identification of N1, P2, and N2. Response windows were consistent with previously reported literature (e.g. Harkrider et al., 2006; Tremblay et al., 2004). N1 was described as the largest negativity occurring between 90 and 150 ms at frontocentral electrodes (Fz, FCz, Cz, FC1, FC2). P2 was defined as the largest positivity following N1 occurring between 130 and 220 ms. Visual inspection of the group average and individual waveforms showed that N2 was well-defined in younger adults but was absent, or was a broad negativity, in many older adults. Therefore, mean N2 amplitude was calculated as the largest mean amplitude from amplitudes within the 240-340 ms latency range in younger adults and within 260-360 ms in older adults at frontocentral electrodes (Fz, FCz, Cz, FC1, FC2). Latency windows were determined by inspection of peak latencies in group and individual waveforms and were defined later in older adults to avoid P2 amplitudes in the calculation of N2. These methods are consistent with previous literature examining N2 in younger and older adults (Bertoli et al. 2005). While this technique may provide an accurate estimate of mean N2 amplitude for the two age groups, we were unable to calculate N2 latencies. Results from one younger participant were excluded due to excess artifact. The active condition was not included for one older participant due to time constraints.

2.5 Processing Speed

Processing speed was assessed using the Purdue Pegboard test and the Connections Test (Salthouse 2000). For the Purdue Pegboard test, participants completed three time trials, during which they placed as many pegs in the board as possible within 30 s using their right hand, then left hand, then both hands. Participants also completed an assembly task, in which they alternate hands, to construct as many “assemblies” as possible within 60 s; an assembly consists of a pin, a washer, a collar, and another washer. Results were averaged across the three time trials to provide single estimates of processing speed for the right hand (dominant), left hand, both hands, and assembly. The Connections test consists of two parts, Connections Simple and Connections Complex. The Connections Simple portion of the test requires participants to connect as many circled letters or numbers in alphabetic and numeric sequence as possible in 20 s. The letters and/or numbers are pseudorandomly organized in a 7×7 array of circles on a sheet of paper, with the next target located at one of the adjacent locations. Participants completed 2 trials of the letter form and 2 trials of the number form. Trial results were averaged to provide the Connections Simple score. Connections Complex requires participants to alternate between drawing a line between a number and a letter (i.e., 1 to A to 2 to B). Participants completed 2 trials starting with a number and 2 trials starting with a letter. Trial results were averaged to provide the Connections Complex score.

2.6 Data Analyses

For the behavioral measure of gap detection, age-related differences in percent detected were assessed with a repeated measures analysis of variance (ANOVA) with age as the grouping variable and gap duration as the repeated measure. Differences in ERP latencies were assessed by ANOVA for N1, and P2, and differences in ERP amplitudes for N1, P2, and N2, with age as the grouping variable and listening condition (active and passive) as the repeated measure. Differences in measures of processing speed were assessed using independent *t*-tests. Associations among variables were assessed using Pearson correlation coefficients to determine the extent to which latencies and amplitudes for active and passive listening and processing speed predicted behavioral gap detection. For all analyses, *p* values of <0.05 were considered statistically significant.

Higher-order attention-related effects can be partly disassociated from age-related differences in early automatic levels of auditory processing by contrasting responses for passive and active listening. Linear regression analyses were performed to examine these effects while controlling for age-related differences in auditory processing. Response latencies or amplitudes during active listening were entered as the dependent variable and response latencies or amplitudes during passive listening were entered as the independent variable. The standardized residual, or the remaining variance in the attended response latencies or amplitudes after removing the variance attributed to passive listening, was used to create an “attention modulation” construct. Pearson correlation analyses assessed the extent to which attention modulation, ERPs, and processing speed predicted behavioral gap detection.

3. Results

3.1 Percent detected and reaction time to gaps in continuous noise

Gap detection increased with increasing gap duration (Figure 3). The 3-ms step size generated steep behavioral response curves for most subjects. The ANOVA revealed a significant main effect of age [$F_{(1,46)} = 8.9, p = .005$] and a significant gap duration by age interaction [$F_{(1,46)} = 7.6, p < .001$]. Post hoc independent samples *t* tests indicated significant age-group differences for the 6 ms [$t = 3.6, p = .001$] and 9 ms [$t = 2.6, p = .014$] gap durations only, with better gap detection for younger than older adults. These group differences were not related to hearing levels, as individual variation in pure-tone thresholds (250 Hz to 8000 Hz) did not predict percent detected in younger or older adults. False positive responses, i.e., those occurring < 75 ms or > 1500 ms post gap onset, were minimal ($< 3\%$) and did not significantly differ across age group or gap duration.

To account for individual differences in gap detection and examine age-related differences in ERPs elicited by equally discriminable stimuli (Alain et al. 2004), age-related differences were assessed at the shortest gap that produced a percent detected within 5% of the asymptote. Asymptote was estimated from the function relating percent detected to gap duration: $[(1-a)/(1 + \text{Exp}[-s(d - m)])]$, where *a* is required to be greater than or equal to 0, *d* is gap duration, *s* determines the slope of the function, *m* is the point where the slope reaches its maximum value, and $(1-a)$ is the asymptotic value of the function (Alain et al. 2004). The gap duration nearest to asymptotic detection during active listening was also used for analyses of passive listening. Across subjects, the shortest gap corresponding to asymptotic performance ranged from 6 to 15 ms. Older adults required significantly longer gaps than younger adults to reach asymptotic performance [$t_{(1,23)} = -3.1, p = .004$], but there were no significant differences with respect to percent detected at asymptote [$t_{(1,23)} = -1.5, p = .143$].

Mean RT and the RT ICV were calculated for younger and older subjects. Differences in RT between younger subjects (mean=351.77ms, SD=124.31) and older subjects (mean=434.68, SD=177.41). Differences in ICV between younger (.53) and older subjects (.40) were not statistically significant. In addition to targeting gap duration closest to asymptote, age-related differences in ERPs were assessed with 15 ms gaps (results not shown).

3.2 ERPs to gaps in continuous noise

During both passive and active listening, clear N1-P2-N2 components were obtained in response to gaps of 6 ms or longer in younger adults. In older adults, the averaged ERP was dominated by the N1 component and was present in response to gaps as short as 9 ms, although in some subjects the ERP was not present until gap duration increased to 12 or 15 ms. The presence of the ERP was consistent with the subject's gap detection; that is, an ERP was more likely to be present for gap durations corresponding to percent detected $\geq 60\%$. Group average ERP waveforms are provided for passive listening (Figure 4A) and active

listening (Figure 4B) for younger adults (Figure 4, left) and older adults (Figure 4, right). Regardless of listening condition (passive and active), grand average ERP waveforms for the younger adults differed from those for the older adults during the initial ~400 ms following gap onset. As seen in the scalp voltage maps (Figure 4D), these differences were most pronounced over fronto-central electrodes, where the response was largest. Response latencies and amplitudes were measured from a subset of fronto-central electrodes (Fz, FCz, Cz, FC1, FC2). Given that there were no significant interactions between electrode and age or experiment, data were collapsed across electrodes and averaged for further analysis.

