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Horváth, J., Gaál, Z. A., & Volosin, M. (2017). Sound offset-related brain potentials show retained sensory processing, but increased cognitive control activity in older adults. *Neurobiology of Aging*, 57, 232–246. <https://doi.org/10.1016/j.neurobiolaging.2017.05.026>
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Sound offset-related brain potentials show retained sensory processing, but increased cognitive control activity in older adults

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Abstract

It has been hypothesized that age-related hearing loss is caused not only by peripheral, but also central changes in the auditory system. Many studies utilized event-related potentials (ERPs) elicited by sound onsets to characterize age-related differences in central auditory processing. Age-related ERP enhancements in such studies have often been interpreted in terms of elevated sensitivity to auditory stimulation. Such ERPs, however, comprise various components reflecting different aspects of auditory and task-related processing. The composition of the waveforms may considerably differ for ERPs elicited by other auditory events. In the present study ERPs elicited by tone-offsets were used to characterize processing differences between younger and older adults in a short-go, tone-duration discrimination paradigm. Whereas the onset-related auditory ERP was enhanced in the older adult group, no age-related differences were found in the offset-related auditory ERPs observable at temporal electrodes. In older adults, however, offset-related processing was dominated by an N2 that could reflect enhanced cognitive control activities. Because N2 was present regardless discrimination difficulty, younger adults may have framed the task as offset-detection, whereas older adults represented the task as “genuine” discrimination.

Keywords: aging, hearing, event-related potentials, cognitive control, T-complex, N2

1. Introduction

Human sensory systems change over the lifespan. Developmental and age-related changes affect the transduction of physical effects, as well as the processing of the resulting sensory signals. Maintaining optimal behavior despite these changes may require adaptation in non-peripheral, or even in non-sensory systems (Pelle & Wingfield, 2016). But because these systems are also affected by aging (Wayne, & Johnsrude, 2015), characterizing age-related changes in the interaction of peripheral and central, as well as sensory and non-sensory processing is not trivial. The deterioration of hearing with age (*presbycusis*, for a review see Gates, & Mills, 2005) has numerous manifestations. Beside the most frequently measured increase in pure tone detection thresholds, various paradigms show reduced temporal resolution (Humes, et al., 2010), and difficulties in speech understanding (see e.g., Humes, 1996; Marshall, 1981). Although some problems may be directly related to hearing threshold increases at higher frequencies (e.g., loss of discrimination ability for phonemes with high frequency components), certain aspects of hearing may be impacted even in the absence of such a threshold change (Bharadwaj, et al., 2015). This suggests that the causes of presbycusis are manifold, and different paradigms may reflect different (combinations of) hearing function changes. Although recent research suggests that some of these changes can be largely attributed to various peripheral causes (e.g., loss of outer hair cells, or cochlear neuropathy; Plack et al., 2016), it has also been suggested that certain aspects of age-related hearing problems are caused by changes in central auditory processing (Humes, et al., 2012). The goal of the present study was to characterize age-related differences in central auditory and non-auditory processing reflected by event-related potentials (ERPs) elicited by tone-offsets in a duration discrimination task.

Sound onsets elicit an ERP waveform comprising various deflections at various latencies (see e.g., Picton, et al., 1974). The late part of this waveform comprises the P1, N1

and P2 deflections (peaking respectively at around 50, 100, and 170 ms). Age-related differences in these ERPs have been investigated in numerous experiments, which mostly showed that these ERPs were enhanced in older adults (or no significant differences were present). Age-related enhancements of P1 or its enhancements magnetic counterpart were found, for example, by Alain et al. (2012), Bertoli et al. (2005), Fabiani et al. (2006), Kovacevic et al. (2005), Pekkonen et al. (1995), Pfefferbaum et al. (1979), and Smith et al. (1980). An N1 amplitude increase with growing age was found among others by Amenedo and Díaz (1998), Anderer et al. (1996, 1998), Ford and Pfefferbaum (1991), and Pfefferbaum et al. (1984); but Goodin et al. (1978) observed age-related reduction of the N1-P2 amplitude (measured from peak-to-peak). Age-related P2-amplitude increases were found, for example, by Ford and Pfefferbaum (1991), Pfefferbaum et al., (1984); but Czigler et al. (1992), and Ross and Tremblay (2009), found lower P2 amplitudes in older than in younger participants.

