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Electrophysiological evidence for age effects on sensory memory processing of tonal patterns

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Abstract

In older adults, difficulties processing complex auditory scenes, such as speech comprehension in noisy environments, might be due to a specific impairment of temporal processing at early, automatic processing stages involving auditory sensory memory (ASM). Even though age effects on auditory temporal processing have been well-documented, there is a paucity of research on how ASM processing of more complex tone-patterns is altered by age. In the current study, age effects on ASM processing of temporal and frequency aspects of two-tone patterns were investigated using a passive listening protocol. The P1 component, the mismatch negativity (MMN) and the P3a component of event-related brain potentials (ERPs) to tone frequency and temporal pattern deviants were recorded in younger and older adults as a measure of auditory event detection, ASM processing, and attention switching, respectively. MMN was elicited with smaller amplitude to both frequency and temporal deviants in older adults. Furthermore, P3a was elicited only in the younger adults. In conclusion, the smaller MMN amplitude indicates that automatic processing of both frequency and temporal aspects of two-tone patterns is impaired in older adults. The failure to initiate an attention switch, suggested by the absence of P3a, indicates that impaired ASM processing of patterns may lead to less distractibility in older adults. Our results suggest age-related changes in ASM processing of patterns that cannot be explained by an inhibitory deficit.

Keywords

aging; audition; sensory memory; MMN; temporal processing

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Introduction

Various studies report that older adults have difficulties compared to younger adults when performing listening tasks that require temporal processing (for review: Martin & Jerger, 2005; Pichora-Fuller, 2003; Pichora-Fuller & Souza, 2003). Sensory memory processing is crucial for temporal processing in the auditory modality (Näätänen & Winkler, 1999). Of particular importance is the long perceptual store of auditory sensory memory (ASM) that maintains the temporal structure of complex sounds, including the sequential order of tones (Cowan, 1984; Massaro, 1972). The current study tests the hypothesis that aging is accompanied by impaired temporal processing associated with ASM. We tested frequency and temporal violations of two-tone patterns, both of which require temporal processing to be detected, in older adults and compared responses with younger adults. We predicted that because detection of both deviations of two-tone patterns requires temporal processing, deviance detection reflected by ASM would be impaired in older adults for both types of deviations.

MMN as a tool to study temporal processing in ASM

ASM can be investigated using the mismatch negativity (MMN) component of the event-related brain potentials (ERPs). ERPs provide a real time measure of information processing, and the methodology is therefore well-suited to investigate processing at several, even automatic, processing stages. MMN is generated by the outcome of a sensory-memory based comparison between a representation of the actual input and a prediction based on the previous stimulation (Schröger, 2005). Regularities, in the previous stimulation (e.g., temporal patterns) are extracted and used to predict the input. MMN is elicited when the actual input deviates from the prediction (the representation in ASM). Thus, MMN is an indirect index for the processing of the sound regularities in ASM. MMN is measured in the difference between the ERP elicited by a frequently occurring standard and the ERP elicited by an infrequent deviant (deviant-minus-standard ERPs). Usually it peaks in a negative deflection 100-200 ms from deviant onset, with topographical maxima at fronto-central electrode sites. Studies that showed MMN to pattern deviations suggest that MMN indexes not only the short, but also the long perceptual store of ASM. Deviations of discrete tone patterns (e.g., Schröger, Näätänen, & Paavilainen, 1992; Sussman, Ritter, & Vaughan, 1998; Sussman, Ritter, & Vaughan, 1999), as well as continuous tone patterns can elicit MMN (Alain, Woods, & Ogawa, 1994; Schröger, 1994; Tervaniemi, Maury, & Näätänen, 1994; Winkler & Schröger, 1995). MMN to tone patterns is also elicited when tone-frequencies (hereafter referred to as “frequency”) or tone durations are interchanged within a pattern. Thus, the overall spectral energy of tone patterns remains the same within the sequence for the standard and the deviant patterns, as no new frequencies are added, and no additional stimulation of new hair cells along the basilar membrane occurs, when the deviant is presented. Accordingly, MMN to interchanged tones within tone patterns cannot solely be explained by simple stimulus-specific adaptation of the neuronal response to repeated standard stimuli (smaller N1 amplitude of standards compared to deviants). Rather MMN can index automatic processing of temporal order in ASM (Bendixen & Schröger, 2008; Sussman et al., 1999; Winkler & Schröger, 1995).

Implications of ASM processing for involuntary attention

The detection of a salient deviation at the level of ASM can elicit an involuntary attention switch. When attention is involuntarily directed to salient or easily discriminated deviations, MMN can be followed by a P3a component (Escera, Alho, Schröger & Winkler, 2000). The P3a is a positive ERP waveform with a fronto-central distribution peaking at about 270 ms that is also measured in the deviant-minus-standard ERP waveform (Friedman, Cycowicz, &

Gaeta, 2001). The P3a reflects activation of an involuntary attention-switching mechanism (Dien, Spencer, & Donchin, 2004; Horváth, Winkler, & Bendixen, 2008; Polich & Criado, 2006). Thus, the P3a, along with the MMN, are valuable tools for assessing attention effects of temporal processing deficits among older adults.

Age effects on temporal processing of complex tone sequences

In older adults, deficits in temporal processing of more complex auditory patterns have been reported, such as those containing speech (Gordon-Salant & Fitzgibbons, 1993; Tun, 1998) and non-speech sounds (Fitzgibbons & Gordon-Salant, 1995; Fitzgibbons & Gordon-Salant, 2010). Gordon-Salant and Fitzgibbons showed that older adults have deficits in recognizing speech degraded by temporal waveform distortion (e.g., reverberant, time-compressed or interrupted speech). Using non-speech stimuli, temporal processing of isolated sound segments has been shown to be even more strongly impaired by age when sounds are presented within a context of a complex sound pattern (Fitzgibbons & Gordon-Salant, 1995; Fitzgibbons & Gordon-Salant, 2004; Fitzgibbons & Gordon-Salant, 2010). Gordon-Salant suggests that older adults problems with processing complex sound sequences might be due to a decrease in the sensitivity to the overall rhythm of a stimulus sequences (Gordon-Salant, 2005). Problems with discriminating changes of the temporal order of sounds observed in older adults are in line with this assumption (Fitzgibbons & Gordon-Salant, 1998; Gordon-Salant & Fitzgibbons, 1999; Shrivastav, Humes, & Aylsworth, 2008; Trainor & Trehub, 1989). Fitzgibbons and colleagues (Fitzgibbons, Gordon-Salant, & Friedman, 2006) found age effects on temporal order recognition to be independent from the stimulus presentation rate (see also: Trainor & Trehub, 1989). They proposed that older adults have a general difficulty with the processing of temporal order of auditory stimuli that is unrelated to age-related differences in processing speed. However, in a temporal order discrimination task, Shrivastav and colleagues (2008) revealed age differences only with fast presentation rates (≥ 5 tones per second) and short tone durations (20 ms). Temporal processing deficits, such as when sounds are embedded in a complex sequence, as well as deficits in temporal order processing observed in older adults suggests that at least some of the performance decline involving temporal processing may not be specific to speech but rather may be linked to temporal processing of complex auditory patterns. Given that the complexity involved in speech processing makes it more difficult to investigate the origin of temporal processing deficits *per se*, non-speech tone-sequences can be used as an alternative (Fitzgibbons & Gordon-Salant, 2010).

Factors contributing to temporal processing deficits

Several factors may contribute to temporal processing deficits observed in older adults. These include a general slowing of cognitive processing (Salthouse, 2000), an inhibitory deficit (Hasher & Zacks, 1988), or an impairment of higher cognitive functions such as working memory and attention (Grady & Craik, 2000). In addition, a specific impairment of sensory processing may also account for observed deficits (Lindenberger, Marsiske, & Baltes, 2000; but see also, Lindenberger & Ghisletta, 2009). However, Schneider and Pichora-Fuller (2000) emphasize that in order to understand causes of age-related deficits, perception and cognition must be seen as an integrated system, where possible interactions must be considered.