Waveforms elicited in response to the gap duration nearest asymptote are provided in Figure 4C for passive (solid) and active listening (dotted) for younger adults (left) and older adults (right). Age-related differences remain significant even after adjusting for differences in behavioral gap detection. The P2 response appears greatly diminished and the N2 response is largely absent in older adults compared to younger adults during both passive and active listening. The P2 and the N2 response are most affected by attention, showing increases in response amplitude and age-dependent changes in response latency in active compared to passive listening.

3.3 N1, P2, and N2 amplitudes: Effects of age and attention

Separate repeated-measures ANOVAs were conducted for N1, P2, and N2 amplitudes in response to the gap duration nearest to asymptotic detection. Similar results were obtained in response to gaps of 15 ms. ANOVA results are summarized in Table 1. Box plots showing response amplitudes are provided in Figure 5 for younger and older subject groups during passive listening (white) and active listening (gray). Amplitudes for N1, P2 and N2 were robustly affected by age with significantly larger response amplitudes for younger than older adults [Main effect of age: (N1: $F_{(1,46)}=13.76$, $p=.001$), (P2: $F_{(1,46)}=29.73$, $p<.001$), (N2: $F_{(1,46)}=21.86$, $p<.001$)]. N1 amplitude was not significantly different between active and passive listening [$F_{(1,46)}=1.04$, $p=.314$]. P2 amplitudes were significantly larger for active than passive listening in younger and older adults [$F_{(1,46)}=4.32$, $p=.043$]. N2 amplitudes showed a significant main effect of listening condition, and an age by listening condition interaction [$F_{(1,46)}=7.78$, $p=.008$]; post-hoc paired t tests revealed significantly larger N2 amplitudes for active than passive listening in younger adults [$t_{(1,23)}=3.2$, $p=.005$] but not in older adults [$t_{(1,23)}=.47$, $p=.96$].

3.4 N1 and P2 response latencies: Effects of age and attention

N1 latencies did not differ significantly between younger and older adults [$F_{(1,46)}=1.10$, $p=.299$], whereas, P2 latencies were significantly shorter in younger than in older adults [$F_{(1,46)}=29.71$, $p<.001$]. The interaction between age and listening condition was not significant for N1 or P2 latencies. However, response latencies for N1 and P2 were significantly shorter in younger adults for active than passive listening [(N1: $t_{(1,23)}=3.02$, $p=.006$), (P2: $t_{(1,23)}=2.33$, $p=.029$)]. The effect of attention on response latencies, particularly P2 latencies, was more variable in older adults, resulting in similar mean response latencies for N1 and P2 in active and passive listening [(N1: $t_{(1,23)}=1.03$, $p=.325$), (P2: $t_{(1,23)}=-0.45$, $p=.657$)].

3.5 Processing speed: Effects of age

Mean scores and standard deviations for Connections and Purdue Pegboard for younger and older participants are provided in Table 2. Measures of processing speed were strongly positively correlated with each other, with Pearson r values ranging from 0.63 to 0.84, ($p<.001$). Processing speed was significantly faster for younger than older adults ($p<.001$), with no evidence of a linear association between age and processing speed within the older adults [(age range: 58.8 to 83.6)($r_{24}=-.10$ to $.06$, ns)]. Individual differences in pure-tone thresholds

did not relate to measures of processing speed in younger subjects, older subjects, or across the sample [$r(48) = -.26$ to $.12$, ns].

3.6 Associations among behavioral gap detection, processing speed, and ERP latencies and amplitudes

Processing speed, as measured by simple and complex Connections, was positively correlated with behavioral gap detection after controlling for differences in processing speed due to age [Connections simple: (*partial r* = .35, $p = .02$); Connections Complex (*partial r* = .37, $p = .01$)]. Adults with faster processing speed had better gap detection. The association among P2 response latencies during active listening, processing speed, and gap detection were driven primarily by results for older adults. P2 response latencies during active listening were negatively correlated with gap detection [*partial r* = -.31, $p = .04$], such that subjects with shorter P2 response latencies had better gap detection. For older subjects, P2 latencies during active but not passive listening were negatively correlated with processing speed, including Connections complex, and the right, left, and assembly conditions on the Pegboard test [$r(24) = -.48$ to $-.50$, $p < .05$]; older subjects with longer latencies had slower processing speed. N2 amplitudes during active but not passive listening were negatively correlated with Pegboard results (right hand, left hand, and both left/right conditions); such that subjects with larger (more negative) amplitudes had faster processing speed [*partial r* = -.29 to $-.36$, $p < .05$]. Associations among gap detection, processing speed, and ERPs may be related to attention, given that no significant correlations were observed during passive listening [$r(48) = -.18$ to $.16$, ns].

3.7 Attention modulation, gap detection, and processing speed

The attention modulation construct was used to clarify the role of attention on ERPs, behavioral gap detection, and processing speed (see Section 2.6 Data Analyses). For P2 latencies, attention modulation was negatively correlated with gap detection [*partial r* = -.39, $p = .009$]. In older adults P2 latency attention modulation was negatively correlated with processing speed [$r(23) = -.40$ to $-.57$, $p < .05$] (Figure 6). Those older adults with P2 latencies that decreased with active listening had better gap detection and faster processing speed than those older adults whose P2 latencies increased with attention (Figure 6). For N2 amplitudes, attention modulation was positively correlated with processing speed in both younger adults and older adults, such that those adults whose N2 amplitudes increased with active listening had faster processing speed than those adults whose N2 amplitudes decreased with active listening (Figure 6).

4. Discussion

We hypothesized that age-related differences in auditory temporal processing are the result of age-related changes in automatic and attention-related processing and that some older adults would be less able to compensate for age-related differences at automatic levels of processing by exerting increased cognitive control and attention. Consistent with this hypothesis, our results show that: (1) older adults are less able than young adults to detect small gaps, (2) neurophysiological response patterns to gap onset were atypical for older adults for active and passive listening, with reduced P2 responses and virtually absent N2 responses, and (3) neurophysiological estimates of attention modulation accounted for a significant portion of the variance in gap detection and processing speed such that faster processing speed in old age appears to limit significant aging effects on gap detection.