Although some of these ERPs reflect the physical characteristics of the stimulation (e.g., louder sounds elicit larger, and earlier N1s, see Näätänen and Picton, 1987), they are also influenced by cognitive factors, for example by the attentional orientation of participants (Hillyard et al., 1973): When participants perform tasks related to one stimulus channel (e.g., a given ear: Woldorff and Hillyard, 1991) N1 amplitude is enhanced for the sounds presented in the given channel. That is, these ERPs reflect the interaction of sensory processing and its top-down modulation. Building on this, if an experiment administers *equivalent* auditory stimulation in two conditions, then between-condition ERP differences would reflect differences in top-down modulation. Indeed, age-related amplitude enhancements have been generally interpreted as signs of a general age-related increase in sensitivity to auditory stimuli. This may reflect a declined ability to inhibit sensory processing (Alain and Woods, 1999; Chao and Knight, 1997; Stothart and Kazanina, 2016), or more generally, to inhibit the processing of irrelevant pieces of information (Gazzaley et al., 2005; Hasher et al., 1999;

Hasher and Sacks, 1988). Such a sensitivity increase may, however, not only reflect a decline, but also an adaptation to a peripheral deficit: some studies presenting *physically* identical sounds to participants with peripheral hearing loss found enhanced auditory ERPs in comparison to participants with normal hearing despite elevated pure tone thresholds (Alain et al., 2014; Harkrider et al., 2006; Morita et al., 2003).

Although the interpretations above seem straightforward, there are a number of inconsistencies. Whereas the sign of the age-related effects on the onset-related waveforms (i.e. amplitude *enhancement* with growing age) is consistent for P1 across studies, for N1, and especially P2, consistency decreases, with more counter-examples showing *reductions* with growing age. It is also important to note that the ERP waveform elicited by other transient events, for example by short gaps in continuous tones shows the opposite pattern as a function of age: gap-related N1 and P2 are markedly reduced in older adults in comparison to younger adults (Harris et al., 2012; Volosin et al., 2017).

Furthermore, the reported onset-related ERP enhancements do not seem to follow a pattern reflecting a single cause: in many studies an age-related enhancement was found for one or two of the waveforms, but not for the other(s). Although these waveforms certainly have generators in auditory areas of the temporal cortex (see e.g., Crowley and Colrain, 2004; Godey et al., 2001; Halgren et al., 1995; Liegeois-Chauvel et al., 1994; Lütkenhöner and Steinsträter, 1998; McEvoy et al., 1994; Nakagawa et al., 2014; Scherg et al., 1989), they nonetheless comprise different components, which may account for the inconsistencies described above. The N1 waveform has at least three sub-components (Näätänen and Picton, 1987). Two of these originate from auditory areas: The supra-temporal component, which exhibits a frontally negative peak and a positive peak at electrodes under the Sylvian-fissure when the EEG is recorded with a nose-reference, is well modeled by a tangential equivalent dipole placed in the supra-temporal cortex (Vaughan and Ritter, 1970). The T-complex

(Wolpaw and Penry, 1975) is mainly observable at temporal sites, with a field well-described by radially oriented equivalent dipolar sources at the lateral sides of the temporal cortices, which may reflect activity in secondary auditory areas (Scherg and Von Cramon, 1986; Ponton et al., 2002). It has been suggested that P2 comprises at least two components as well (Verkindt et al., 1994). Further ERP components overlapping the N1 and P2 can be found in different stimulation and task arrangements (Näätänen and Picton, 1987). In tasks requiring sound-based decisions, the deflection descriptively labeled as N1 may actually receive contributions from the processing negativity (PN, Näätänen et al., 1978; or negative difference – Nd, see Hansen and Hillyard, 1980) or N2 (Horváth, 2016) components. Whereas PN probably reflects processing related to the matching of the incoming sound to a voluntarily maintained auditory template, an *attentional trace* (Näätänen, 1982, 1990), N2 may reflect the evaluation of the stimulus in terms of the given task (Ritter et al., 1979). The positive waveform descriptively labeled as P2 may actually receive contributions from an overlapping PN or N2 (Czigler et al., 1992), which reduce its amplitude (or even make it unobservable, if the task-related N2 is much larger than the P2, see e.g., Experiment 3 in Horváth, 2016); or it can be enhanced by a P3a, which is elicited by unpredictably occurring stimuli (Friedman et al., 2001). That is, sounds presented in different experimental paradigms may have different processing demands, which are also reflected in the component-structure underlying the ERP waveforms. Consequently, age-related ERP differences may have markedly different causes across paradigms.