Alain and colleagues suggest that automatic central auditory processing is impaired in older adults (Alain, McDonald, Ostroff, & Schneider, 2004; for review: Alain, Dyson, & Snyder, 2006). Alain et al. (2004) recorded ERPs to gap stimuli in passive and active listening conditions, along with behavioral measures in the active condition. They minimized peripheral effects by making the stimuli equally discriminable to all participants. In the passive condition no MMN was elicited by the near-threshold deviant gaps in older adults.

However, in the active condition, older adults' neurophysiological responses were similar to the younger adults (N2b, P3b component), and they had similar gap detection behavioral performance. Alain et al. (2004) suggested that the lack of MMN to near-threshold deviant gaps in the passive condition was due to a deficit in automatic central auditory processing. They argued that the age-invariant results when participants performed a task, indicated deficits in automatic processing could be compensated for by top-down control. Importantly, studies that separated groups by age and several degrees of hearing loss showed that differences in auditory processing at the ASM level between younger and older adults could not be explained solely by impaired peripheral auditory processing in older adults (e.g., Abel, Krever, & Alberti, 1990; Gordon-Salant & Fitzgibbons, 1993; Gordon-Salant & Fitzgibbons, 2004).

Age effects on sensory memory processing

ASM processing has been mainly investigated in oddball paradigms using discrete tones. MMN amplitude reduction in older adults has been reported for deviants in duration (Karayanidis, Andrews, Ward, & Michie, 1995; Kiang, Braff, Sprock, & Light, 2009; Pekkonen et al., 1996; Schroeder, Ritter, & Vaughan Jr, 1996; Woods, 1992; for review: Pekkonen, 2000), inter-stimulus-interval (ISI) (Kisley, Davalos, Engleman, Guinther, & Davis, 2005), for deviance detection of short gaps in stimuli (Alain et al., 2004; Bertoli, Smurzynski, & Probst, 2002), and for frequency deviations. However, several studies have reported reduced MMN amplitude evoked by frequency deviants only when long (> 3 sec), but not when short (≤ 1.5 sec) ISIs are used (Gunter, Jackson, & Mulder, 1996; Mueller, Brehmer, von Oertzen, Li, & Lindenberger, 2008; Pekkonen, Jousmäki, Partanen, & Karhu, 1993; Pekkonen et al., 1996; Schroeder et al., 1996; Verleger, Neukäter, Kömpf, & Vieregge, 1991). While age effects on ASM processing of temporal deviations with short ISIs can be explained by an impairment of the automatic comparison mechanism, age effects with long ISIs might be due to a faster decay of the sensory memory trace in older adults (Cooper et al., 2006; Pekkonen, 2000, for review). Pekkonen (2000) suggested that only the automatic discrimination of duration deviation is impaired with age, whereas frequency deviation processing is more resistant. However, other studies found frequency MMN amplitude reduction also with short ISIs (Alain & Woods, 1999; Cooper et al., 2006; Czigler, Csibra, & Csontos, 1992; Schiff et al., 2008).

There is some controversy over why the MMN amplitude is reduced for detection of these feature deviants in aging adults. It has been suggested that reduced MMN amplitude in older adults is partly due to age effects on N1 amplitudes of standard stimuli (larger N1 amplitude), resulting in a smaller deviant-minus-standard wave (e.g., Alain & Woods, 1999). The P1-N1-P2 complex is seen as index of detection of an acoustic event by neurons in auditory cortex (Burkard & Eggermont, 2007). Larger N1 amplitude in older adults might be due to inefficient filtering (sensory gating) or impaired inhibition of irrelevant information (Amenedo & Diaz, 1999; Fabiani, Low, Wee, Sable, & Gratton, 2006; Sable, Low, Maclin, Fabiani, & Gratton, 2004). This would be in line with the inhibitory deficit hypothesis (Hasher & Zacks, 1988). Besides modulation of the sensory input (N1) caused by an inhibitory deficit, the sensory input might also be modulated by a more specific impairment of temporal processing. Thus, age might not only modulate the ASM mechanism, but already the sensory input to the MMN generators.

In conclusion, age effects on sensory memory processing have mainly been investigated in oddball paradigms using separated tones and temporal (duration, gap) or frequency deviants. These studies provide evidence for an impairment of sensory memory processing of temporal aspects of simpler sound deviations in older adults (Pekkonen, 2000), but do not address the temporal processing skills associated with more complex sequence or pattern detection.

Aims of the present study

Using a passive listening paradigm, we employed two-tone patterns to investigate age effects on auditory temporal processing in ASM. Unique to our study, we tested age effects on sensory memory processing of patterns deviations, when the deviation is evoked by temporal and frequency parameters separately. We tested the hypothesis that age modulates the processing of frequency and temporal deviations of tones embedded in a two-tone pattern differently than reported for frequency versus temporal deviations of single tones (for review, Pekkonen, 2000). To test this hypothesis, MMN was recorded to sounds that deviated in the spectral regularity (frequency deviants) and in the temporal regularity (temporal deviants) of two-tone patterns. If, as reported for separated tones (Pekkonen, 2000), frequency deviance detection is more resistant to impairments, then we should see an asymmetry with impaired ASM processing of temporal, and preserved ASM processing of frequency aspects of tone patterns in older adults. In this case, older adults are expected to show smaller MMN amplitudes compared to younger adults to the temporal, but not to the frequency pattern deviants. However, because pattern processing involves the long perceptual store of ASM (Cowan, 1984; Massaro, 1972), and pattern deviants might violate an integrated sensory memory representation of temporal and frequency features (Alain, Cortese, & Picton, 1999; Gomes, Bernstein, Ritter, Vaughan, & Miller, 1997), deviations within patterns might be modulated differently by age than simple deviations on single tones, overall resulting in similar age effects for both deviants. Then we expect that older adults will have smaller amplitudes for both temporal and frequency pattern MMN compared to younger adults. In addition, we will investigate consequences of age effects on ASM processing (MMN) on the attention-switching mechanism (P3a). As involuntary attention-switching to a salient deviation requires prior detection of the deviation in ASM, we expected smaller MMN amplitudes in older adults compared to younger adults to go along with smaller P3a amplitudes.

Materials and Methods

Participants

14 healthy younger and 17 healthy older adults participated in the study. All of them were right-handed. Three participants were excluded from the study who had hearing thresholds higher than 35 decibels effective sound pressure (dB SPL_{eff}; i.e., the root mean square of the instantaneous sound pressure over a given interval in time) at frequencies of 250, 500, 1000 and 2000 Hz (Hickish, 1989). In addition, one older participant was excluded due to technical problems (1 male), and one younger participant (1 female) due to excessive EEG artefacts. The results reported in the following are based on a sample of 13 younger participants (7 female, mean age: 25.23 years, sd: 3.54 years) and 13 older participants (7 female, mean age: 66.62 years, SD: 2.84 years). There were no reported histories of neurological or psychiatric diseases and none of the participants used drugs that would affect central nervous system functions. At the time of testing, all participants were in a condition of good health. However, some of the older participants and one of the younger participants had histories of illnesses (coronary heart disease, younger: n=1; hypertension, older: n=4; hypothyreosis, younger: n=1, older: n=4; prostatahyperplasie, older: n=2 and mild diabetes type II, older: n=2, with no reported side effects of the medication). The Mini-Mental State examination (MMSE; Folstein et al., 1990) was performed on all participants (a score higher 27 points was required). Performance in the MMSE did not differ between groups (younger mean: 29.54, sd: 0.66; older mean: 29.15, sd: 0.90; Kruskal-Wallis-Test with $\alpha = .05$: $p = .27$). Participants were matched according to years of overall, school-/university- and musical-education (none of the participants was an expert musician) (table 1). Additionally, the subtest Digit-Span of the German version of the Wechsler Memory Scale Revised (WMS-R; Härtling et al., 2000) was conducted as measure of working memory performance.