4.1 Aging affects both automatic and cognitive processes

Neurobiological explanations for age-related differences in auditory temporal processing have focused largely on age-related differences in early or automatic levels of processing

during passive listening, and have attributed age-related differences in auditory temporal processing to impaired inhibition, temporal jitter, declines in neural synchrony, and/or neuronal loss or disintegration of synaptic connectivity in auditory cortices (e.g., Harkrider et al. 2005; Harris et al. 2008; Tremblay et al. 2004). Age-related changes in the structure and function of the central auditory system are well documented (e.g., Boettcher et al. 1996; Caspary et al. 1995; Harris et al. 2009a; Walton et al. 1997; Walton et al. 2002). The robust differences between younger and older adults ERPs observed during passive listening are consistent with the premise that aging affects the neural representation of temporal cues at automatic stages of auditory processing.

Older adults who maintain normal performance on relatively simple listening tasks may recruit cognitive control systems to compensate for changes at automatic levels of processing (Alain et al. 2004; Eckert et al. 2008). However, even with focused attention, large age-related differences in ERP amplitude and latency of the ERP and gap detection were observed in the current study, suggesting that the gap detection task used in the current study may have been more difficult for older than younger adults. With increased task difficulty greater demands are placed on cognitive resources to compensate for changes in auditory processing. With increased task difficulty, the cognitive control systems of some older adults may not be able to compensate for changes in automatic levels of processing, resulting in declining performance (Harris et al. 2009b). These results suggest a complex relationship between the effects of age on automatic and cognitive processing.

4.2 N2 as a marker of sustained attention

The most obvious difference in ERP waveforms of younger and older adults was the absence of the N2 response in many older subjects. Although larger or similar N2 amplitudes have been observed in older adults (Alain et al. 2004), the N2 peak most often shows a marked decrease in amplitude with age (Bertoli and Probst 2005; Ceponiene et al. 2008; De Chicchis et al. 2002). Unlike previous studies where gap duration was randomized within an experimental block (Michalewski et al. 2005; Pratt et al. 2005), gap durations in the present study were held constant within a stimulus block, such that the same gap duration was presented sequentially for 250 consecutive trials, followed by the next gap duration for 250 trials, and so on. When gap duration varies from trial to trial, a robust P3 or P300 is generated in response to the attended gap stimuli (Michalewski et al. 2005; Pratt et al. 2005). Presenting the same gap duration throughout an experimental block had profound effects on the physiological response, including a lack of, or significant reduction in a P3 response, and possible effects on the N2 response. By grouping the stimuli in this manner the task becomes more monotonous and the gaps may be less exogenously alerting. Similar effects on ERP components have been reported in the go/no-go N2-P3 literature, particularly while participants performed the Sustained Attention to Response Task (SART) (O'Connell et al. 2008; van Veen et al. 2002). Differences observed between the SART fixed versus the SART random are relevant to the current study. The SART is a continuous performance task in which a series of digits (from 1 to 9) is presented visually and subjects are required to press a button upon seeing each digit, except when the digit 3 appears, in which case the subjects must withhold a response. In the random version, the numbers are presented randomly and the number 3 occurs infrequently. In the fixed version, the numbers are presented sequentially with equal likelihood of occurrence (e.g., 1, 2, 3, 4). An N2-P3 component is generated during the SART random condition in comparison to the fixed condition where only an N2 response is observed (Dockree et al. 2005b; O'Connell et al. 2008). By making the task more routine demands on the frontally driven sustained attention networks may have increased (Manly et al. 2003). Thus, the N2 may be an index of these proactive control processes and may represent performance monitoring (O'Connell et al.

2008; van Veen and Carter 2002), whereas the P3 may reflect later stages of processing related to response selection and/or response inhibition.

The N2 is thought to be generated from medial frontal areas, including anterior cingulate cortex (Bekker et al. 2005; Jonkman et al. 2007a), and the right ventral and dorsolateral prefrontal cortex (Lavric et al. 2007). Karch et al. (2010) conducted a simultaneous EEG and fMRI study and reported that the N2 amplitude was associated with BOLD responses in medial frontal brain regions and the putamen. Furthermore, differences in brain activation patterns (PET and fMRI studies) elicited by SART fixed and random suggest that SART fixed places increased demands on sustained attention networks, including right dorsolateral prefrontal cortex (Manly et al. 2003), left inferior frontal cortex, right angular gyrus, left insula, and medial frontal gyrus (Fassbender et al. 2004). These studies collectively emphasize the importance of frontal attention-related brain regions in the generation of the N2. The large age-related differences in N2 amplitude and/or absence of the N2 in older adults, and the increased variability in attention modulation of N2 amplitudes in older adults, may represent an age-related change in the structure and function of frontal attention networks.

N2 amplitudes may also be affected by temporal expectations and/or implicit cueing that was generated by the regular spacing of the gaps in the continuous noise (Rimmele et al. 2011). The temporal regularity of an auditory signal may automatically engage ventral frontal parietal areas used in search tasks (Shulman et al. 2010), generating the frontally dominant N2 response. Thus, age-related differences in N2 amplitudes could relate to differences in temporal cuing. However, reaction times collected from button presses by older adults to gap detection remained relatively constant within a block, which rules out effects of temporal expectations or anticipation.

4.2 Associations among gap detection, processing speed, and ERPs

The associations among attention modulation, processing speed, and gap detection variables support our previous findings (Harris et al. 2010a) and suggest that age-related differences in gap detection stem in part from differences in attention networks. The auditory P2 has been associated with sensory arousal and attentional orienting and is likely susceptible to top-down modulatory control (Ceponiene et al. 2005a). More so, P2 latency may be a salient marker for attention-related decrements with age and has been shown to correlate with accuracy during attention and working memory tasks (Finnigan et al. 2011). This is consistent with the hypothesis that modality-specific attentional processing and brain processes supporting attention can occur even at very early sensory levels (Gazzaley et al. 2008; Gazzaley et al. 2005; Mesulam 2000; Roland 1982). The auditory N2 is proposed to reflect higher order sensory processing (Ceponiene et al. 2005b; Karhu et al. 1997) and may be affected by age-related changes in local connectivity and top-down modulations. Larger N2 amplitudes have been shown to be associated with better auditory target detection (Ceponiene et al. 2008) and better performance on measures of sustained attention (Dockree et al. 2005a). The relationship between the N2 response and processing speed suggest that similar structural and functional cortical networks may be involved in N2 response generation (Bekker et al. 2005; Jonkman et al. 2007b; Lavric et al. 2007) and processing speed (Eckert et al. 2010; Kennedy et al. 2009). Our future studies will examine the extent to which age-related differences in ERPs and gap detection are the result of changes in the structure of attention networks or related to changes in auditory cortex that may limit top-down modulation.