The present study is based on the idea that different types of stimulations may require different patterns of processing, which may also be reflected in the composition of the auditory ERPs. Alain et al. (1997), for example, showed that N1 subcomponents indexed processes with different temporal integration times, which was reflected in their amplitudes when tone durations were varied in the 8-72 ms range. Although studies on age-related

changes in auditory processing mostly used sound onsets to elicit P1, N1 and P2, auditory ERPs can also be elicited by other types of auditory events. In the present study, instead of focusing on ERPs elicited by sound onsets, we focused on ERPs elicited by sound offsets.

The processing of sound onsets and offsets includes common, as well as event-specific processes. Neural responses to offsets have been identified in animal studies at all stages of the auditory pathway from the cochlear nucleus (e.g., Suga, 1964), to the auditory thalamus (He, 2001, 2002) and the auditory cortex (e.g., Fishman and Steinschneider, 2009; Qin et al., 2007; Recanzone, 2000; for a recent overview, see Ramamurthy and Recanzone, 2017). It has also been shown that onset and offset responses in the auditory cortex - even if produced by the same neurons - are likely driven by separate sets of synapses (Scholl et al., 2010; O'Connell et al., 2011).

ERP waveforms elicited by onsets and offsets are largely similar (Davis and Zerlin, 1966; Hillyard and Picton, 1978; Onishi and Davis, 1968). The magnetic reflections of these ERPs have overlapping generator structures according to some studies (Hari et al., 1987; Pantev et al., 1996; Yamashiro et al., 2011), whereas others (Noda et al., 1998) suggest the involvement of separate structures. The onset-related auditory ERP signal features a positivity at around 100 ms post-onset at temporal electrodes (the Ta sub-component of the T-complex), which is followed by a negativity (the Tb, at around 150 ms, Wolpaw and Penry, 1975), while a negativity is observable at the fronto-central electrodes at around 100 ms (reflecting - at least in part - the supra-temporal N1 subcomponent). Whereas onset-related auditory ERPs are readily observable in most paradigms, most previous studies suggested that offset-related ERPs are mainly observable when tone durations are long (i.e. longer than 1 s, Näätänen and Picton, 1987). A recent set of studies, however, demonstrated that attended sound offsets elicit a positive-negative-positive waveform with similar temporal structure as the onset-related P1-N1-P2 ERP (Horváth, 2014). Although the between-deflection intervals were very similar to

those observable in a typical onset-related waveform, the waveform itself was uniformly delayed by about 50 ms (i.e., the P1 peaked at about 100 ms, and the N1 at about 150 ms after the start of the offset transient). Interestingly, the waveform was most prominently observable at temporal sites (Horváth, 2016). Because of its topographical distribution and timing, it was suggested that the offset-related waveform may be analogous to the T-complex rather than to the typical onset-related waveform, in which the fronto-central negativity at 100 ms is the most pronounced. The experiments by Horváth (2016) also revealed that the negative part of the offset-related waveform was composed of two components: one reflecting sensory offset-processing (N1), and one reflecting the processing of the offsets in task-related terms (N2). Whereas N1 was most clearly distinguishable at temporal sites, it was dominated by an N2 at central electrodes (forming a monolithic N1/N2 waveform) when the stimulation was more complex (i.e. pitch or stimulus presentation rate varied during the experiment). In a study investigating age-related differences in distraction, a similar offset-related P1-N1-P2 waveform was found, which seemed to be delayed by about 80 ms in older adults (Horváth et al., 2009). These results show that offset-related ERPs may allow different insights on age-related differences in sound processing from that offered by onset-related ERPs. The present study was a targeted investigation of the results by Horváth et al. (2009), which omitted the distraction aspect of their paradigm, used multiple durations, and administered the task to larger younger and older adult groups than the previous studies (Horváth et al., 2009, and Horváth, 2016).

Based on Horváth et al. (2009), we hypothesized that offset-related processing will be delayed in the older adult group, which will be reflected by the delayed elicitation of the offset-related ERP waveform. To separate N1 and N2 contributions, ERPs from trials with faster and slower-than-median responses were separately averaged. Because N2 latency is

known to covary with response latency, we hypothesized that this would allow the separation of the two components.