Younger participants scored higher on the Digit-Span subtest (younger: mean: 18.54, sd: 3.26; older: mean: 15.00, sd: 4.24; Kruskal-Wallis-Test with $\alpha = .05$: $p < .05$). According to the declaration of Helsinki, written informed consent was obtained from each participant prior to the experiment.

The present experiment was part of a larger study that included another experiment with five-tone patterns. Results from the five-tone pattern experiment will be reported elsewhere.

Stimuli and procedure

Stimuli

Sounds were presented continuously in a two-tone pattern with a temporal and a frequency regularity (Fig. 1). Tones had a 40 ms tone-duration (5% rise-fall time). The temporal regularity was a two-tone ISI pattern: 210 ms, 560 ms. The frequency regularity was a two-tone frequency pattern: 392 Hz, 349 Hz. Rare temporal pattern deviants (T condition) (two-tone ISI pattern: 100 ms, 560 ms) and rare frequency pattern deviants (F condition) (two-tone frequency pattern: 392 Hz, 440 Hz) occurred with a 8.3 % probability per deviant type. Another condition was used to derive standard stimuli to calculate the deviant-minus-standard ERP waveforms. This “standard condition” presented the two-tone deviant patterns equally distributed (physically matched to the temporal pattern deviant, $p = .5$, and to the frequency pattern deviant, $p = .5$).

Sounds were generated and presented continuously using Matlab 7.1 (Mathworks). Sounds were calibrated (HEADacoustics HMS III.0) and stimulus intensity was adjusted to 57 dB above the individual hearing threshold (table 2). The individual hearing threshold was measured using an automated psychoacoustic test procedure (Tucker-Davis-Technologies [TDT, System III]) and associated software (RPvdsEx) from the “Leipziger Inventar für Patientenpsychoakustik” (LIPP; Bungert-Kahl, Biedermann, Dörrscheidt, von Cramon, & Rübsamen, 2004). Audiograms were obtained using a yes/no (heard/not-heard) paradigm. Thresholds were measured by applying an adaptive up-down method (Levitt, 1971). The individual hearing threshold was calculated by averaging over tone-frequencies relevant for the experiment (250 and 500 Hz) and the left and right ear (table 2).

Procedure

Participants were seated in a comfortable chair in a sound-attenuated room. Stimuli were presented binaurally through headphones (Sennheiser, HD 25-1, 70 Ω). Participants were instructed to ignore the auditory stimulation and watch a self-selected silent (subtitled) movie during electroencephalography (EEG) recordings. The computer screen was placed behind a glass pane outside the chamber at a distance of 172 cm. There were three blocks for each condition. Each condition contained 1800 patterns (For the condition that contained deviants we used 150 deviant patterns and 1650 non-deviant patterns. For the “standard condition” we used 900 temporal and 900 frequency standard patterns). Blocks were presented randomized within the whole experiment for each participant. Prior to the experiment measures of the individual hearing threshold and tests were conducted (see participants section). Therefore, the total session time including all six conditions, all tests, electrode placement and breaks, was approximately 4 hours (experiment duration ~ 128 min).

Electrode placement and EEG recording

The EEG was recorded continuously with an electrode cap using the following scalp locations (modified 10-20 International system; Picton, Alain, Otten, Ritter, & Achim, 2000) Fz, Cz, Pz, Oz, Fp1, Fp2, AF3, AF4, F7, F8, F3, F4, Fc5, Fc6, Fc1, Fc2, T7, T8, C3, C4,

Cp5, Cp6, Cp1, Cp2, P7, P8, P3, P4, PO3, PO4, O1, O2. Additional electrodes were placed at the tip of the nose and at the right (RM) and left (LM) mastoids. The EOG was recorded using a montage with three monopolar EOG channels (Schlögl et al., 2007). The three EOG electrodes were positioned above the nasion, and below the outer canthi of the eyes, forming a rectangular triangle. Horizontal and vertical EOG components were captured through bipolar EOG channels “left-central” and “central-right”. EEG and EOG signals were amplified by BioSemi Active-Two amplifiers and sampled at 512 Hz.

Data reduction and analysis

Event-related potentials

ERP data for deviants and standards was re-referenced to the average of the mastoids ((LM + RM)/2) to increase the signal-to-noise ratio at the electrodes used for statistical analyses (Schröger, 2005). For the purpose of eye correction, the EEG and EOG were filtered off-line using a 1-100 Hz band-pass filter (Kaiser window), then filtered again using a 20 Hz low-pass filter (Kaiser window) before generating epochs. Epochs of 750 ms were created, which include a 100 ms pre-stimulus period. The epochs began at the stimulus onset of the first tone of the two-tone pair that preceded the frequency pattern deviant/standard, or the temporal pattern deviant/standard (Fig. 1), and were averaged separately for each stimulus type (deviant and standard) in each condition (T, F). With these epochs, the frequency deviant/standard onset was at 250 ms, while the temporal deviant/standard onset was at 140 ms. The pre-stimulus period served as the baseline for the amplitude measurements. Epochs with amplitude changes exceeding $\pm 75 \mu\text{V}$ were rejected from further processing. Deviant-Standard ERPs were calculated by subtracting the average ERP for each participant elicited by standard stimuli from that elicited by deviant stimuli each averaged over the respective time window, separately for MMN and P3a component and separately for the conditions.

Global field power

The Global Field Power (GFP) provides a reference-independent measure of response strength (Hamburger & Burgt, 1992; Lehmann & Skrandies, 1984; Murray, Brunnet & Michel, 2008). Furthermore, as the GFP is a global measure of the electrical field at the scalp, it is not prone to the experimenters' selection of a single electrode or set of electrodes for the analysis. The GFP was calculated as the root-mean square across the average-referenced electrode values of the standard ERP waves for evaluating the P1 wave, and for the deviant-standard ERP difference waves to evaluate the MMN and P3a components, separately for each age group in each condition (Lehmann & Skrandies, 1984). As the GFP calculation uses all scalp electrode positions, noisy electrode channels were interpolated for two participants at single blocks of the experiment (one older: electrodes F8, O1; one younger: electrodes Oz, O2).

For the purposes of statistical analyses, individual peak latencies and amplitudes were measured for each participant on the basis of the peaks obtained using the GFP calculations. The peaks of power were labeled referring to the respective component peaks visible in the ERP waveforms, i.e. P1, N1, MMN and P3a. Due to the fast stimulation rate, the N1 wave was not visible in the GFP and thus not further analyzed. Table 3 shows the peak latency (and time window) used to calculate the mean amplitude of the P1 component evoked by the first tone, and the MMN and P3a components evoked by the second tone. One-sample Students t-tests were conducted to determine whether the mean amplitudes of the GFP in the latency range of the P1, MMN and P3a components were significantly greater than zero (one-tailed criterion, 95% confidence interval). Mixed model repeated-measures ANOVA were conducted to analyze effects of age-group (between-subjects factor age: younger,

older) and deviant type (within-subjects factor condition: T, F) on the P1, MMN and P3a amplitude.

When components were statistically present (significantly greater than zero amplitude), and latency differences between age groups or conditions were evident by visual inspection, the peak latencies of the components were compared using a jackknife-based analysis (Kiesel, Miller, Joliceur, & Brisson, 2008; Miller, Ulrich, & Schwarz, 2009). Component latencies were measured using the following time windows: P1: 30-100 ms post-stimulus onset; MMN: T condition 100-190 ms and F condition 100-220 ms post stimulus onset; P3a younger adults: T condition: 200-360 ms and F condition: 220-360 ms post-stimulus onset). The jackknife-based method was used to scale the peak latency in the GFP measured at subsets of the grand-average ERP. Subsets were generated by using data from an iteration of $n-1$ participants (N -different-leave-out-one subsets) of the original sample included in the grand-average ERP (Miller et al., 2009). This way the standard error of the estimated component peak time was derived. In order to compare the T and F conditions relative to similar onset, the MMN latencies in the T condition were subtracted by 140 ms, and subtracted by 250 ms in the F condition. For the purpose of statistical analysis, estimates of the individual participants latencies (o_1, \dots, o_n) were calculated from the sub average scores (j_1, \dots, j_n) using the following equation: $o_i = n \bar{J} - (n-1)j_i$ (Smulders, 2010) (see Table 4). Mixed-model repeated-measures ANOVAs were conducted to examine effects of age (between-subjects factor age: younger, older) and deviant type (within-subjects factor condition: T, F) on the P1 and MMN latency. Effects of deviant type on the P3a component were only tested for younger adults, as there was no defined P3a peak visible in older adults (ERP and GFP).

