

Electrophysiological Correlates of Adult Age Differences in Attentional Control of Auditory Processing

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In addition to sensory decline, age-related losses in auditory perception also reflect impairments in attentional modulation of perceptual saliency. Using an attention and intensity-modulated dichotic listening paradigm, we investigated electrophysiological correlates of processing conflicts between attentional focus and perceptual saliency in 25 younger and 26 older adults. Participants were instructed to attend to the right or left ear, and perceptual saliency was manipulated by varying the intensities of both ears. Attentional control demand was higher in conditions when attentional focus and perceptual saliency favored opposing ears than in conditions without such conflicts. Relative to younger adults, older adults modulated their attention less flexibly and were more influenced by perceptual saliency. Our results show, for the first time, that in younger adults a late negativity in the event-related potential (ERP) at fronto-central and parietal electrodes was sensitive to perceptual-attentional conflicts during auditory processing (N450 modulation effect). Crucially, the magnitude of the N450 modulation effect correlated positively with task performance. In line with lower attentional flexibility, the ERP waveforms of older adults showed absence of the late negativity and the modulation effect. This suggests that aging compromises the activation of the fronto-parietal attentional network when processing the competing and conflicting auditory information.

Keywords: aging, attention, auditory perception, conflict monitoring, ERP

Introduction

When listening to someone amidst a conversational background, for example, at a cocktail party, different speech streams are competing for the brain's limited processing resources. The competition between these sensory inputs can be biased either by perceptual saliency or attentional control (Desimone and Duncan 1995; Kastner and Ungerleider 2000). Perceptually salient inputs can capture attentional orienting mechanisms more easily for further processing than nonsalient stimuli (e.g. Theeuwes 1992, 1994; Fan et al. 2002; Posner and Rothbart 2007). At the same time, mechanisms that selectively focus attention on specific sensory inputs, for instance, the speech stream from a conversational partner, also facilitate perceptual processing (Peterson and Kramer 2001; Fan et al. 2002; Posner and Rothbart 2007; Whiting et al. 2007). Perceptual saliency and attentional control dynamically interact with each other. Attentional control demands are low when relevant perceptual information is easily accessible, but high

when irrelevant information is more salient and has to be suppressed (Desimone and Duncan 1995; Miller and Cohen 2001).

A Paradigm to Study the Interplay Between Perceptual Saliency and Attentional Control on Auditory Processing

In research on auditory perception, recent studies showed that a dichotic listening (DL) task in which attentional focus and perceptual saliency of the auditory inputs are manipulated in a fully crossed design is well suited for investigating the interaction between auditory perception and attention (Tallus et al. 2007; Westerhausen et al. 2009, 2010; Passow et al. 2012). In this paradigm, 2 different consonant–vowel (CV) syllables are presented simultaneously to the right and left ears (RE and LE). The relative perceptual saliency of the auditory inputs from either ear is manipulated by varying the degree of intensity difference between the ears, either favoring the RE or the LE. Attentional focus is varied by instructing the participants to focus either on the RE (focused right [FR]) or on the LE (focused left [FL]), or attend to both ears (neutral-focus [NF]). In line with the biased competition model of Desimone and Duncan (1995), the demand for attentional control can be systematically varied in this paradigm. The demand is low when perceptual saliency and attentional focus favor the same ear, but high when perceptual saliency conflicts with attentional focus (e.g. when the RE syllable is perceptually more salient, but the instruction mandates that attention is directed to inputs from the LE). In this case, the perceptual saliency of the nonattended ear has to be suppressed to selectively attend to the weaker perceptual inputs from the instructed ear.

Behavioral studies using DL paradigms that manipulate both perceptual saliency and attentional focus have shown that younger adults are able to flexibly direct their attention as requested by the instructions. Even in conditions with high conflict between attentional focus and perceptual saliency, younger adults can selectively attend to the instructed ear quite easily (Tallus et al. 2007; Westerhausen et al. 2009, 2010; Passow et al. 2012). This ability, however, deteriorates from early to late adulthood. Passow et al. (2012) showed that older adults did not direct their attention flexibly, so that their performance was primarily driven by perceptual saliency. In other words, older adults tended to report perceptually more salient syllables irrespective of attentional focus. These findings are in line with multiple studies showing age-related attentional

deficits across a broad range of tasks (e.g. Kray and Lindenberger 2000; Hugdahl et al. 2001; Spieler et al. 2006; e.g. Thomsen et al. 2004; Whiting et al. 2007; Takio et al. 2009).

Decrements in top-down attentional selection with advancing adult age may reflect age-related deficits in flexibly recruiting relevant brain circuitries according to the attentional control demands. Using the aforementioned variant of the DL task that crosses perceptual saliency and attentional focus, a recent functional magnetic resonance imaging (fMRI) study of younger adults identified 2 distinct top-down control brain networks that are involved in auditory attention, a fronto-parietal network, and a medial-lateral frontal network (Westerhausen et al. 2010). The authors showed that the activity in these 2 networks was modulated by perceptual-attentional conflicts. The blood oxygen level-dependent (BOLD) signal increased in conditions of the high attentional control demand in which perceptual saliency and attentional focus conflicted with each other, but did not change or even decreased in conditions of low attentional control demand conditions in which both perceptual saliency and attentional focus favored the same ear. Thus far, findings from this fMRI study are the only direct evidence for which brain networks are involved in the DL task. Information about the time course of the neural processes implementing top-down control of auditory perception in this paradigm is, however, still lacking.

Classical DL studies in younger adults without any perceptual or attentional manipulation showed clear P1, N1, and P2 event-related potential (ERP) components in response to simple CV syllables (e.g. Eichele et al. 2005; Sandmann et al. 2007; Bayazit et al. 2009). ERP analyses often focused solely on the N1 component as an indicator of early prelexical auditory processing. Hemispheric differences in N1 amplitude and latency were shown to reflect hemispheric lateralization effects already at the prelexical speech processing level (Eichele et al. 2005; Sandmann et al. 2007). Bayazit et al. (2009), in contrast, compared early and late ERP components between dichotic (different syllables to both ears) and diotic (identical syllables to both ears) stimulus presentation. They did not find any differences in early ERPs between those 2 stimulus presentations. Regarding later time windows, a late negativity of approximately 450–550 ms after stimulus onset at frontal sites was more pronounced in dichotic compared with diotic stimulus presentation. The finding has been interpreted in terms of this late negativity's sensitivity to sensory conflict in the dichotic inputs (Bayazit et al. 2009). Thus far, there is no ERP study that investigated how this late negativity is modulated by different attentional control demands in DL, for example, induced by conflicts between perceptual saliency and attentional control, and age differences therein.

Late Negative-Going ERP Deflection and Attentional Control Demands

Electroencephalogram (EEG) studies of cognitive control (e.g. color-naming Stroop task) have revealed a late fronto-central ERP modulation effect that approximately peaked at 450 ms after stimulus onset that is sensitive to the attentional control demand. Specifically, compared with congruent trials, the conflicts between competing response options in incongruent trials (e.g. when color and color-word are incongruent) required more attentional control. The need for greater attentional control in the incongruent relative to the congruent

condition reliably evoked an increased negativity referred to as the N450 (e.g. West and Alain 1999; Liotti et al. 2000; Hanslmayr et al. 2008; Larson et al. 2009).

Studies using other conflict paradigms have found a more parietal N450 (Schirmer and Kotz 2003; Frühholz et al. 2009). Frühholz et al. (2009) asked their participants to make fast valence judgments while presented with learned (congruent) or unlearned (incongruent) face-color combinations. The parietal manifestation of the N450 elicited by incongruent face-color combinations was interpreted as an indicator of enhanced attentional processing in incongruent trials. The more posterior distribution of the N450 compared with what has been observed with Stroop paradigms was explained by task-specific functional differences in attentional control. ERP source analyses point to the anterior cingulate cortex as the neural generator of the N450 in both Stroop-like and other paradigms (Liotti et al. 2000; Frühholz et al. 2009).