4.5 Challenges in studies of gap detection, attention, and aging

The neurophysiological response to gap onset may have unique morphology and underlying generators that differ from those to marker onset (Michalewski et al. 2005). The ERP elicited by a gap is generated in response to the change from noise against no input; however, our current understanding of the physiological response to gap stimuli is largely influenced by the response to the marker onset. The brain's ability to signal the offset of a signal is important in many aspects of speech recognition. Results from the current study suggest that older adults exhibited markedly different responses to gap onset than younger adults. Although responses to marker onset were not available, little to no age-related differences have been observed in cortical responses to the onset of simple stimuli, such as tones (Tremblay et al. 2004) even for a similar continuous presentation paradigm (Harris et al. 2007; Harris et al. 2008) when a slow inter-stimulus interval is used.

5. Conclusions

Results from the current study are broadly consistent with previous findings that older adults exhibit significantly poorer gap detection than younger adults in challenging tasks. Task difficulty in the current study may have been increased in older adults by the regularity of the task, which may have increased demands on sustained attention networks. Even after adjusting for poorer gap detection, older and younger adults showed robust differences in their electrophysiological responses to sound offset. These differences were present with both passive and active listening. Furthermore, the degree to which attention modulated the ERP was associated with individual variation in measures of processing speed and gap detection. Taken together, these results suggest an age-related deficit in early or automatic levels of auditory temporal processing and that some older adults may be less able to compensate for declines in processing by attending to the stimulus. These results extend our previous findings (Harris et al. 2010b) and support the hypothesis that age-related differences in cognitive or attention-related processing, including processing speed, contribute to an age-related decrease in gap detection.

References

- Alain C, McDonald KL, Ostroff JM, et al. Aging: a switch from automatic to controlled processing of sounds? *Psychol Aging*. 2004; 19:125–133. [PubMed: 15065936]
- ANSI. Specification for Audiometrics. New York: American National Standards Institute; 2004.
- Bekker EM, Kenemans JL, Verbaten MN. Source analysis of the N2 in a cued Go/NoGo task. *Brain Res Cogn Brain Res*. 2005; 22:221–231. [PubMed: 15653295]
- Berg P, Scherg M. A multiple source approach to the correction of eye artifacts. *Electroencephalogr Clin Neurophysiol*. 1994; 90:229–241. [PubMed: 7511504]
- Bertoli S, Heimberg S, Smurzynski J, et al. Mismatch negativity and psychoacoustic measures of gap detection in normally hearing subjects. *Psychophysiology*. 2001; 38:334–342. [PubMed: 11347878]
- Bertoli S, Probst R. Lack of standard N2 in elderly participants indicates inhibitory processing deficit. *Neuroreport*. 2005; 16:1933–1937. [PubMed: 16272882]
- Boettcher FA, Mills JH, Swerdloff JL, et al. Auditory evoked potentials in aged gerbils: responses elicited by noises separated by a silent gap. *Hear Res*. 1996; 102:167–178. [PubMed: 8951460]
- Caspary DM, Milbrandt JC, Helfert RH. Central auditory aging: GABA changes in the inferior colliculus. *Exp Gerontol*. 1995; 30:349–360. [PubMed: 7556513]
- Ceponiene R, Alku P, Westerfield M, et al. ERPs differentiate syllable and nonphonetic sound processing in children and adults. *Psychophysiology*. 2005; 42:391–406. [PubMed: 16008768]
- Ceponiene R, Westerfield M, Toriki M, et al. Modality-specificity of sensory aging in vision and audition: evidence from event-related potentials. *Brain Res*. 2008; 1215:53–68. [PubMed: 18482717]

- Cerella J. Information processing rates in the elderly. *Psychol Bull.* 1985; 98:67–83. [PubMed: 4034819]
- Craik FI. Changes in memory with normal aging: a functional view. *Adv Neurol.* 1990; 51:201–205. [PubMed: 2403713]
- De Chicchis AR, Carpenter M, Cranford JL, et al. Electrophysiologic correlates of attention versus distraction in young and elderly listeners. *J Am Acad Audiol.* 2002; 13:383–391. quiz 400-381. [PubMed: 12199514]
- Dockree PM, Kelly SP, Robertson IH, et al. Neurophysiological markers of alert responding during goal-directed behavior: a high-density electrical mapping study. *Neuroimage.* 2005; 27:587–601. [PubMed: 16024257]
- Eckert MA. Slowing down: age-related neurobiological predictors of processing speed. *Front Neurosci.* 2011; 5:25. [PubMed: 21441995]
- Eckert MA, Keren NI, Roberts DR, et al. Age-related changes in processing speed: unique contributions of cerebellar and prefrontal cortex. *Front Hum Neurosci.* 2010; 4:10. [PubMed: 20300463]
- Eckert MA, Walczak A, Ahlstrom J, et al. Age-related Effects on Word Recognition: Reliance on Cognitive Control Systems with Structural Declines in Speech-responsive Cortex. *J Assoc Res Otolaryngol.* 2008; 9:252–259. [PubMed: 18274825]
- Fassbender C, Murphy K, Foxe JJ, et al. A topography of executive functions and their interactions revealed by functional magnetic resonance imaging. *Brain Res Cogn Brain Res.* 2004; 20:132–143. [PubMed: 15183386]
- Finnigan S, O'Connell RG, Cummins TD, et al. ERP measures indicate both attention and working memory encoding decrements in aging. *Psychophysiology.* 2011; 48:601–611. [PubMed: 21039584]
- Folstein MF, Robins LN, Helzer JE. The Mini-Mental State Examination. *Arch Gen Psychiatry.* 1983; 40:812. [PubMed: 6860082]
- Gazzaley A, Clapp W, Kelley J, et al. Age-related top-down suppression deficit in the early stages of cortical visual memory processing. *Proc Natl Acad Sci U S A.* 2008; 105:13122–13126. [PubMed: 18765818]
- Gazzaley A, Cooney JW, Rissman J, et al. Top-down suppression deficit underlies working memory impairment in normal aging. *Nat Neurosci.* 2005; 8:1298–1300. [PubMed: 16158065]
- Harkrider AW, Plyler PN, Hedrick MS. Effects of age and spectral shaping on perception and neural representation of stop consonant stimuli. *Clin Neurophysiol.* 2005; 116:2153–2164. [PubMed: 16043402]
- Harris KC, Dubno JR, Keren NI, et al. Speech recognition in younger and older adults: a dependency on low-level auditory cortex. *J Neurosci.* 2009; 29:6078–6087. [PubMed: 19439585]
- Harris KC, Eckert MA, Ahlstrom JB, et al. Age-related differences in gap detection: effects of task difficulty and cognitive ability. *Hear Res.* 2010; 264:21–29. [PubMed: 19800958]
- Harris KC, Mills JH, Dubno JR. Electrophysiologic correlates of intensity discrimination in cortical evoked potentials of younger and older adults. *Hear Res.* 2007; 228:58–68. [PubMed: 17344001]
- Harris KC, Mills JH, He NJ, et al. Age-related differences in sensitivity to small changes in frequency assessed with cortical evoked potentials. *Hear Res.* 2008; 243:47–56. [PubMed: 18597958]
- He NJ, Horwitz AR, Dubno JR, et al. Psychometric functions for gap detection in noise measured from young and aged subjects. *J Acoust Soc Am.* 1999; 106:966–978. [PubMed: 10462802]
- Humes LE. Do 'auditory processing' tests measure auditory processing in the elderly? *Ear Hear.* 2005; 26:109–119. [PubMed: 15809539]
- Jonkman LM, Sniedt FL, Kemner C. Source localization of the Nogo-N2: a developmental study. *Clin Neurophysiol.* 2007; 118:1069–1077. [PubMed: 17368096]
- Karch S, Feurecker R, Leicht G, et al. Separating distinct aspects of the voluntary selection between response alternatives: N2- and P3-related BOLD responses. *Neuroimage.* 2010; 51:356–364. [PubMed: 20171291]
- Karhu J, Herrgard E, Paakkonen A, et al. Dual cerebral processing of elementary auditory input in children. *Neuroreport.* 1997; 8:1327–1330. [PubMed: 9172129]