Significance was tested with a two-tailed criterion and a 95% confidence interval.

Topography

The global dissimilarity (DISS) provides an index of the difference between two electric fields after normalizing the field strength (Lehmann & Skrandies, 1984; Murray et al., 2008). The DISS allows identifying potential age group differences in the ERP components topography. Numbers closer to 2 indicate topographic incongruence and numbers closer to 0 indicate topographic homogeneity. The DISS was calculated as the square root of the mean of the squared differences between average-referenced ERPs of each age group at all scalp electrodes after normalizing the data by dividing the mean voltage at the respective components time window by its own GFP (Murray et al., 2008).

Spherical spline interpolated isocontour voltage maps (VM) of the grand-average ERPs averaged over the respective time window were derived to show the P1, MMN, and P3a topography separate for the age groups and conditions. As the VM calculation uses all scalp electrode positions, noisy electrode channels were interpolated for two participants at single blocks of the experiment (one older: electrodes F8, O1; one younger: electrodes Oz, O2).

Results

Effects of age and condition on P1 component

In both age groups P1 was visible in the ERPs (Fig. 2) and significantly present in the GFP (calculated at standard ERPs) in both the T and F conditions ($p < .01$) (Fig. 4 a). There were no significant effects on the GFP amplitude (main effect of condition, $p = .46$; main effect of age group, $p = .27$; interaction of condition \times age group, $p = .29$) or latency (main effect of condition, $p = .52$; interaction of condition \times age group, $p = .89$) in the range of P1 component. However, there was a tendency toward a shorter P1 latency in the older adults (main effect of age group, $F(1,24) = 4.01$, $p = .06$, $\eta_p^2 = 0.14$). The DISS indicated

homogeneous topographies in the range of P1 for the younger and older adults in both the T (DISS = 0.29) and the F (DISS = 0.30) conditions. Voltage maps show a maximal amplitude of P1 component over fronto-central electrode sites for both age groups and conditions (Fig. 5 a).

N1 wave

In both age groups and both conditions N1 wave was visible, but very small and positively shifted, in the ERP (Fig. 2). However, no peak could be identified in the GFP in the range of N1 (calculated at standard ERPs) (Fig. 4 a), which was likely due to the rapid presentation rate (Sussman, Steinschneider, Gumenyuk, Grushko, & Lawson, 2008).

Effects of age and condition on MMN component

In both age groups and both conditions MMN was visible in the deviant-standard ERP (Fig. 3) and significantly elicited in both conditions in the GFP ($p < .01$) (calculated at deviant-standard ERPs) (Fig. 4b). Younger adults had greater signal strength (larger GFP amplitude) in the range of MMN compared to older adults (main effect of age group, $F(1,24) = 5.00$, $p < .05$, $\eta_p^2 = 0.17$). There was no main effect of condition on the GFP amplitude ($p = .65$) and there were no interactions (interaction of condition \times age group, $p = .68$). There were no main effects or interactions on the MMN latency (main effect of condition, $p = .53$; main effect of age group, $p = .93$; interaction of condition \times age group, $p = .41$). The DISS index indicated somewhat homogeneous configurations of MMN comparing younger and older adults in both the T (DISS = 0.82) and the F (DISS = 0.65) conditions. Voltage maps show maximal MMN amplitude over the fronto-central scalp in both age groups and conditions (Fig. 5 b).

Effects of age and condition on P3a component

P3a was visible in the ERP in both conditions only in the younger age group (Fig. 3). Thus, P3a was only tested against zero in the younger group. P3a was significantly present in younger adults in both conditions in the GFP ($p < .01$) (calculated at deviant-standard ERPs) (Fig 4 b). The GFP amplitude in the range of P3a was larger in the younger compared to older adults (main effect for age group, $F(1,24) = 20.05$, $p < .01$, $\eta_p^2 = 0.46$). Additionally, the GFP amplitude was larger in the T compared to the F condition (main effect condition, $F(1,24) = 4.59$, $p < .05$, $\eta_p^2 = 0.16$). This effect was due to a larger GFP amplitude in the T compared to the F condition in younger adults (interaction of condition \times age group, $F(1,24) = 6.08$, $p < .05$, $\eta_p^2 = 0.20$). As there was no defined P3a peak in older adults, P3a latency was only analyzed in younger adults. Younger adults showed shorter latencies in the T compared to the F condition (main effect of condition, $F(1,12) = 14.05$, $p < .01$, $\eta_p^2 = 0.54$). The DISS indicated relatively homogeneous topographies in the range of P3a for younger and older adults in the T (DISS = 0.64) and slightly inhomogeneous topographies in the F (DISS = 1.06) conditions. In the younger group voltage maps show maximal P3a amplitudes over the fronto-central scalp in both conditions (Fig. 5 c).

Discussion

Automatic processing of temporal and frequency pattern deviations was demonstrated by MMN elicitation in younger and older adults. Our results are consistent with previous findings in younger adults showing passive detection of temporal and frequency deviations to tone-patterns (e.g., Alain et al., 1999; Sussman et al., 1998; Winkler & Schröger, 1995). Our results are also consistent with Alain and Woods (1999) who found automatic processing of frequency pattern deviations in older adults. Importantly, we extend their findings by showing that temporal deviations of two-tone patterns are also automatically processed in older adults.

Less robust processing of pattern deviations in older adults

Even though MMN was elicited in younger and older adults, MMN amplitude was reduced in older adults, consistent with Alain and Woods (1999). One explanation for the decline in MMN amplitude in older adults is that it is at least in part due to an increase in the amplitude of the standard (N1) ERP seen in older adults (e.g., Alain & Woods, 1999; Fabiani et al., 2006; Amenedo & Diaz, 1999; Sable et al., 2004). Thus, when the standard is subtracted from the deviant, the result would be a smaller MMN amplitude. In the current study, however, the N1 wave to standards (first tone) was strongly attenuated in the ERPs, and not visible in the GFP. Previous research showed that at fast stimulus presentation rates (ISI: 150 ms) only the P1 component of the P1-N1-P2 complex is elicited in adults (Sussman et al., 2008). Thus, P1 can be seen as a more reliable indicator of sound onset detection in auditory cortex when fast stimulus presentation rates are used. Although, in the current study only P1 component to standards (first tone) was analyzed, visual inspection showed no age effects on the N1 wave (first tone) in the ERPs. Although visual inspection showed slightly larger P1 amplitude in older adults, P1 amplitude was not statistically modulated by age. There was a tendency toward a shorter P1 latency in older adults. This would be in line with the assumption of an inhibitory deficit in older adults, whereas the inhibition of irrelevant sounds in younger adults results in attenuation as well as a delay of the neuronal response. However, age effects on the P1 latency were not statistically present. Our results match with a study that did not find age effects on P1 and N1 using rapid stimulus presentation rates (Papanicolaou, Loring, & Eisenberg, 1984). Furthermore, our results are in line with evidence that early sensory gating is preserved in older adults (Guerreiro, Murphy & Van Gerven, 2010; Thomas et al., 2010). Guerreiro and colleagues suggest that older adults do not show inefficient filtering, i.e. an inhibitory deficit, when irrelevant sounds are ignored and thus filtered at an early processing stage. Beyond that the age invariant N1 amplitude to standard stimuli in our paradigm could be due to the use of tone patterns, which minimize stimulus-specific adaptation and thus age differences in the stimulus-specific adaptation of the neural response to the standard stimuli. Alternatively, different characteristics of the two-tone pattern regarding stimulus-specific adaptation and age effects on stimulus-specific adaptation compared to unpaired stimuli have to be considered (Loveless & Hari, 1993). In contrast to an unpaired paradigm Loveless and Hari found the transient magnetic response (N100m) to abrupt acoustic events (noise burst) in a paired stimulus paradigm to be not only modulated by the stimulus presentation rate, but also the perceptual grouping of the tones. In conclusion our results suggest that the smaller MMN amplitude in older adults cannot be solely explained by an inhibitory deficit or changes in the stimulus-specific adaptation of the neuronal response to the standard stimuli (i.e. larger N1 to standards) in older adults, but was either caused by an impaired deviant representation in ASM (i.e. impaired regularity extraction) or by an impairment of the comparison mechanism itself.