Analyses focusing on earlier ERP components (e.g. the P3) using Stroop paradigms failed to show any differences in amplitude or latency between congruent and incongruent trials (Duncan-Johnson and Kopell 1981; Ilan and Polich 1999; Rosenfeld and Skogsberg 2006). This leads to the suggestion that the interference effect and the effects of attentional control captured by ERP components are related to the later processing stages of higher-order cognitive processing rather than to stimulus evaluation processes.

Age-Related Differences in Attentional Control and Their Neural Correlates

Past research has demonstrated an age-related decline in attentional control using tasks, such as Go-Nogo (Hämmerer et al. 2010) and Stroop tasks (see Macleod 1991 for review; Spieler et al. 1996; West and Baylis 1998), where the degree of response conflict was manipulated between conditions. Using a cued Go-Nogo task while simultaneously recording EEG, Hämmerer et al. (2010) found that older adults showed higher indices of attentional distraction than younger adults as reflected in a larger P3a component after infrequent NonCue stimuli as well as reduced conflict monitoring signals reflected in a reduced Nogo N2 component. Regarding the Stroop task, West and Baylis (1998) showed an increased Stroop interference effect (e.g. increased reaction time and error rate) in older adults but only in conditions of high attentional control demand, when the proportion of incongruent trials was high, and not in conditions of low attentional control demand, when incongruent trials were less frequent. The authors suggest that this pattern of results reflects older adults' difficulties in maintaining the color-naming strategy to guide performance, thus pointing to an age-related deficit in attentional control. Spieler et al. (1996) used a process dissociation procedure to show independent estimates of the contribution of either color or word information to task performance in older and younger adults. They argue that the increased Stroop interference effect in older adults results from an increase in the contribution of word information, suggesting a deficit in efficient inhibitory control of word information on incongruent trials. Correspondingly, ERP data revealed a strong age-related attenuation of the N450, reflecting a decline in the activity of a neural system supporting the suppression of word information during incongruent trials in the Stroop task (West and Alain 2000; West 2004). In

contrast, ERP modulation reflecting the processing of color information and selection processes appeared to be well preserved in older adults (West and Alain 2000).

Study Aims and Hypotheses

To perform well on the attention and intensity-modulated DL task, particularly in conditions with high perceptual-attentional conflict, it is essential to keep the attentional focus on the instructed ear across a large number of trials while inhibiting distracting and salient auditory input presented to the other ear. Specifically, the perceptually more salient syllable of the nonattended ear has to be suppressed to adhere to the attentional focus and report the syllable from the to-be-attended ear. The palpable adult age differences observed with this task (Passow et al. 2012) are fully consistent with the age-related increase in Stroop interference. Hence, one might expect that age differences in ERP modulations would be similar as well.

This study aimed at investigating the electrophysiological correlates of different degrees of attentional control demand in the attention and intensity-modulated DL paradigm and their relations to individual differences in task performance. Based on previous findings showing that effects of attentional control are related to the later processing stages of higher-order cognitive processing (Duncan-Johnson and Kopell 1981; West and Alain 1999; Liotti et al. 2000; Schirmer and Kotz 2003; Rosenfeld and Skogsberg 2006; Frühholz et al. 2009; Larson et al. 2009), we expected effects for later ERP components. As reported above, during classical DL, a late negativity of approximately 450–550 ms after stimulus onset in response to sensory conflict in dichotic input is present, at least in younger adults (Bayazit et al. 2009). In light of an increased negativity (N450) in response to conflicts between competing response options in incongruent Stroop trials in the same time window, we expected the amplitude of this late negativity to be sensitive to attentional control demands. In younger adults, based on previous findings, we hypothesized a more negative-going deflection under the conditions of high attentional control demand relative to that of low attentional control demand. Furthermore, we assumed that the sensitivity of this latent negativity to the attentional control demand (hereafter referred to as the N450 modulation effect) would correlate with task performance. In light of older adults' lack of flexible attentional control in this task (Passow et al. 2012), we expected a substantial attenuation of the N450 modulation effect in older adults.

Materials and Methods

Participants

Twenty-six right-handed younger and 29 right-handed older adults participated in 2 testing sessions. Participants first completed an extensive behavioral version of the DL task with 9 levels of interaural intensity differences (for more details see Experimental Procedure). The dense sampling of intensity differences allowed us to compute an independently assessed selective attention index (ATTIndex) to investigate the neural-behavioral relations. In a second session, EEG was recorded, while the participants conducted a modified version of the DL task (for more details see Experimental Procedure). Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield 1971). All participants were screened for hearing acuity and sensitivity to interaural threshold differences for the frequencies 250, 500, 1000, 2000, and 3000 Hz by using a pure-tone audiometer (MAICO

Diagnostics MA 51, Berlin, Germany). To reduce the selectivity of our older adult sample, we relaxed the common exclusion criterion of >25 to >35 dB HL for the 5 frequencies tested and adapted the stimulus intensity individually.

Two older adults had to be excluded due to exceeding hearing thresholds (>35 dB HL) and interaural threshold differences (>10 dB HL). Consequently, they did not take part in the follow-up ERP study. After artifact rejection (for more details see Electrophysiological Data Recording and Analyses), one older and one younger participants had to be excluded because the proportion of trials that needed to be rejected due to movement artifacts was too large (>30%). Thus, the effective sample consisted of 25 younger adults aged 22–35 years (mean age 25.8 ± 2.7 years; 12 women) and 26 older adults aged 63–76 years (mean age 70.0 ± 4.1 years; 12 women). Prior to the DL experiment, cognitive covariates including a marker of perceptual speed (Digit Symbol Substitution test; Wechsler 1981) and a marker of verbal knowledge (Spot-A-Word; Lehrl 1977) were assessed. In line with 2-component theories of lifespan intelligence (Horn 1968; Baltes 1987; Cattell 1971) and empirical evidence (Schaie et al. 1998; Li et al. 2004) contrasting the fluid mechanics and crystallized pragmatics of cognition, our results showed a significant age-related decline in perceptual speed (younger adults: 71.5 ± 13.9 , older adults: 48.3 ± 11.3 ; $t(49) = 6.54$, $P < 0.001$, $d = 1.83$) and significant higher scores in verbal knowledge for older adults (younger adults: 18.2 ± 5.3 , older adults: 23.7 ± 4.3 ; $t(49) = -4.02$, $P < 0.001$, $d = 1.12$), confirming the age typicality of our samples. Mean educational levels were 13.1 (± 2.3) years for younger adults and 12.2 (± 4.2) years for older adults. All participants were native speakers of German, gave informed consent, and were paid for participation. The Ethics Committee of the Max Planck Institute for Human Development, Berlin, Germany approved the study.

Experimental Procedure

Two different CV syllables were presented simultaneously to both ears. The CV syllables consisted of 3 voiced (/b/, /d/, /g/) and 3 unvoiced (/p/, /t/, /k/) consonants that were combined with the vowel /a/. Only syllables with the same voicing were combined, resulting in 12 different dichotic syllable pairs. All syllables were spoken by a young adult male speaker with constant intonation and intensity and by a mean duration of 400 ms. The 2 syllables were temporally synchronized to have the same onset times of the LE and RE channel. Most of the spectral energy of these CV syllables is within a frequency range of 250–5000 Hz (Hugdahl 2003), with the highest amplitude in all of the 6 CV syllables being present in the frequency range of <1000 Hz. Thus, pure-tone thresholds at 500 Hz (mean of the range from 0 to 1000 Hz) were taken for individual adjustments of input intensity. This was done by adding a constant of 65 dB to each participant's personal hearing threshold. Since we included older adults with mild hearing loss (≤ 35 dB HL), we also checked for the differentiability of the syllables by conducting a syllable discrimination task prior to the experiment. The 6 syllables were presented diotically, and the participants had to choose 1 of 6 corresponding buttons. The chance level of this task was 16.7% (1 of the 6 possible choices), and all participants performed well above chance at a mean accuracy level of over 90%.