- Kennedy KM, Raz N. Aging white matter and cognition: differential effects of regional variations in diffusion properties on memory, executive functions, and speed. *Neuropsychologia*. 2009; 47:916–927. [PubMed: 19166865]
- Lavric A, Clapp A, Rastle K. ERP evidence of morphological analysis from orthography: a masked priming study. *J Cogn Neurosci*. 2007; 19:866–877. [PubMed: 17488210]
- Lehmann D, Skrandies W. Reference-free identification of components of checkerboard-evoked multichannel potential fields. *Electroencephalogr Clin Neurophysiol*. 1980; 48:609–621. [PubMed: 6155251]
- Lister J, Besing J, Koehnke J. Effects of age and frequency disparity on gap discrimination. *J Acoust Soc Am*. 2002; 111:2793–2800. [PubMed: 12083214]
- Lister JJ, Roberts RA. Effects of age and hearing loss on gap detection and the precedence effect: narrow-band stimuli. *J Speech Lang Hear Res*. 2005; 48:482–493. [PubMed: 15989406]
- Manly JJ, Touradjji P, Tang MX, et al. Literacy and memory decline among ethnically diverse elders. *J Clin Exp Neuropsychol*. 2003; 25:680–690. [PubMed: 12815505]
- Manly T, Owen AM, McAvinue L, et al. Enhancing the sensitivity of a sustained attention task to frontal damage: convergent clinical and functional imaging evidence. *Neurocase*. 2003; 9:340–349. [PubMed: 12925947]
- Mesulam M. Brain, mind, and the evolution of connectivity. *Brain Cogn*. 2000; 42:4–6. [PubMed: 10739582]
- Michalewski HJ, Starr A, Nguyen TT, et al. Auditory temporal processes in normal-hearing individuals and in patients with auditory neuropathy. *Clin Neurophysiol*. 2005; 116:669–680. [PubMed: 15721081]
- O'Connell RG, Bellgrove MA, Dockree PM, et al. Self-Alert Training: volitional modulation of autonomic arousal improves sustained attention. *Neuropsychologia*. 2008; 46:1379–1390. [PubMed: 18249419]
- Pichora-Fuller MK, Schneider BA, Benson NJ, et al. Effect of age on detection of gaps in speech and nonspeech markers varying in duration and spectral symmetry. *J Acoust Soc Am*. 2006; 119:1143–1155. [PubMed: 16521775]
- Picton TW, Bentin S, Berg P, et al. Guidelines for using human event-related potentials to study cognition: recording standards and publication criteria. *Psychophysiology*. 2000; 37:127–152. [PubMed: 10731765]
- Poth EA, Boettcher FA, Mills JH, et al. Auditory brainstem responses in younger and older adults for broadband noises separated by a silent gap. *Hear Res*. 2001; 161:81–86. [PubMed: 11744284]
- Pratt H, Bleich N, Mittelman N. The composite N1 component to gaps in noise. *Clin Neurophysiol*. 2005; 116:2648–2663. [PubMed: 16221565]
- Rimmele J, Jolsvai H, Sussman E. Auditory target detection is affected by implicit temporal and spatial expectations. *J Cogn Neurosci*. 2011; 23:1136–1147. [PubMed: 20146603]
- Roland PE. Cortical regulation of selective attention in man. A regional cerebral blood flow study. *J Neurophysiol*. 1982; 48:1059–1078. [PubMed: 7175557]
- Salthouse TA. Aging and measures of processing speed. *Biol Psychol*. 2000; 54:35–54. [PubMed: 11035219]
- Salthouse TA, Ferrer-Caja E. What needs to be explained to account for age-related effects on multiple cognitive variables? *Psychol Aging*. 2003; 18:91–110. [PubMed: 12641315]
- Schneider BA, Hamstra SJ. Gap detection thresholds as a function of tonal duration for younger and older listeners. *J Acoust Soc Am*. 1999; 106:371–380. [PubMed: 10420628]
- Shulman GL, Pope DL, Astafiev SV, et al. Right hemisphere dominance during spatial selective attention and target detection occurs outside the dorsal frontoparietal network. *J Neurosci*. 2010; 30:3640–3651. [PubMed: 20219998]
- Tombaugh TN, McIntyre NJ. The mini-mental state examination: a comprehensive review. *J Am Geriatr Soc*. 1992; 40:922–935. [PubMed: 1512391]
- Tremblay KL, Billings C, Rohila N. Speech evoked cortical potentials: effects of age and stimulus presentation rate. *J Am Acad Audiol*. 2004; 15:226–237. quiz 264. [PubMed: 15119463]

- Tremblay KL, Piskosz M, Souza P. Aging alters the neural representation of speech cues. *Neuroreport*. 2002; 13:1865–1870. [PubMed: 12395081]
- van Veen V, Carter CS. The anterior cingulate as a conflict monitor: fMRI and ERP studies. *Physiol Behav*. 2002; 77:477–482. [PubMed: 12526986]
- Walton JP, Frisina RD, Ison JR, et al. Neural correlates of behavioral gap detection in the inferior colliculus of the young CBA mouse. *J Comp Physiol [A]*. 1997; 181:161–176.
- Walton JP, Simon H, Frisina RD. Age-related alterations in the neural coding of envelope periodicities. *J Neurophysiol*. 2002; 88:565–578. [PubMed: 12163510]