Furthermore, the current results are in line with the assumption that deficits in temporal processing in older adults are due to impaired central auditory processing and cannot solely be explained by changes in peripheral hearing (Alain et al., 2006; Gordon-Salant & Fitzgibbons, 1993; Gordon-Salant & Fitzgibbons, 2004). In the current study participants passed an extensive hearing screening, whereas older participants' had higher hearing thresholds compared to younger participants only at high frequencies (2000 Hz), but not at low frequencies (250, 500, 1000 Hz). To compensate for potential differences in peripheral hearing, sound intensities were adjusted to the individual hearing threshold.

Similar age effects on the processing of temporal and frequency pattern deviations

MMN amplitudes evoked by both temporal and frequency pattern deviants were attenuated in older adults. As mentioned previously, for single tones that are not embedded in a tone pattern, it has been suggested that the MMN mechanism for temporal (duration, ISI, gap)

deviants is impaired, whereas the frequency MMN mechanism is preserved (Gunter et al., 1996; Karayanidis et al., 1995; Kiang et al., 2009; Mueller et al., 2008; Pekkonen et al., 1996; Schroeder et al., 1996; Verleger et al., 1991; for review: Pekkonen, 2000). This assumption of asymmetric age effects on ASM processing between temporal and frequency deviations of tones seems not to hold for the processing of tone patterns. A possible reason that age effects on processing pattern deviations differ from processing single tone feature deviants might be that different features of tone patterns are represented in a more unified sensory memory representation (Alain et al., 1999; Gomes et al., 1997). Because pattern processing involves the detection of the temporal order of tones, impaired processing of pattern deviations likely resulted in less robust processing of both temporal and frequency deviations of the two-tone patterns.

Time invariant processing of pattern deviations in older adults

There were no age effects on the latency of the MMN responses. This is in line with previous research findings (Schiff et al., 2008). However, other studies showed a latency increase for frequency MMN (Cooper et al., 2006; Verleger et al., 1991), and also for duration MMN (Cooper et al., 2006). In contrast to a general slowing account (Salthouse, 2000), our results suggest that the processing at the level of ASM is not necessarily decelerated with age.

Age effects on involuntary attention

In the younger adults, the P3a was significantly elicited to both temporal and frequency pattern deviants, but the P3a amplitude was significantly larger when elicited by temporal pattern deviants. Thus, although both types of pattern deviations were detectable (indexed by MMN), temporal pattern deviants that deviate more strongly from the rhythm of the stimulation might have been more disruptive in the passive listening condition, and therefore stronger in triggering an attention switch (observed as a larger amplitude P3a).

In contrast to younger adults, P3a was not observed in older adults to either of the pattern deviants. As suggested by the attenuated MMN amplitude in older adults, deviants might have been processed to a lesser degree in older adults, and therefore have been perceived as less salient. Our results are in line with the assumption that there is diminished attentional orienting in older adults (Fjell & Walhovd, 2004). Several studies report reduced P3a amplitude in older adults in active and passive paradigms (Gaál, Csuhaj, & Molnár, 2007; Knight, 1987; Kiang et al., 2009; Fjell & Walhovd, 2004). Absence of P3a in older adults in a passive auditory paradigm has been reported previously (Czigler et al., 1992). Czigler and colleagues speculated that the deviant was not processed beyond automatic deviant detection because of a smaller processing capacity (Light, 1991) or a higher threshold for stimulus orienting in the older. Furthermore, there is evidence of a P3a delay in older adults (Fjell & Walhovd, 2004; Gaál et al., 2007; Horváth, Czigler, Birkás, Winkler, & Gervai, 2009). Our P3a results suggest that impaired sensory memory processing impacts the allocation of involuntary attention, by decreasing the distractibility (Dien et al., 2004; Polich & Criado, 2006). In contrast there is also evidence for an increase in distractibility in older adults, which can be explained by the inhibitory deficit hypothesis and might be related to deteriorated frontal lobe functions (Andrés, Parmentier, & Escera, 2006). According to the inhibitory deficit hypothesis (Hasher & Zacks, 1988) a decrease in the ability to inhibit irrelevant information in older adults may cause an increase in distractibility. However, Guerreiro et al. (2010) suggest that in audition an early pre-attentive filtering mechanism (e.g. thalamus, brainstem, cochlea) is preserved in old age, whereas there seems to be a deficit in later filtering. Older adults do only show higher distractibility when the stimulation is attended and thus filtered at later processing stages, but not if it is already filtered at early processing stages. In our study irrelevant standard stimuli were ignored and

might have been efficiently filtered at early processing stages. However, our results show that deviations triggered an attention switch in younger (P3a) but not in older adults. Diminished distractibility due to less robust sensory memory processing does not contradict the idea of a general less efficient cognitive control in older adults, but suggests a more complex interplay between lower, rather perceptual and higher cognitive processing that cannot be explained by the inhibitory deficit hypothesis. Thereby, a reduced distractibility by complex task-irrelevant stimuli might be disadvantageous, as well as advantageous in certain situations, such that older adults might be less distracted by changes in the sound environment (Healey, Campbell, & Hasher, 2008). However, many situations are imaginable where the lack of orienting towards deviations in the non-attended sound environment might be disadvantageous, such as when driving a car and not detecting changes in the car engine noise.

In conclusion, the current results provide evidence that automatic detection of temporal as well as frequency deviations of two-tone patterns in sensory memory (indexed by MMN) is less robust in older compared to younger adults. We did not find asymmetric age effects on the processing of temporal and frequency pattern deviants, which is in contrast to sensory memory processing of temporal and frequency deviants observed in simple oddball paradigms (for review: Pekkonen, 2000). In the current study, both the temporal and the frequency deviations of two-tone patterns required pattern processing, which was observed to be less robust in the older adults. Furthermore, these results suggest that impaired sensory memory processing may have an impact on attentional orienting (indexed by P3a), which might lead to perceptual deficits in everyday situations.

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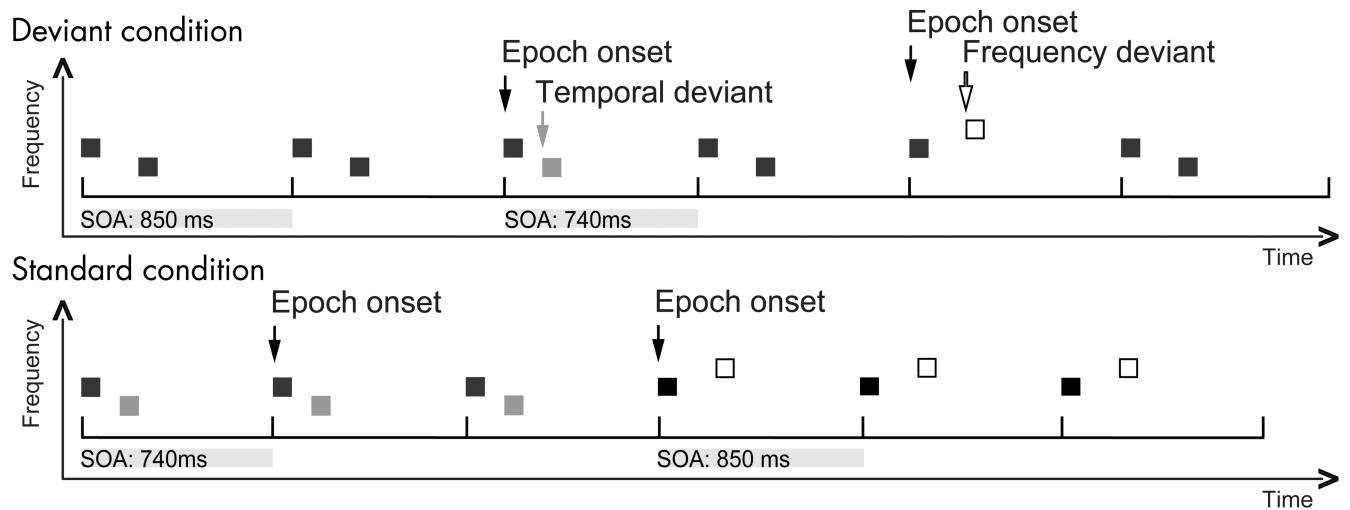