In the extensive behavioral version of this task, perceptual saliency of the syllables was manipulated by varying the intensity difference between the ears. The interaural intensity difference was varied by decreasing the intensity of either the RE or the LE in 5 dB steps until a maximum of 20 dB was reached (comparable with Passow et al. 2012). Thus, there were 4 conditions favoring the LE, L > R ([−20], [−15], [−10], [−5]), 4 conditions favoring the RE, R > L ([+20], [+15], [+10], [+5]), and 1 neutral condition (same input intensity to both ears, L = R ([0]). The neutral condition served as baseline intensity and was adapted to each participant's individual hearing threshold at 500 Hz (see above).

To obtain more trials per conditions in the EEG version of the task, the 9 perceptual saliency conditions in the behavioral study were reduced to 3 conditions and varied by decreasing the intensity of either the RE or the LE by 10 dB. Thus, there was 1 condition favoring

the LE, L>R ([-10]), 1 condition favoring the RE, R>L ([+10]), and 1 condition was neutral (same input intensity to both ears, L=R ([0]). Each of the 12 dichotic syllable pairs was presented 9 times for each of the 3 perceptual saliency conditions, resulting in a total of 324 intensity stimulus pairs for each attentional condition which were further split into 4 testing blocks of 81 trials each. The interstimulus interval was variable and varied between 3500 and 4000 ms. Trial order was randomized within and between blocks.

Attentional focus was manipulated by 3 different attentional instructions (Hugdahl and Andersson 1986): NF, FR, and FL. In the NF condition, participants were asked to report the syllables they heard most clearly. In the focused-attention conditions, they were asked to attend either to the RE (FR) or to the LE (FL) and to report only the syllable presented to the to-be-attended ear. The NF blocks were always completed first to avoid carry-over effects from the FR or FL conditions to the NF conditions (Hiscock and Stewart 1984). Afterwards, FR and FL blocks were intermixed and individually counterbalanced in 2 presentation orders (i.e. ABBABAAB or BAABABBA). Due to the simultaneous perceptual and attentional manipulation, the need for attentional control was varied. The attentional control demand was low when perceptual saliency and attentional focus favor the same ear (FR [+10] and FL [-10]) and high when perceptual saliency conflicts with the attentional focus (FR [-10] and FL [+10]).

All testing was performed in a sound-attenuated booth. Presentation of the stimuli and response collection were controlled via E-Prime 1.1 software. All stimuli were presented via insert earphones (ER 3A Insert Earphone, Etymotic Research, Inc., Elk Grove Village, IL, United States of America).

Electrophysiological Data Recording and Analyses

EEG was recorded continuously (BrainAmp DC amplifiers, Brain Products GmbH, Gilching, Germany) from 64 Ag/AgCl electrodes placed according to the 10–10 system in an elastic cap (Braincap, BrainVision) using BrainVision Recorder. The sampling rate was 1000 Hz with a bandpass filter applied in the range of 0.01–100 Hz. EEG recordings were referenced online to the right mastoid. The ground was positioned above the forehead. Impedances were kept <5 k Ω . Vertical and horizontal electro-oculograms were recorded next to each eye and below the left eye. Using BrainVision Analyzer software (Version 2.0, Brain Products), the recorded data were digitally re-referenced to a linked mastoid reference. EEG recordings were bandpass-filtered (0.05–25 Hz) and segmented into stimulus-locked time epochs of 100 ms prestimulus to the 800-ms postonset. Thereafter, the epochs were corrected for eye movements using the Gratton and Coles algorithm (Gratton et al. 1983), and further artifacts were rejected based on a maximum admissible voltage step (50 μ V), and a maximum admissible absolute difference between 2 values in a segment (150 μ V). Consequently, across all conditions an average of $12.12 \pm 0.90\%$ of the trials had to be removed from the EEG data, for younger adults: $11.21 \pm 1.27\%$ and for older adults: $13.03 \pm 1.27\%$. The number of rejected trials did not significantly differ between conditions and age groups (all $P \geq 0.05$). Baseline corrections were applied automatically on the epoched data with respect to a 100-ms prestimulus baseline. ERPs were then obtained by separately averaging across trials for each electrode and condition for each subject first, and then across subjects within each age group.

Previous studies have shown that effects of attentional control demands are unlikely to be observed in early ERP components (Duncan-Johnson and Kopell 1981; Ilan and Polich 1999; Rosenfeld and Skogberg 2006). Nevertheless, we also tested for age differences in early auditory processing of CV syllables, as reflected by differences in latency and amplitude of the P1, N1, and P2 components. Informed by previous findings (Ceponiene et al. 2008) and in line with the scalp topographies derived from the present data, which showed nonlateralized fronto-central scalp distributions of the P1, N1, and P2 component in all experimental conditions for younger and older adults, our analyses thus focused on mean amplitudes that were averaged across FCz, C1, and C2. After visual inspection of the grand average ERP data, peak amplitude and peak latency of the P1, N1, and P2 for each of the 2 low attentional control demand stimuli

(FR [+10] and FL [-10]) and for each of the 2 high attentional control demand stimuli (FR [-10] and FL [+10]) were defined as the most positive (P1 and P2) or negative peak (N1) in the individual averages in the following time windows: P1: 80–120 ms, N1: 120–200 ms, and P2: 200–300 ms after stimulus onset.

To identify the relevant electrode sites for the N450 modulation effect, topographical raw voltage maps and current source density (CSD) maps of the difference waveforms between high minus low attentional control demand conditions were analyzed (as depicted in Fig. 3). The CSD maps were computed using the Laplacian transformation with Brain Vision Analyzer. The signal was interpolated with a spherical spline interpolation procedure (Perrin et al. 1989; order of splines: 2; maximal degrees of Legendre polynomials: 10; approximation parameter λ : $1e-5$). Based on previous results (Larson et al. 2009) and on the topographical raw voltage, CSD maps derived from the present data, our analyses focused on the fronto-central (FCz, C1, C2) and parietal (Pz, P3, P4) sites. ERP peak amplitudes for analyzing the late negativity were defined as the most negative peak in the individual averages between 450 and 550 ms after stimulus onset across all attentional control demand conditions. All ERP mean amplitudes in each condition were parameterized as the mean voltage in a range of 25 ms before and 25 ms after each individual peak across trials. ERP mean latencies in each condition were indexed as the averaged time of the individual ERP peak amplitude across trials. ERP mean amplitudes and ERP mean latencies of all components were averaged across sites prior to analyses (Larson et al. 2009), resulting in the fronto-central and parietal region of interests (ROIs). To correlate neural activity to performance in this task, a measure reflecting the amplitude modulation was computed (cf. Rutman et al. 2010). Specifically, this measure was defined as the difference between ERP mean amplitudes in conditions of high and low attention control demands (mean ERP_{high demand} – mean ERP_{low demand}) in the time window of 450–550 ms after stimulus onset. We referred to this measure as the N450 modulation effect, and the effect was assessed for the fronto-central and parietal ROIs separately.

Statistical Data Analysis

The behavioral and ERP data obtained using the EEG version of the task were analyzed to examine age differences in: 1) The interaction between perceptual saliency and attentional focus; 2) performance in high versus low attentional control demand conditions; 3) the N450 modulation effect; and 4) the relations between individual differences in performance and the N450 modulation effect.