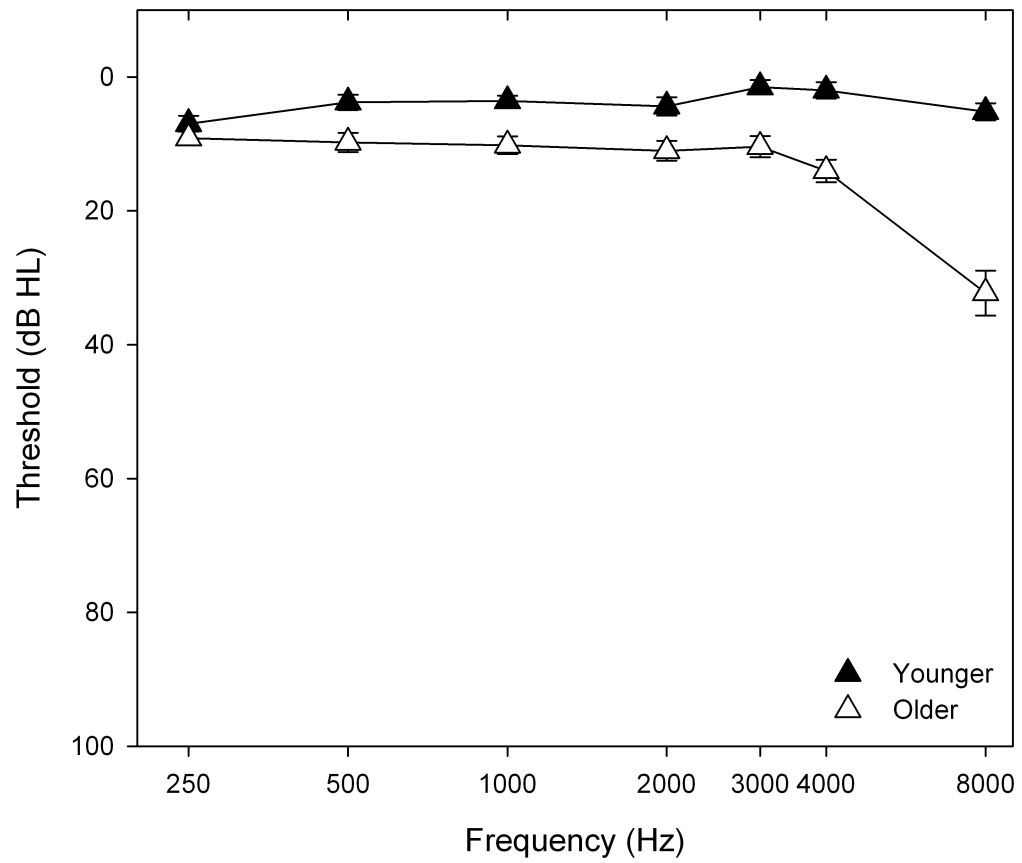


Figure 1. Mean pure-tone thresholds (dB HL) and standard errors (± 1 S.E.M) for the test (right) ear of younger adults (open) and older adults (filled) plotted as a function of frequency (Hz).

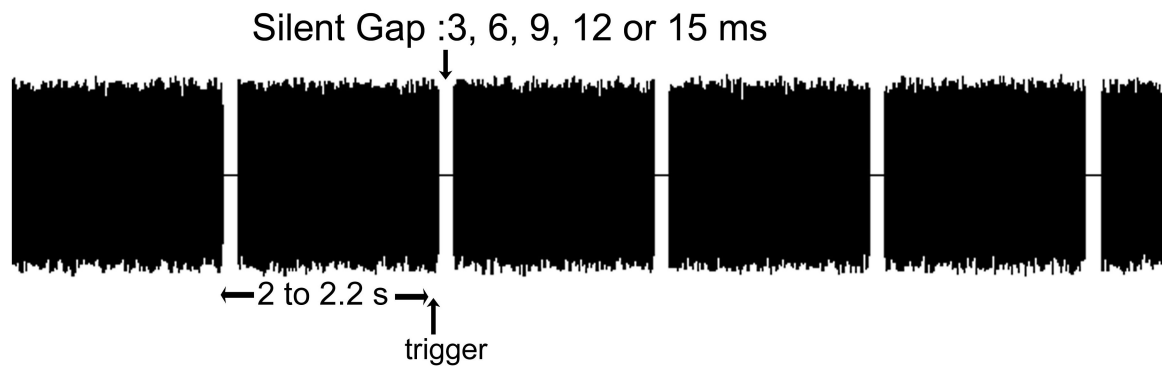


Figure 2. A schematic of a segment of the stimulus sequence. Continuous noise was presented with silent gaps distributed every 2 to 2.2 seconds. Averaging of the ERP was triggered 100 msec (baseline) prior to gap onset.