Figure 1. Schematic of the stimulus paradigm

Time is displayed along the x-axis and frequency along the y-axis. In the deviant condition two-tone patterns were interspersed with infrequent temporal and frequency deviants. The stimulus onset-asynchrony (SOA) of patterns was 850 ms for the standard and the frequency deviant patterns and 740 ms for the temporal deviant patterns (highlighted by grey bars). In the standard condition patterns were physically matched to the temporal pattern deviants ($p = .5$), respective the frequency pattern deviants ($p = .5$). Arrows point toward the epoch onset, as well as the stimulus onset of the temporal and the frequency pattern deviants.

Temporal condition ERPs

Frequency condition ERPs

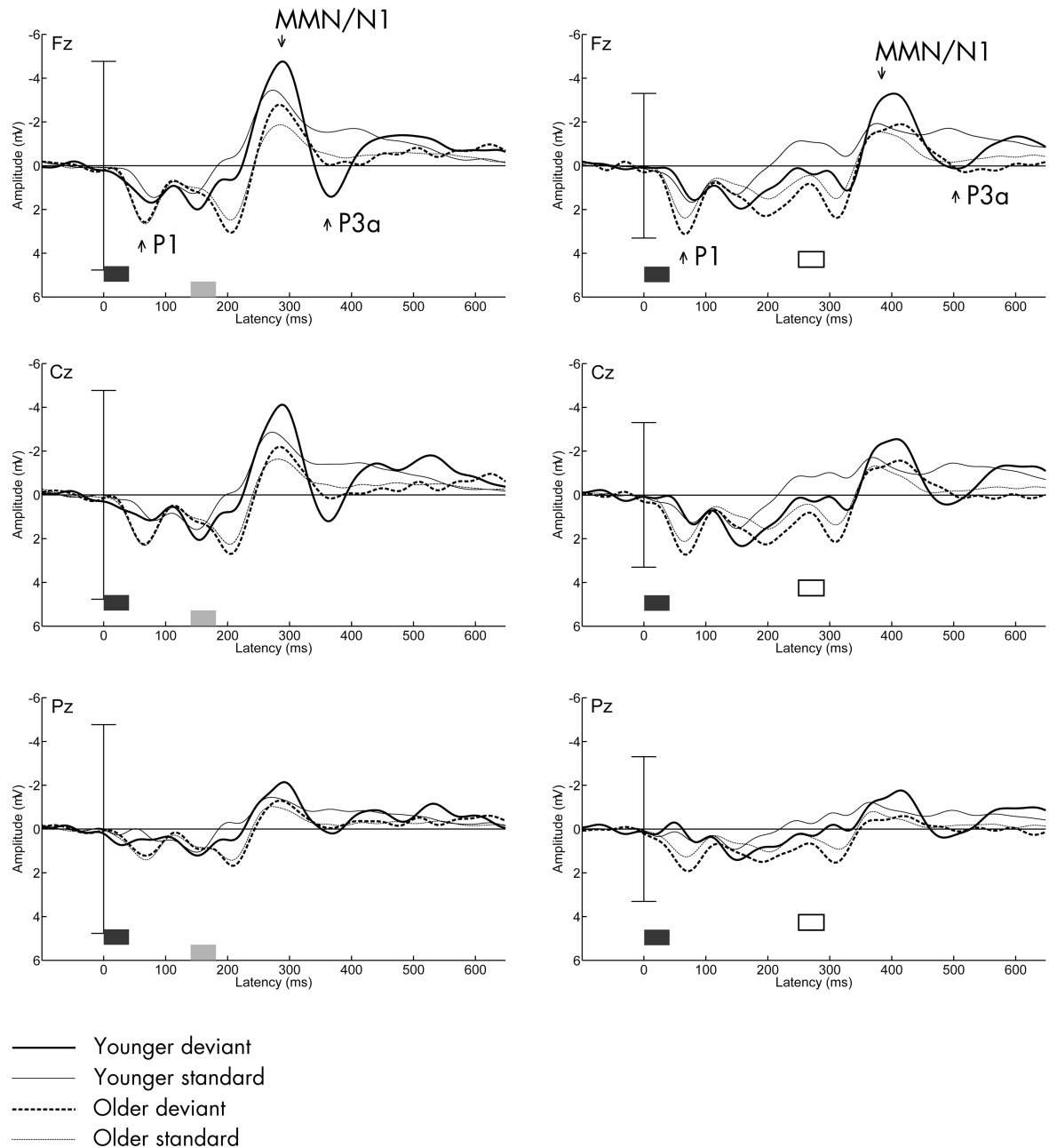
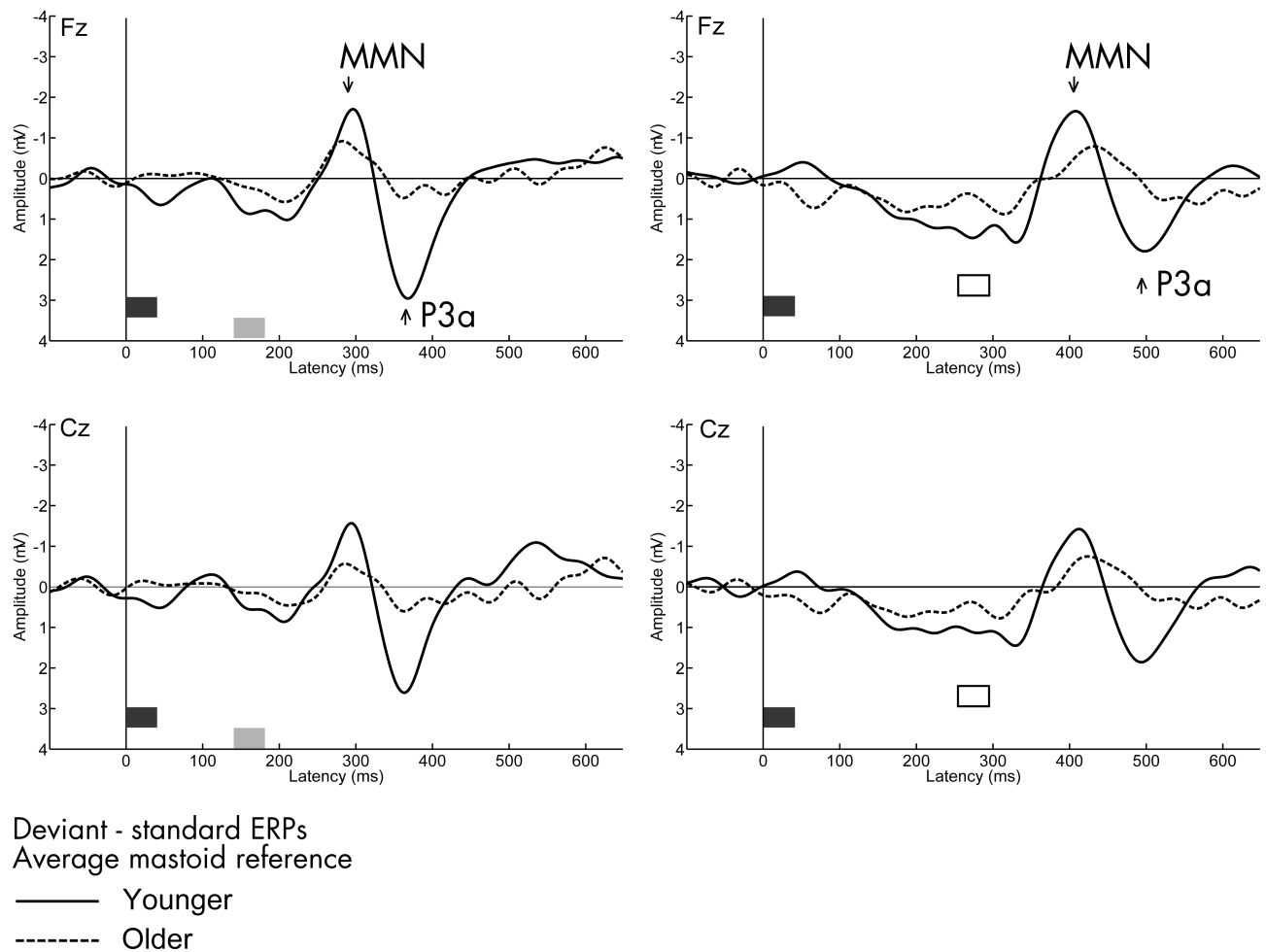