Behavioral Analysis

Age differences in the interaction between perceptual saliency and attentional focus in auditory perception were analyzed by using the auditory laterality index. The laterality index represents the extent of correct RE reports in relation to correct LE reports (i.e. $[RE - LE] / [RE + LE] \times 100$). It is used as an index of hemispheric lateralization in verbal processing and ranges from -100% to 100% (Marshall et al. 1975). Positive laterality indices indicate a RE advantage (REA, more report from the RE), whereas negative laterality indices indicate a LE advantage (LEA, more report from the LE). The laterality indices for younger adults and older adults were analyzed in a repeated-measures analysis of variance (ANOVA) with attentional focus (NF, FR, and FL) and number of perceptual saliency conditions (3 conditions) as within-subject factors and age group and sex group as between-subject factors. Age differences in performance in high versus low attentional control demand conditions were analyzed based on the percentage of correct reports. Performance under high attentional control demand was defined by the number of correctly reported syllables presented to the to-be-attended ear in conditions when perceptual saliency favored the nonattended ear (FR [-10] and FL [+10]), whereas performance under low attentional control demand (FR [+10] and FL [-10]) was defined by correct reports in conditions when perceptual saliency also favored the to-be-attended ear. A repeated-measures ANOVA with attentional control demand (low, high) and attended ear (FR, FL) as within-subject factors and age group and sex group as between-subject factors was calculated. Conflict costs were

calculated as ratio scores between correct reports in high and low attentional control demand conditions separately for FR and FL (i.e. [correct report low – correct report high]/[correct report high + correct report low] × 100).

As a general measure of auditory attentional flexibility, we computed an ATTIIndex, derived from the more extensive behavioral version of the task including 9 conditions of perceptual saliency. The ATTIIndex is based on the laterality indices for all 3 attentional conditions (NF, FR, and FL) across all 9 levels of perceptual saliency, defined as:

ATTIIndex

$$= \frac{\sum_{|IAI|=1}^9 [LI_{IAI}(FR) - LI_{IAI}(NF)] + \sum_{|IAI|=1}^9 [LI_{IAI}(NF) - LI_{IAI}(FL)]}{2 \cdot 9}$$

The ATTIIndex reflects the extent to which the participant could selectively attend either to the RE or to the LE stimulus.

In addition, we computed the percentage of correct reports in conditions with the high attentional control demand (CorrectReportIndex) derived from the ERP study as a direct measure of performance in this task. The CorrectReportIndex is based on the mean percentage of correct reports across FR and FL when perceptual saliency favored the nonattended ear. Pearson product-moment correlations were used to analyze the relations between each of the 2 performance indices and the magnitude of the N450 modulation effect at parietal sites. The N450 modulation effect was reflected (multiplied with –1) to facilitate the interpretation of the correlation indices.

EEG Analyses

To examine age differences in P1, N1, and P2 components and the N450 modulation effect, mean latencies and mean amplitudes were analyzed in a repeated-measures ANOVAs with attentional control demand (low, high) and attended ear (FR, FL) as within-subject factors and age group and sex group as between-subject factors. Sex as a between-subject factor in the repeated-measures ANOVAs did not reveal any main or interaction effects (all $P > 0.05$). Hence, sex was omitted as a factor in all subsequent analyses. Given that we were mostly interested in testing differences between different attentional control demand conditions and age differences therein, we focused on main effects of age and attentional control demand and on age group × attentional control demand interactions. The analysis of the N450 modulation effect was done separately for each ROI.

Whenever sphericity assumptions were violated ($P < 0.05$, Mauchly's test), the Greenhouse–Geisser correction was applied, and adjusted degrees of freedom and P -values of the analyses are reported. Effect sizes of main or interaction effects are given as η^2 , representing the proportion of variance of the dependent factor explained by the independent variable. Effect sizes of follow-up t -tests were given as Cohen's d . For all analyses, the alpha level was set at $P = 0.05$.

Results

Age Differences in the Interaction Between Perceptual Saliency and Attentional Focus

Three-way repeated-measures ANOVA analyzing the laterality indices revealed a significant 3-way interaction between perceptual saliency, attentional focus, and age group, $F_{2,23,109,20} = 4.76$, $P < 0.05$, $\eta^2 = 0.01$, indicating age differences in the interactions between perceptual saliency and attentional focus (Fig. 1).

The results of follow-up analyses for each age group indicated reliable main effects of attentional focus in both age groups, but with considerably larger effect sizes in younger, $F_{2,18,28,39} = 30.48$, $P < 0.05$, $\eta^2 = 0.45$, than in older adults, $F_{1,87,46,86} = 5.77$, $P < 0.05$, $\eta^2 = 0.03$, as well as main effects of perceptual saliency, but with higher effect sizes in older

$F_{1,27,31,78} = 98.29$, $P < 0.05$, $\eta^2 = 0.64$, compared with younger adults, $F_{1,26,30,21} = 87.79$, $P < 0.05$, $\eta^2 = 0.31$. In line with earlier findings (Passow et al. 2012), these results indicate that older adults were not as flexible in regulating their attentional focus as younger adults and that their performance was mainly driven by perceptual saliency.

Age Differences in the Effects of Attentional Control Demand due to Perceptual–Attentional Conflict

Regarding age-related performance differences between high versus low attentional control demand conditions, the repeated-measures ANOVA revealed a main effect of age group, $F_{1,49} = 13.31$, $P < 0.05$, $\eta^2 = 0.07$, attentional control demand, $F_{1,49} = 167.83$, $P < 0.05$, $\eta^2 = 0.58$, and attended ear, $F_{1,49} = 14.45$, $P < 0.05$, $\eta^2 = 0.06$. Importantly, the attentional control demand × age group interaction was reliable, $F_{1,49} = 16.26$, $P < 0.05$, $\eta^2 = 0.06$. Follow-up analyses confirmed that correct reports in high attentional control demand conditions were reliably lower in older adults than in younger adults, FR: $t(49) = -4.45$, $P < 0.05$, $d = 1.25$; FL: $t(49) = -3.59$, $P < 0.05$, $d = 1.00$, whereas age differences under low attentional control demand conditions were not significant, FR: $t(49) = -0.87$, $P > 0.05$; FL: $t(49) = -0.19$, $P > 0.05$ (Fig. 2A).

We also computed ratio scores of conflict costs, which reflect reduction in performance due to the perceptual–attentional conflict. Conflict costs were significantly lower in younger adults than in older adults across both conditions, FR: $t(49) = -4.64$, $P < 0.05$, $d = 1.31$; FL: $t(49) = -4.08$, $P < 0.05$, $d = 1.15$ (Fig. 2B).

Age Differences in Early Event-Related Potentials

In both age groups, the auditory CV stimuli elicited a typical sequence of P1, N1, and P2 ERP peaks (Figs 4 and 5). Regarding the P1 and N1 components, analysis of the grand average ERP data did not reveal any significant main effects of age group or interaction effect including age group (all $P > 0.05$). In contrast, the results of the repeated-measures ANOVAs based on P2 mean latencies showed a significant main effect of age group, $F_{1,49} = 50.93$, $P < 0.05$, $\eta^2 = 0.50$, reflecting reliably longer latencies in older compared with younger adults across all conditions (all $P < 0.05$). Similarly, the analysis of the P2 amplitude also revealed a significant main effect of age group, $F_{1,49} = 4.11$, $P < 0.05$, $\eta^2 = 0.08$, reflecting higher amplitudes in younger compared with older adults across all conditions (all $P < 0.05$). The mean P2 amplitudes and latencies are shown in Table 1.