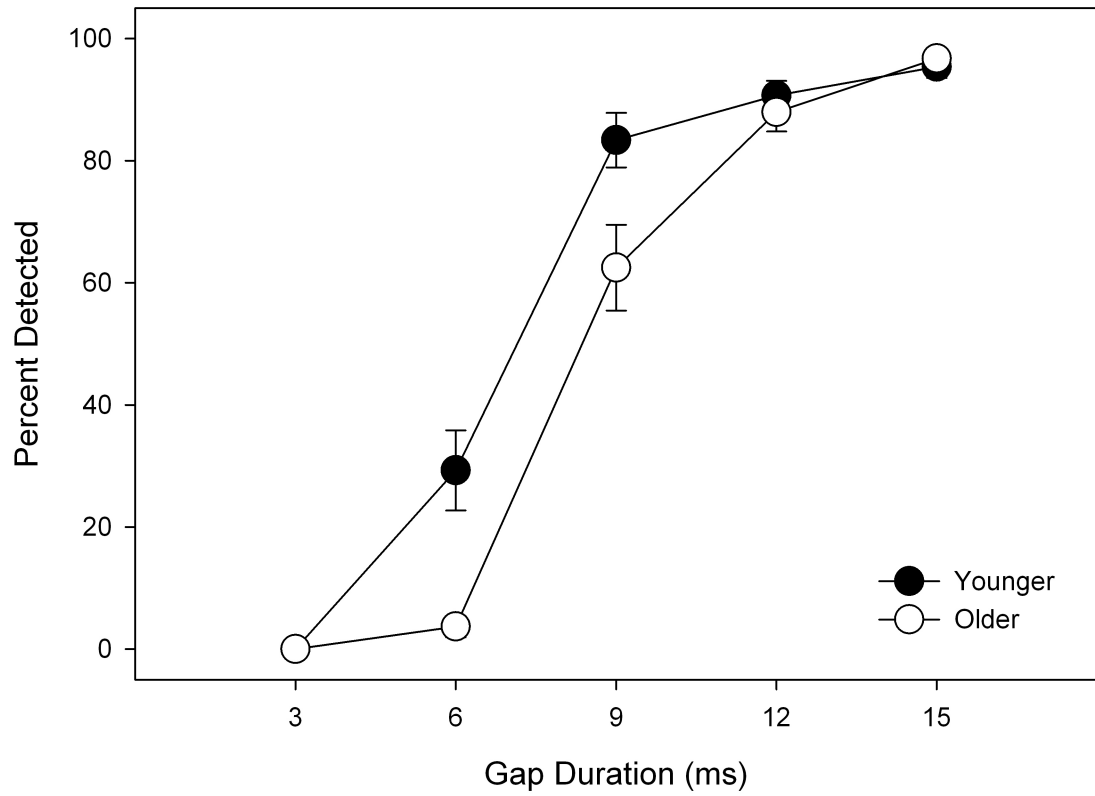


Figure 3. Percent detected (percent correct) as a function of gap duration (ms) for younger adults (open) and older adults (filled). Significant differences in percent detected between younger and older adults were observed only for 6 ms and 9 ms gaps.

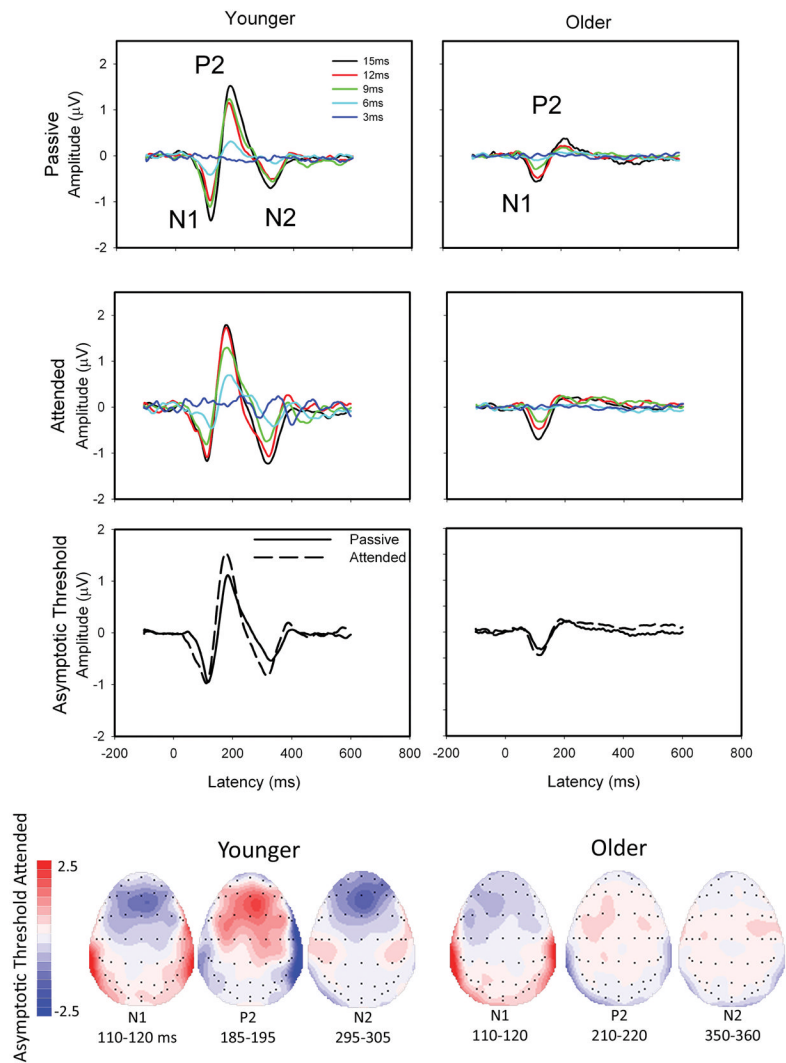


Figure 4. Waveforms and scalp voltage maps. A-B. Group average waveforms for younger and older adults during passive (A) and active (B) listening for each gap duration recorded and averaged from a cluster of fronto-central electrodes (Fz, FCz, Cz, FC1, FC2). C. Group average waveforms for younger and older adults during passive and active listening at the gap duration nearest to the asymptotic threshold (see text). D. Group average scalp voltage maps for younger and older adults elicited by the gap duration closest to asymptotic threshold during active listening. Voltage maps display scalp topography of the ERP components at their peak latencies. Given its anterior scalp distribution and negative deflection, an argument can be made that the component labeled as N2 is in fact a second N1 response to the onset of the second marker. However, pronounced differences in the voltage maps for N1 and N2, and the differential effects of attention and gap duration on the N2, as compared to the N1, support the identity of the N2 response.