Figure 2. Effects on deviant and standard ERPs

Grand-average waveforms are displayed at midline (Fz, Cz, Pz) electrodes by stimulus type (deviant black thick line; standard black thin line) and age group (younger adults solid lines; older adults dashed lines) for conditions (left column: T, right column: F). Negative polarity is plotted upwards. ERPs in the range of P1 (response to the first tone of the tone-pair), MMN and P3a (response to the second tone of the tone-pair) are labeled at Fz electrode, with arrows pointing toward the peak of the components. Rectangles above the x-axis illustrate the time course of the tone presentation (black rectangle: standard; gray rectangle: temporal pattern deviant; transparent rectangle: frequency pattern deviant).

Temporal condition

Frequency condition

**Figure 3. Effects on the deviant-standard difference waves**

Grand-average deviant-standard difference waves are displayed at midline (Fz, Cz) electrodes for both conditions (left column: T, right column: F) and for both age groups (younger adults solid lines; older adults dashed lines). Negative polarity is plotted upwards. MMN and P3a (response to the second tone of the tone-pair) are labeled at Fz electrode, with arrows pointing toward the peak of the components. Rectangles above the x-axis illustrate the time course of the tone presentation (black rectangle: standard; gray rectangle: temporal pattern deviant; transparent rectangle: frequency pattern deviant).

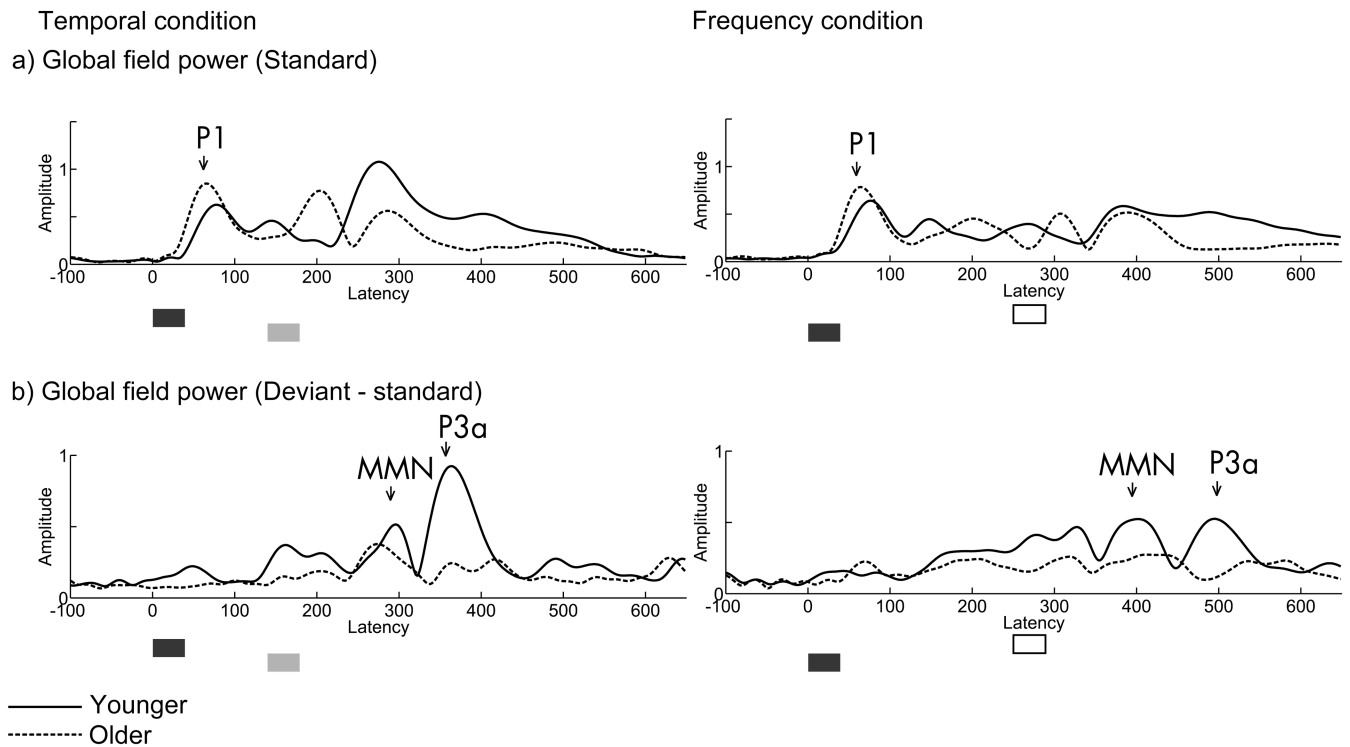


Figure 4. Age and condition effects on the global field power

The Global field power (GFP) is calculated as root mean of the squared voltage deviations across electrode recordings from the entire scalp to provide a reference-free measure of the components. **a)** The GFP measured at the grand-average standard ERPs is displayed for both conditions (left column: T, right column: F) and for both age groups (younger adults solid lines; older adults dashed lines). P1 is labeled with arrows pointing toward the peak of power referring to the respective component peaks visible in the ERP waveforms (Fig. 2). **b)** The GFP measured at grand-average deviant-standard difference waves is displayed for both conditions (left column: T, right column: F) and for both age groups (younger adults solid lines; older adults dashed lines). MMN and P3a are labeled with arrows pointing toward the peak of power referring to the respective component peaks visible in the ERP waveforms (Fig. 3). Rectangles below the x-axis illustrate the time course of the tone presentation (black rectangle: standard; gray rectangle: temporal pattern deviant; transparent rectangle: frequency pattern deviant).