Age Differences in Later Event-Related Potential

The topographical raw voltage (top panel) and CSD (bottom panel) maps showing the distribution of the difference between high and low attentional control demand conditions for younger and older adults are shown in Figure 3. The observed distributions are in line with earlier results and provided the basis for focusing the analysis of N450 modulation effects on fronto-central (FCz, C1, and C2) and parietal (Pz, P3, and P4) sites.

Stimulus-locked ERP grand average waveforms as a function of different degrees of attentional control demand in FR and FL are shown separately for younger and older adults in fronto-central (Fig. 4) and parietal ROIs (Fig. 5). In younger adults, a clear negativity starting at about 450 ms and lasting until about 550 ms after stimulus onset can be identified

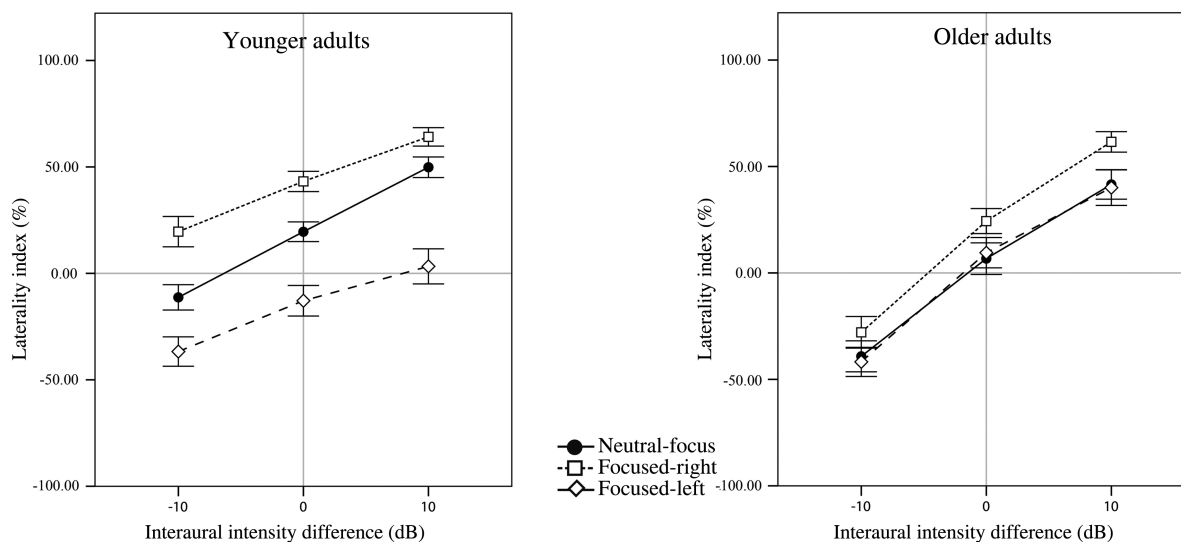


Figure 1. Mean laterality index (LI) for younger adults (left panel) and older adults (right panel) across 3 conditions of perceptual saliency and for each attentional focus: NF, FR, and FL. Error bars indicate 1 standard error (SE) of the mean.

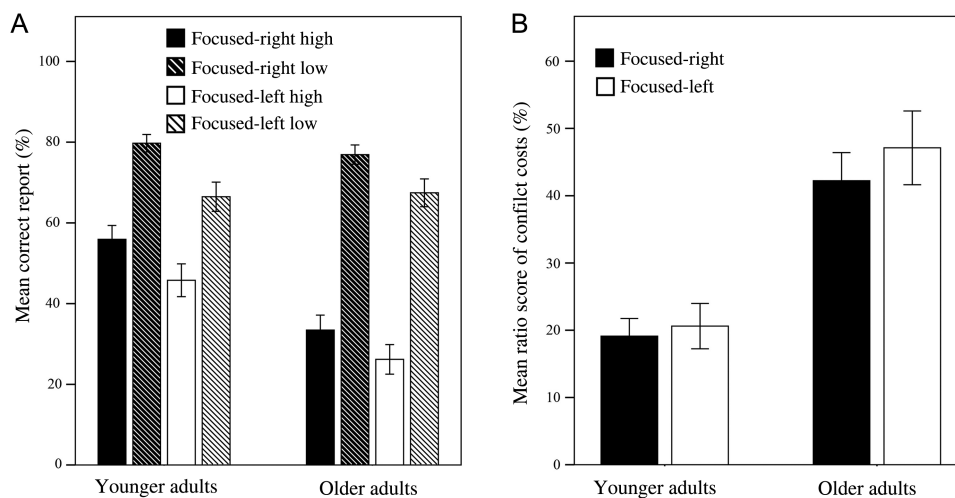


Figure 2. (A) Mean correct report (report of the syllable presented to the instructed ear) for younger adults (left) and older adults (right) in FR high, FR low, FL high, and FL low attentional control demand condition; (B) mean ratio score of conflict costs (correct report low – correct report high)/(correct report high + correct report low) \times 100 for younger adults (left) and older adults (right) for FR and FL conditions. Error bars indicate 1 SE of the mean.

across all conditions. In contrast, across all conditions, ERP grand average waveforms for older adults do not show a negative deflection. Crucially, in younger adults, amplitude of the late negativity varied as a function of attentional control demand.

With respect to mean ERP latencies, the repeated-measures ANOVA did not yield any significant main or interaction effect (all $P > 0.05$). Regarding the mean ERP amplitude in the fronto-central ROI, the results of the repeated-measures ANOVA revealed a statistically significant main effect of age group, $F_{1,49} = 16.35$, $P < 0.05$, $\eta^2 = 0.25$. Analyzing the age groups separately revealed a significant main effect of the attentional control demand in younger adults, $F_{1,24} = 8.42$, $P < 0.05$, $\eta^2 = .02$, but not in older adults ($P = 0.19$). Follow-up paired sample t -tests in younger adults showed larger negative deflections under conditions of high attentional control

demand relative to conditions of low attentional control demand in both focused-attention conditions, FR: $t(24) = -1.94$, $P = 0.06$, $d_z = 0.39$; FL: $t(24) = -2.15$, $P < 0.05$, $d_z = 0.43$ (Fig. 4).

Similarly, at the parietal ROI, the results of the repeated-measures ANOVA revealed a significant attentional control demand \times age group interaction, $F_{1,49} = 4.14$, $P < 0.05$, $\eta^2 = 0.01$. Results of follow-up ANOVAs separately for younger and older adults indicated a main effect of attentional control demand in younger adults, $F_{1,24} = 14.38$, $P < 0.05$, $\eta^2 = 0.04$, but not in older adults ($P = 0.50$). Follow-up t -tests in younger adults again revealed a significantly larger negative deflection under the conditions of high attentional control demand compared with the conditions of low attentional control demand for both focused-attention conditions, FR: $t(24) = -2.18$, $P < 0.05$, $d_z = 0.44$; FL: $t(24) = -3.37$, $P < 0.05$, $d_z = 0.67$ (Fig. 5).

Table 1

Mean (± 1 SE of the mean) P2 peak amplitudes and peak latencies for younger (YA) and older adults (OA) across all attentional control demand conditions

	P2 latency (ms)	P2 amplitude (nV)
FR high		
YA	252.92 \pm 2.90	5.50 \pm 0.64
OA	278.73 \pm 2.43	3.83 \pm 0.55
FR low		
YA	253.24 \pm 3.43	5.39 \pm 0.65
OA	271.31 \pm 3.17	3.80 \pm 0.62
FL high		
YA	251.841 \pm 3.83	5.62 \pm 0.63
OA	274.42 \pm 2.57	3.52 \pm 0.60
FL low		
YA	251.84 \pm 2.92	5.65 \pm 0.71
OA	273.42 \pm 2.61	4.03 \pm 0.61

OA, older adults; YA, younger adults.