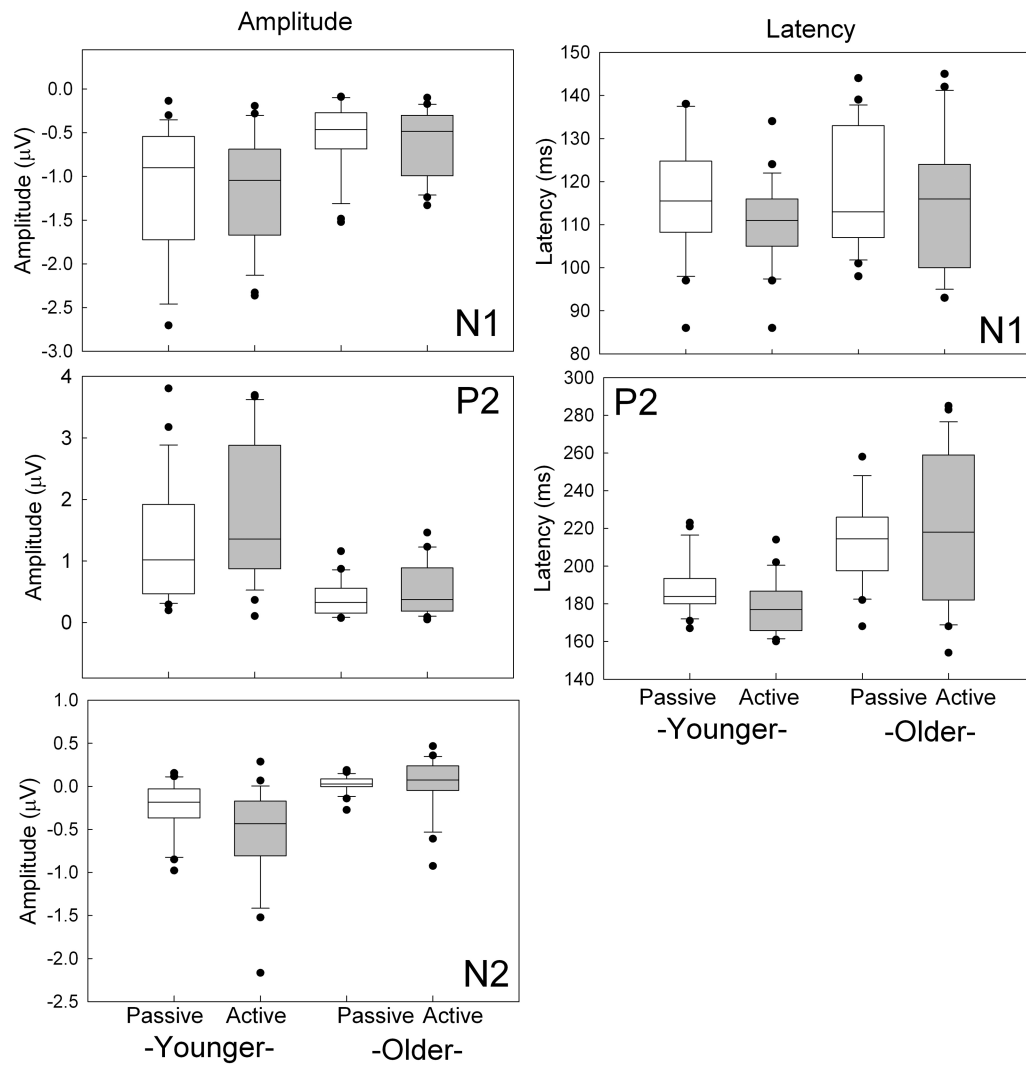


Figure 5. Median values (line in center of box), 25th and 75th percentiles (box boundary), and 10th and 90th percentile (error bars) for N1, P2, and N2 response amplitudes and N1 and P2 response latencies. Within each panel, data are provided for younger (left) and older (right) participants during passive (white) and active (gray) listening.

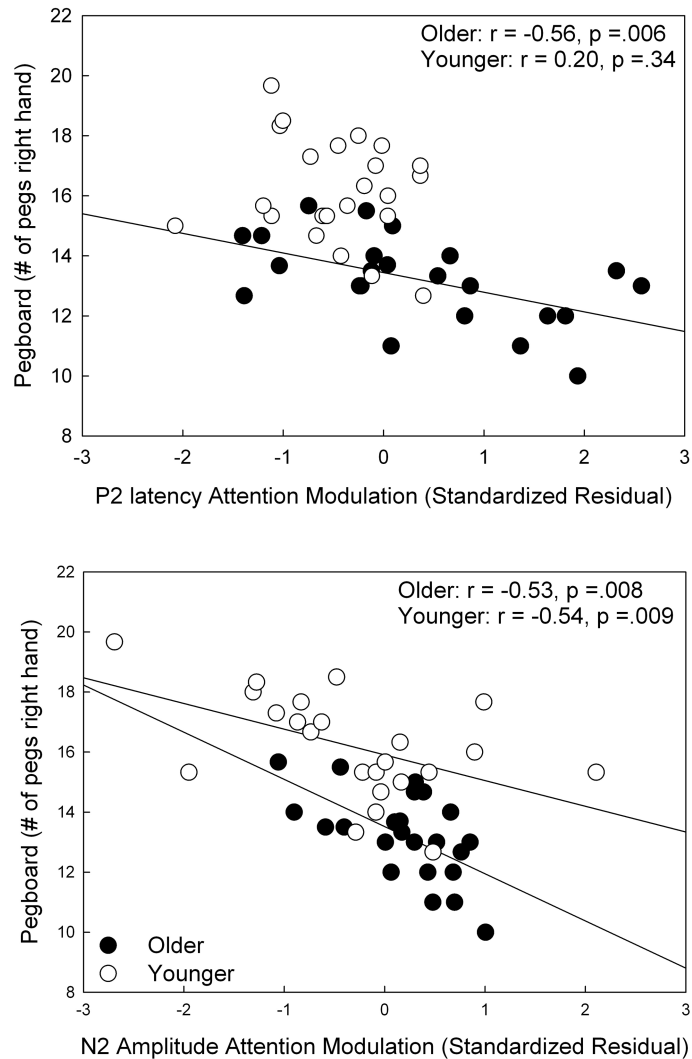


Figure 6.

Pegboard measure of processing speed plotted against P2 latency (top) and N2 amplitude (bottom) estimates of attention modulation for younger adults (open) and older adults (filled). Attention modulation was defined as the standardized residual, or the remaining variance in the attended response latencies or amplitudes after removing the variance attributed to passive listening. Significant negative correlations reveal that older adults with P2 latencies that decreased with attention (more negative residuals) had faster processing speeds, whereas older adults with P2 latencies that increased with attention (more positive residuals) had slower processing speeds (top). Similar relations between attention modulation and processing speed were obtained for N2 amplitudes for younger and older subjects (bottom). Age-related differences in attention may compound age-related differences at automatic levels of processing, contributing to the age effects observed during challenging listening tasks. We examined age-related differences in and associations among gap detection, processing speed, and cortical ERP elicited by gaps in a continuous noise under passive and active listening. Age-related differences in gap detection and ERPs during active and passive listening suggest that early or automatic levels of auditory temporal processing are reduced for older adults, and that some older adults may be less able to compensate for declines in processing by attending to the stimulus.

Table 1
Summary of ANOVA results for amplitudes and latencies of N1, P2, and N2

Main Effects	Amplitude			Latency	
	N1	P2	N2	N1	P2
Age (Older vs. Younger)	■	■	■		■
Listening condition (Passive vs. Active)			■		■
Interactions: Age x listening condition			■		

■ p<.05

Table 2

Mean and standard deviations for Connections (number of items) and Purdue Pegboard (number of assemblies or units) for younger and older adults.

	Older Participants		Younger Participants	
	Mean	SD	Mean	SD
Connections				
Simple	22.42	5.83	36.60	5.26
Complex	12.25	3.93	20.21	6.79
Pegboard				
Right Hand	13.30	1.63	16.18	1.66
Left Hand	12.38	1.75	14.77	1.42
Both Hands				
Assembly	29.68	5.87	44.08	4.64

Differences across all measures of processing speed between younger and older adults were significant at $p < .001$.