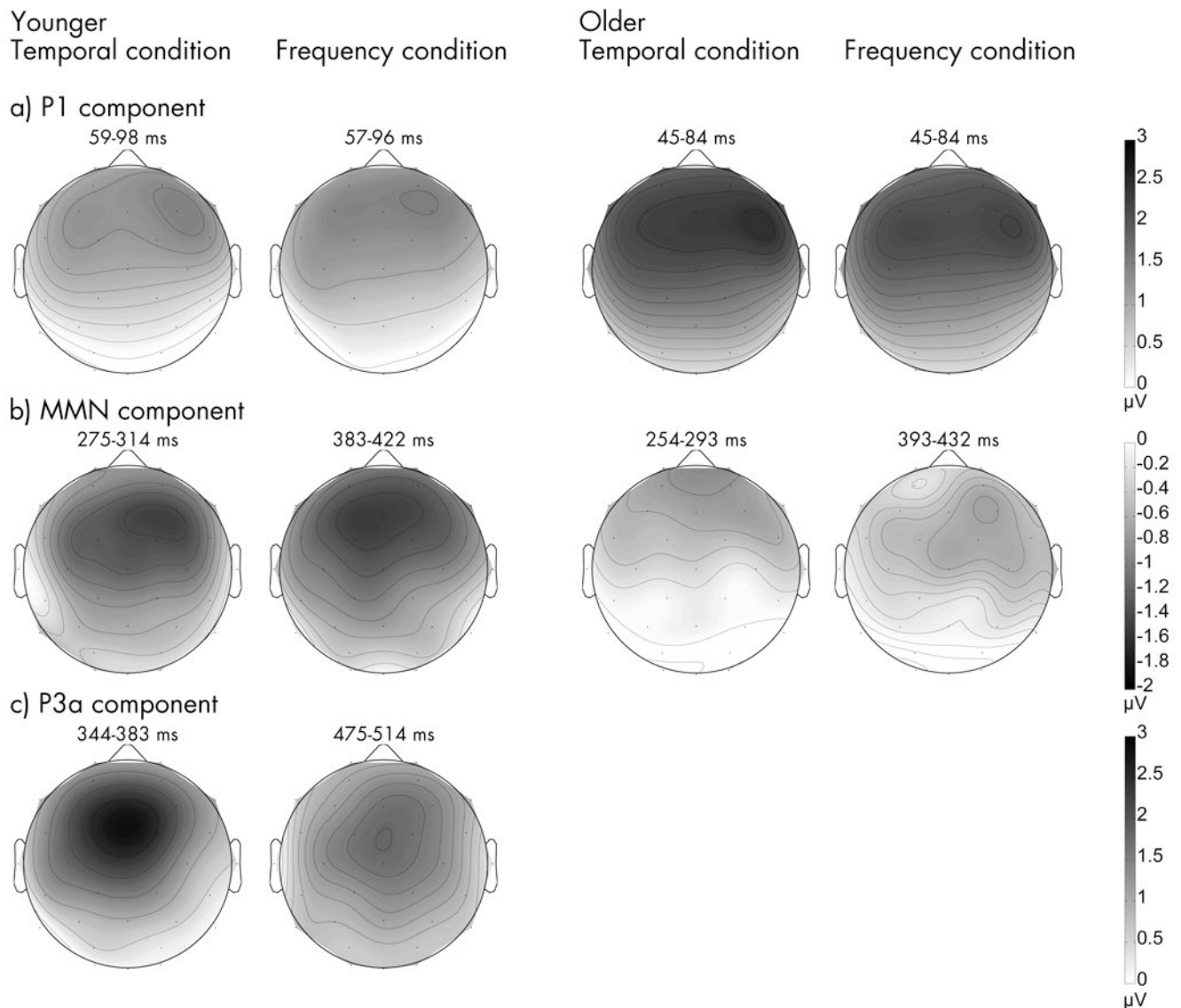


Figure 5. Topographies of the P1, MMN and P3a components

a) Spherical spline interpolated isocontour voltage maps of the grand-average of the P1 component are shown for each condition (T, F) and for both age groups (younger, older). Voltage maps were computed on the standard ERPs at the latency of the average component peak amplitudes (averaged over a 40 ms time window) (younger: T: 78 ms, F: 76 ms; older: T: 64 ms, F: 64 ms), and are displayed on a 0-3 μ V scale (black: positive polarity). **b)** Spherical spline interpolated isocontour voltage maps of the grand-average of the MMN component are shown for each condition (T, F) and for both age groups (younger, older). Voltage maps were computed for the deviant-standard ERPs at the latency of the average component peak amplitudes (averaged over a 40 ms time window) (younger: T: 295 ms, F: 402 ms; older: T: 273 ms, F: 412 ms), and are displayed on a -2-0 μ V scale (black: negative polarity). **c)** Spherical spline interpolated isocontour voltage maps of the grand-average of the P3a component are shown for the younger adults for each condition (T, F). Voltage maps were computed for the deviant-standard ERPs at the latency of the average component peak amplitudes (averaged over a 40 ms time window) (younger: T: 363 ms, F: 494 ms), and are displayed on a 0-3 μ V scale (black: positive polarity).

Table 1
Sample Demographics

	Age Groups		Significance ^c
	Younger	Older	
N	13	13	
Age			
Mean (SD) in years	25.23 (3.54)	66.62 (2.84)	$p < .01$
Span	21 - 31	60-72	
Gender ^b			
male	6 (46%)	6 (46%)	
Highest degree ^b			
No degree	0 (0%)	0 (0%)	
Hauptschulabschluss	0 (0%)	0 (0%)	
mittlere Reife	0 (0%)	5 (38%)	
A-levels	13 (100%)	8 (67%)	
University degree Education ^b	11 (85%)	10 (77 %)	
School-/University education ^a	16.31 (2.98)	15.38 (3.67)	$p = .52$
Professional education ^a	0.23 (0.83)	2.04 (1.59)	$p < .01$
Overall education ^a	16.85 (3.28)	17.42 (3.19)	$p = .57$
Occupation ^b			
Full-time employed	3 (23 %)	0 (0%)	
Part-time employed	1 (8 %)	1 (8%)	
Student	9 (69 %)	0 (0%)	
Trainee	0 (0%)	0 (0%)	
Army/Civilian servant	0 (0%)	0 (0%)	
Retiree	0 (0%)	11 (85%)	
Homemaker	0 (0%)	0 (0%)	
Unemployed	0 (0%)	1 (8%)	
Musical education ^a	3.08 (5.37)	2.73 (3.50)	$p = .76$

Note:

^a In years; mean and standard deviation (in parentheses);

^b Frequencies and percentage in the respective age group (in parentheses);

^c Significant differences in the distribution tested with the Kruskal-Wallis-Test; $\alpha = .05$.

Table 2
Mean hearing thresholds separate for the younger and older group

Mean hearing thresholds			
	Younger Group	Older Group	significance
L 250 Hz	18.1 (6.42)	20.9 (4.73)	p = .21
R 250 Hz	15.4 (5.64)	14.2 (7.77)	p = .82
L 500 Hz	11.5 (7.61)	15.1 (8.35)	p = .13
R 500 Hz	9.9 (6.87)	10.2 (7)	p = .76
L 1000 Hz	7.3 (9.29)	12.8 (9.88)	p = .32
R 1000 Hz	4.8 (9.59)	10.0 (8.83)	p = .31
L 2000 Hz	8.9 (6.71)	15.1 (7.18)	p < .01
R 2000 Hz	6.8 (6.53)	15.0 (7.65)	p < .01
Mean individual ht	13.7 (6.08)	15.1 (4.56)	p = .39

Note: L: left ear presentation, R: right ear presentation. Mean individual ht: mean of individual threshold averaged over left, right ear and 250, 500 Hz. Independent samples Students t-tests were conducted to test differences between the young and old group.

Table 3
Peak latencies and time intervals used to measure the components, separately for each group and condition

Condition	Younger Group	Older Group
P1¹peaks (ms)		
T	78 (58-98)	64 (44-84)
F	76 (56-96)	64 (44-84)
MMN²peaks (ms)		
T	295 (275-315)	273 (253-292)
F	402 (382-422)	412 (392-432)
P3a²peaks (ms)		
T	363 (343-383)	363 (343-383)
F	494 (474-514)	494 (474-514)

Note: Time intervals were measured at the grand-average global field power (GFP).

¹ Measured at the GFP of standard ERPs;

² Measured at the GFP of deviant-standard difference waves.

Table 4
Mean of individual peak latencies retrieved from the jackknife-based latency measure

Condition	Younger Group	Older Group
P1¹ latencies (ms)		
T	80 (21.06)	67 (12.16)
F	78 (16.57)	66 (13.53)
MMN² latencies (ms)		
T	298 (15.24)	276 (21.06)
F	403 (52.27)	421 (162.21)
P3a² latencies (ms)		
T	366 (24.18)	-
F	497 (20.38)	-

Note: Time intervals and standard deviations were measured at the grand-average global field power (GFP).

¹ Measured at the GFP of standard ERPs;

² Measured at the GFP of deviant-standard difference waves. To derive the MMN and P3a latency related to the deviant/standard onset 140 ms have to be subtracted in the T and 250 ms in the F condition.