Neural–Behavioral Correlations Between the N450 Modulation Effect and Performance

We computed an N450 modulation effect defined as the difference between ERP mean amplitudes in response to high and low attentional control demand conditions (high minus low) in the time window of 450–550 ms after stimulus onset. Pearson product–moment correlations between the N450 modulation effect and the independently assessed AT-Index in the behavioral session and the index of correct report (CorrectReportIndex; report of CVs from the to-be-attended ear) assessed in the EEG session were calculated separately for younger and older adults. In both age groups, the 2 performance indices correlated with each other, younger adults: $r = 0.45$, $P < 0.05$; older adults: $r = 0.48$, $P < 0.05$. The N450 modulation effect in younger adults was positively correlated with the ATIndex, $r = 0.40$, $P < 0.05$, and with the CorrectReportIndex, $r = 0.64$, $P < 0.05$ (Fig. 6). In older adults, the corresponding correlations were not reliable, ATIndex, $r = 0.20$, $P > 0.05$; CorrectReportIndex, $r = 0.08$, $P > 0.05$.

Discussion

This study sheds new light on the neural correlates of age-related deficits in attentional control of auditory perception. In younger adults, our results provide the first evidence for the N450 modulation effect during auditory perception. Crucially, individual differences in the magnitude of this N450 modulation effect were predictive of 2 performance measures, indicating flexibility in attentional regulation and performance accuracy. In contrast, the ERP waveforms of older adults did not show an identifiable late negativity. Analyses of condition effects around the 450–550 ms time window also did not reveal any amplitude modulation by attentional control demands in older adults.

Older Adults Show Less Efficient Attentional Control and More Reliance on Perceptual Salience

As has been found before, the younger adults participating in this study were capable of exerting attentional control to suppress salient but conflicting auditory stimuli (Tallus et al. 2007; Westerhausen et al. 2009, 2010; Passow et al. 2012). In contrast, older adults were much less able to flexibly regulate their auditory attentional focus. The age-related decline in

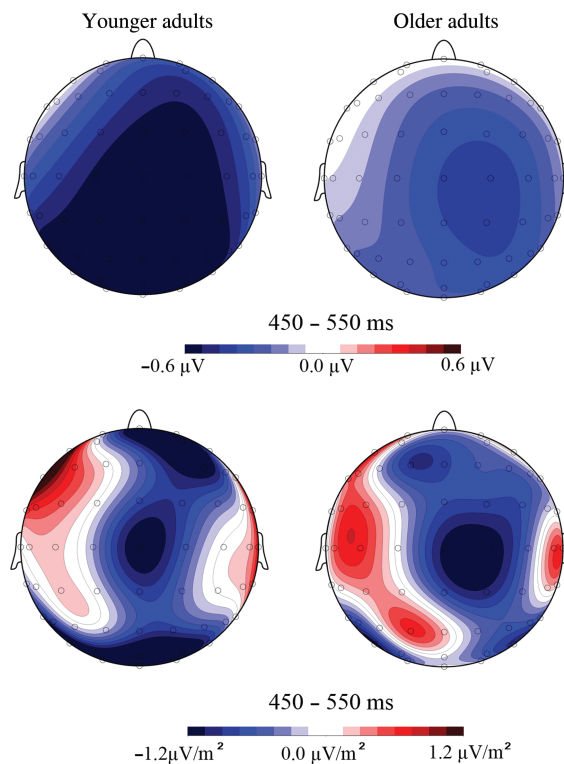


Figure 3. Topographical voltage (upper panel) and Laplacian (CSD) maps (lower panel) of the difference waveforms in the time window of the N450 modulation effect. Maps display top views of the scalp for the distribution of the difference between high minus low attentional control demand conditions for younger adults (left) and older adults (right) in the time window of 450–550 ms after stimulus onset. Based on this, the fronto-central (FCz, C1, C2; left panel) and parietal (Pz, P3, P4; right panel) ROIs were defined.

attentional flexibility reported here parallels the findings from earlier studies reporting age-related declines in cognitive control across a broad range of tasks (e.g. West and Baylis 1998; Kray and Lindenberger 2000; Hugdahl et al. 2001; Gazzaley et al. 2005; Spieler et al. 2006; Whiting et al. 2007; Gazzaley et al. 2008; Anderson et al. 2011). West and Baylis (1998), for instance, showed an increased Stroop interference effect in older adults in a context of high attentional control demand when frequently confronted with incongruent trials and not in a context of low attentional control demand when incongruent trials were rare. The increased Stroop interference effect is thought to result from older adults' inability to actively sustain attention on color-naming strategy across a high number of incongruent trials to support efficient task performance (West and Baylis 1998).

Furthermore, in both younger and older adults, the percentage of correct reports was lower when attentional control demand was high than when it was low. This indicates that both younger and older adults experienced greater difficulties in conditions when perceptual saliency and attentional focus were in conflict with each other. Older adults, however, were much more affected by such conflict than younger adults, showing a greater performance reduction in high conflict conditions. Relative to younger adults, older adults were less able to suppress salient perceptual influences from the nonattended ear in order to focus on syllables from the to-be-attended ear. Hence, older adults' behavior was

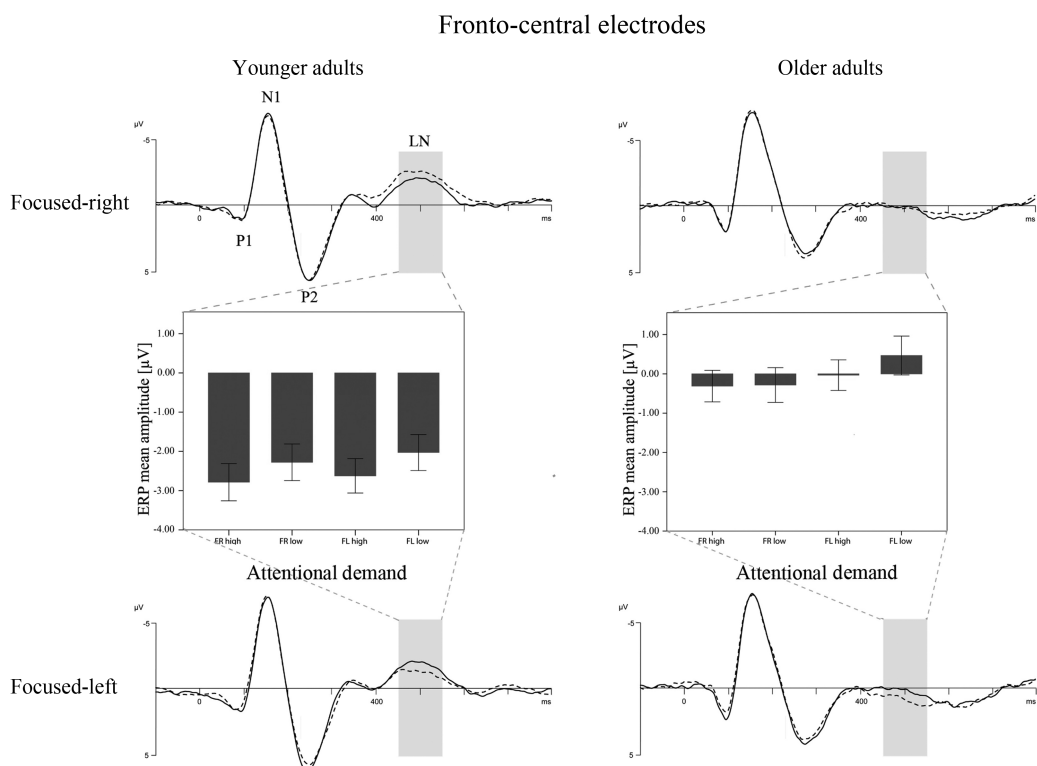


Figure 4. Grand averages of the stimulus-locked ERP waveforms at fronto-central electrodes for younger adults (left panel) and older adults (right panel) separately for FR (upper panel) and FL (lower panel) conditions. ERPs are shown as a function of interaural intensity difference: RE > LE (solid line) and LE > RE (dashed line). Insets indicate mean ERP amplitude separately for each age group across high and low attentional control demand conditions in FR and FL conditions. Error bars indicate 1 SE of the mean.

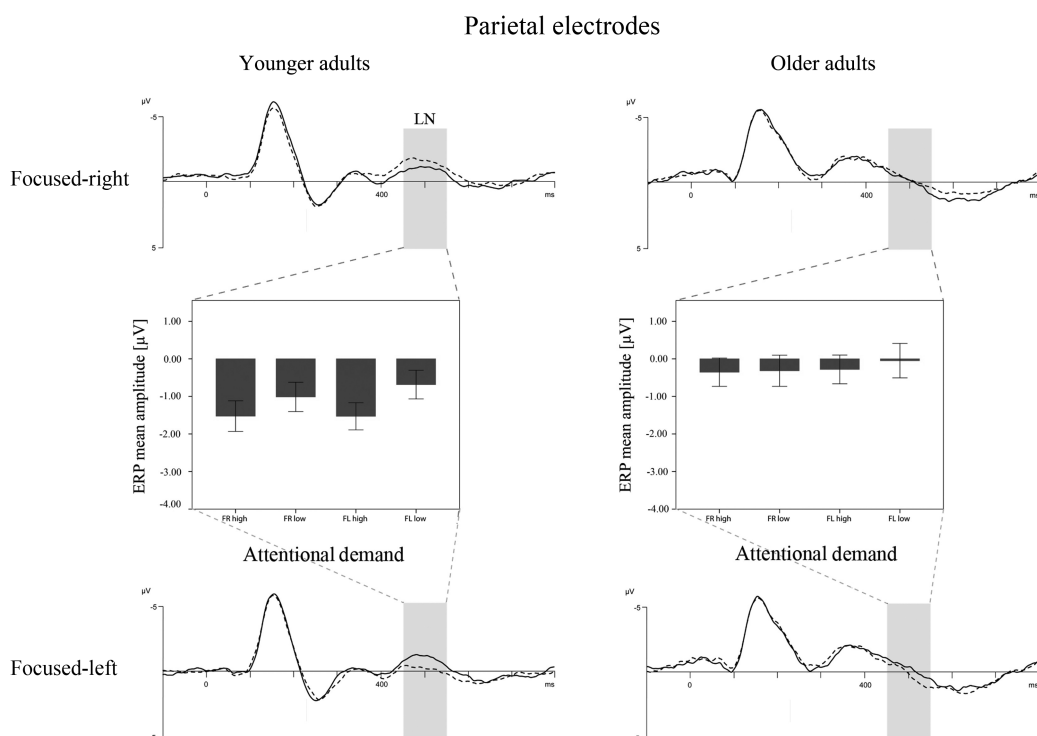


Figure 5. Grand averages of the stimulus-locked ERP waveforms at parietal electrodes for younger adults (left panel) and older adults (right panel) separately for FR (upper panel) and FL (lower panel) conditions. ERPs are shown as a function of interaural intensity difference: RE > LE (solid line) and LE > RE (dashed line). Insets indicate mean ERP amplitude separately for each age group across high and low attentional control demand conditions in FR and FL conditions. Error bars indicate 1 SE of the mean.

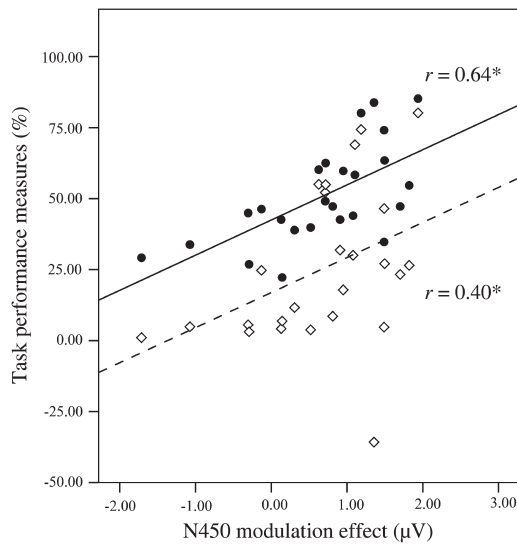


Figure 6. Scatter plot showing the relations between the reflected N450 modulation effect and (A) the selective attention index (ATTIndex; open rhombs, dashed line); and (B) the proportion of correct reports in the high attentional control conditions (CorrectReportIndex; black circles, solid line). Data refer to younger adults only. In older adults, no reliable correlations were observed; * $P < 0.05$.

primarily driven by perceptual saliency. The age-related stronger reliance on perceptual saliency parallels findings from a visual selective attention search task which showed that older adults were notably more susceptible to bottom-up attentional capture effects driven by cue validity than younger adults, particularly when multiple top-down strategies have to be maintained (Whiting et al. 2007). More recently, the neural correlates of age differences in suppressing task-irrelevant representations have also been studied in the context of visual working memory (Gazzaley et al. 2005, 2008; Jost et al. 2011). In an fMRI study, older adults showed a prominent deficit in suppressing cortical responses to task-irrelevant representations compared with their younger counterparts (Gazzaley et al. 2005). Using EEG, it has also been shown that this age-related suppression deficit appears to be restricted to the early visual processing stages (Gazzaley et al. 2008; Jost et al. 2011), suggesting that efficient filtering is delayed in older adults. These results corroborate the claim that attentional suppression is particularly vulnerable to the adverse effects of aging (e.g. Hasher and Zacks 1988).

From a more general perspective, the sensory and motor impairments associated with aging likely increase the need for attentional control in everyday life. At the same time, the present findings and related earlier results (Passow et al. 2012) show that the ability to effectively exert attentional control also declines with age. The combination of these 2 trends represents a major challenge for aging individuals (Lindenberger et al. 2000).

Early Auditory Processing is Fairly Resistant to Aging

As for early ERP components, in line with previous findings, we found that dichotically presented CV stimuli elicited a typical sequence of P1, N1, and P2 ERP peaks (Eichele et al. 2005; Sandmann et al. 2007; Bayazit et al. 2009) in both younger and older adults. However, these components were not sensitive to attentional control demands. The absence of a

significant main effect of condition on these components is in line with previous results that also did not find differences in amplitude or latency of earlier ERP components between congruent and incongruent Stroop trials (Duncan-Johnson and Kopell 1981; Ilan and Polich 1999; Rosenfeld and Skogsberg 2006). Taken together, these results suggest that effects of attentional control as reflected in our paradigm and Stroop tasks and as captured by ERP components are related to later processing stages of higher-order cognitive processing.

Furthermore, the effect of aging on these early ERP components was negligible in our data. Younger and older adults did not differ significantly with respect to the amplitude and latency of the P1 and N1 components, whereas an effect was found for the P2 component. The absence of a significant difference between the 2 age groups parallels the finding that the earlier processing stages, P1 and N1 ERP components, are relatively resistant to neurobiological aging in the auditory domain (Bertoli et al. 2005; Ceponiene et al. 2008). However, it might also be the case that age-related differences in early processing stages simply could not be captured by analyzing ERP components. Previous studies revealed evidence for an increased intertrial phase stability (Sander et al. 2012) and higher phase locking (Müller et al. 2009) during early sensory processing that reflected a stronger dependency on external stimuli in older adults. Thus, future research should examine whether older adults' increased dependency on the perceptual saliency of the stimuli in the present study may be related to age-related differences in oscillatory activity. Regarding the P2 component, parallel to previous findings (Anderer et al. 1996; Tremblay et al. 2003; Bertoli et al. 2005), we found that, relative to younger adults, older adults showed significantly diminished amplitudes and prolonged latencies. Tremblay et al. (2003) reported an age-related delay of P2 latencies in response to CV syllables but not to tones. The authors interpret this finding as reflecting age-associated neural impairments in detecting more complex acoustic signals, such as CV syllables. In general, however, studies investigating age-related changes of the P2 component revealed equivocal results, and the functional significance of the P2 is still not fully understood (Bertoli et al. 2005). Future studies are needed to better understand adult age differences in the amplitude and latency of the P2 when present.

Late N450 Amplitude is Sensitive to Attentional Control Demand in Younger Adults Only

Bayazit et al. (2009) found a late negativity elicited in a classical DL task without perceptual or attentional manipulation and interpreted this result in terms of this component's sensitivity to sensory conflict in the dichotomous inputs. In agreement with this general finding, the grand average ERP waveforms of younger adults showed a clear negativity in the time window of 450–550 ms after stimulus onset. More importantly, extending the results of Bayazit et al. (2009), the amplitude of this negativity was modulated by attentional control demands. Specifically, the amplitude of the negativity was larger in high attentional control demand when compared with low attentional control demand conditions. This N450 modulation effect is consistent with the increased negativity in response to incongruent Stroop trials (N450; e.g. West and Alain 1999; Liotti et al. 2000; Larson et al. 2009). In color-naming Stroop tasks, for instance, the color and the word

compete for the response. Thus, in incongruent trials, the automatic process of word reading needs to be suppressed to correctly name the color of the word. The high attentional control demand condition in our study resembles the incongruent trials in the sense that more salient, distracting perceptual inputs from the nonattended ear also have to be suppressed to report the less salient syllable from the to-be-attended ear.

In younger adults, the N450 modulation effect was present both at fronto-central and parietal sites. The fronto-central distribution is in line with previous studies using classical Stroop paradigms (West and Alain 1999; Liotti et al. 2000; Larson et al. 2009). In contrast, the more posterior parietal distribution parallels the results of studies using other conflict paradigms (Schirmer and Kotz 2003; Frühholz et al. 2009). Frühholz et al. (2009) interpreted the posterior shift reported in their study as a correlate of functional differences in attentional control between their paradigm and classical Stroop paradigms. In a recent fMRI study, it was found that both fronto-central and parietal regions are sensitive to attentional control demands assessed with the modified DL paradigm used in the present study (Westerhausen et al. 2010). Based on these findings, the authors posit that fronto-parietal and medial-lateral frontal networks are involved in DL performance. The N450 modulation effect at fronto-central and parietal sites observed in the younger adults of the present study is consistent with this claim.

Crucially, the N450 modulation effect was reliably correlated with 2 behavioral measures of selective attention. Younger adults who efficiently exerted their attentional control in an independently assessed variant of the DL task showed higher differences between ERP mean amplitudes in response to high versus low attentional control demand conditions in the ERP variant of the task. Furthermore, the behavioral performance derived from the ERP variant of the task also correlated positively with the N450 modulation effect, which suggests that the amplitude modulation reflects performance accuracy, with correct responses being associated with larger amplitude modulation. These neural-behavioral correlations are in line with the finding, showing that decreased performance on incongruent trials in a color-naming Stroop task is accompanied by an attenuated N450 in major depressive disorder patients (Holmes and Pizzagalli 2008). Taken together, the brain-behavior correlations observed in younger adults provide novel evidence for the auditory domain that the modulation of the late negativity in response to high versus low attentional control demands is a valid indicator of attentional processing in the context of the modified DL paradigm used in the present and other studies (Westerhausen et al. 2009, 2010; Passow et al. 2012).

In contrast to younger adults, the grand average ERP waveforms did not show a late negativity in the time window of 450–550 ms after stimulus onset under any of the conditions in older adults. Furthermore, the ERP mean amplitudes in the respective time window were not reliably sensitive to attentional control demands in older adults either. The absence of an N450 modulation effect in older adults confirms previous adult age differences in ERP studies that used the Stroop paradigm. These studies consistently found that the sensitivity of the N450 to attentional control demand was greatly reduced in older adults (West and Alain 2000; West 2004). Furthermore, these findings are paralleled by age differences in the N2 component, for tasks that require conflict monitoring

(Falkenstein et al. 2002; Bertoli et al. 2005; Hämmerer et al. 2010; Wascher et al. 2011). For instance, in a cued Go-Nogo task, the N2 amplitude difference between Nogo and Go trials (Nogo > Go), reflecting more conflict in Nogo than Go trials, was greatly attenuated in older adults (Hämmerer et al. 2010). Similarly, Wascher et al. (2011) showed that the N2, presumably reflecting the suppression of irrelevant cue processing in the context of an inhibition of return task, was absent in older adults. This finding was interpreted to indicate deficient inhibition of irrelevant stimuli in older adults. Thus, the severe attenuation of the late negativity and the absence of an N450 modulation effect reported here further support a decrease in conflict processing with advancing adult age. More specifically, the age-related attenuation of the respective neural correlates at fronto-central and parietal sites may reflect a deficit in flexibly recruiting the frontal-parietal attention network according to attentional control demands (Westerhausen et al. 2010; for related findings in the visual domain, see Prakash et al. 2009). In contrast to younger adults, the magnitude of the N450 modulation effect did not correlate significantly with the 2 behavioral measures of selective attention in older adults. These findings are expected, given that older adults made fewer correct responses, indicating a clear impairment in exerting top-down attentional control. Individual differences in cognitive functioning increase with advancing adult age, even within the normal or healthy range of functioning (de Frias et al. 2007; Lindenberger et al. forthcoming). Additional studies with larger and more heterogeneous older adult samples are needed to explore whether high-performing older adults would yield an N450 modulation effect that is more akin to the findings observed in younger adults.

Past research has shown that auditory selective attention modulates alpha oscillatory activity in the auditory cortex (see Weisz et al. 2011 for review). For instance, decreases in alpha oscillatory activity have been functionally attributed to the amplification of relevant and the inhibition of irrelevant properties of somatosensory (Babiloni et al. 2004) and auditory (Hartmann et al. 2012) inputs. Thus, future research exploring effects in the time-frequency domain may elucidate how focusing attention on relevant inputs from the attended ear and suppressing irrelevant inputs from the nonattended ear may modulate cortical oscillatory activity, and to what extent age-related differences in early sensory processing may be related to a deficit in synchronization of cortical activities. Furthermore, individual differences in the decline of neurotransmitter systems, possibly related to genetic factors, may contribute to individual differences in auditory attention among older adults (Bäckman et al. 2010) and should be taken into consideration. For instance, computational studies showed that aging-related declines in dopaminergic modulation reduce the representational distinctiveness of memory and perceptual stimuli (e.g. Li et al. 2001, 2006). Less distinctive perceptual representations could contribute to older adults' great susceptibility to salient but irrelevant auditory inputs and add further demands on older adults' suboptimal attentional control mechanisms.

Conclusion

This is the first study that provides evidence on neural correlates of adult age differences in overcoming perceptual-attentional conflicts during auditory perception. Using a DL task that manipulated perceptual saliency and attentional focus in

a fully crossed design, we found that older adults compared with younger adults exert attentional control less effectively and are less able to suppress distracting perceptual influences. As a consequence, older adults rely more on perceptual saliency when making perceptual decisions than younger adults. Crucially, only younger, but not older adults, showed a reliable N450 modulation effect. We conclude that the attentional control of auditory perception shows marked deficits in old age, presumably reflecting age-related changes in the fronto-parietal network engaged in attentional control of auditory perception. The generality and modifiability of these deficits remain to be determined.

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Notes

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