2. Materials & Methods

2.1 Participants

Participants reported no history of neurological disorders, and gave written informed consent after the experimental procedures were explained to them. 21 younger adult volunteers, recruited by a student part-time job-agency, and 22 older adult volunteers, recruited from the participant database of the department participated in the experiment for monetary compensation. All of them were right-handed women. Data from two older adult participants were not used in the analyses because of extensive eye-movements resulting in the loss of more than 80% of the EEG epochs during artifact-rejection (see below). The remaining participants were aged 20-24 years (mean 22, standard deviation 2) in the younger, and 61-73 years (mean 66, standard deviation 3) in the older adult group. The mean IQ scores (measured by the Hungarian version of the Wechsler Adult Intelligence Scale, Fourth Edition, WAIS-IV completed in a separate session) were higher than average in both groups, as shown by a two-tailed t-test against 100: ($t[19] = 6.346, p < .001$ for the older, and $t[20] = 2.680, p = .014$ in the younger adult group); the mean IQ scores were also higher in the older than in the younger adult group (see Table 1). The participants had no more than 10 dB hearing threshold difference between the two ears at 500, 1000, and 2000 Hz (measured by an SA-6 audiometer, Mediroll, Debrecen, Hungary). The mean thresholds were higher in the older than in the younger adult group at all measured frequencies (see Table 1).

2.2 Stimuli and procedures

The stimulation was largely similar to that used previously by Horváth (2014, 2016). Participants were sitting in an armchair in a sound-proofed room. Tones comprising three

harmonics (700, 1400 and 2100 Hz sinusoids with relative amplitudes of 0, -3, and -6 dB) were presented through headphones (HD-600, Sennheiser, Wedemark, Germany). The experiment consisted of three conditions. In each condition, pseudo-randomized sequences of short and long tones were presented. The duration of the long tone was 750 ms in each condition, whereas the short tone was either 150, 300, or 450 ms long in the given condition. All tones included 2.5-2.5 ms linear rise and fall times. The intensity of the tones was individually adjusted to 50 dB above hearing threshold level using a continuous version of the tone presented in the experiment. The conditions were presented in random order for each participant. Each condition was divided into 5 stimulation sequences comprising 87 short- and 87 long tones presented in a pseudo-randomized order with an onset-to-onset interval of 1300 ms. The first four stimuli of each sequence comprised a “short-long-short-long” micro-sequence to demonstrate the duration-difference to the participants, who were informed of this introduction sequence. Participants were instructed to press a button held in their dominant (right) hand as fast as possible when the short tone was presented, while maintaining a low false alarm rate, but not to respond to long tones. They also had to keep their gaze on a fixation puppet placed in front of them to minimize eye-movements. Consecutive stimulation sequences were separated by short breaks as needed, with longer breaks between conditions. Before and after the electrode-cap was mounted, participants practiced the task in pseudo-randomized sequences consisting of 42 short (450 ms), and 42 long (750 ms) tones. At the end of each sequence, feedback on the correct response rate and reaction time distribution was provided and discussed. Due to a software problem, tone presentation randomly, occasionally stopped for 5 seconds in some of the blocks (on average, 15% of the blocks were affected by such an irregularity). Responses to the three stimuli following such hang-ups, as well as responses to the first four tones of each block were excluded from the analyses.

2.3 Behavioral data analysis

In each condition, trials were categorized as hits, false alarms, correct rejections and misses based on the presence or absence of responses in the 50-850 ms interval following the timepoints of potential short-tone offsets. Overall, this selection procedure resulted in the inclusion of 98.1% of the trials in the analyses. d' sensitivity scores (according to Signal Detection Theory, for a summary, see Macmillan and Creelman, 2005) were calculated for each condition and each participant. Hit rates of 1 and false alarm rates of zero were adjusted to $1 - (1/(2N))$ and $1/(2N)$, respectively (where N is the number of stimuli requiring a response, see Macmillan and Creelman, 2005) to avoid infinite values in the calculations. To compensate for the potentially skewed individual reaction time distributions, participants' reaction times were calculated as the median of their reaction times for hits. d' scores and reaction times were analyzed in two-way mixed analyses of variance (ANOVA) with group as a between-group factor and condition as a three-level, repeated measures factor. Greenhouse-Geisser-correction was applied as appropriate (epsilon values are reported with the uncorrected degrees of freedom). Generalized eta-squared effect sizes (Olejnik and Algina, 2003; Bakeman, 2005) are reported.

2.4 EEG-recording and analysis

The electroencephalogram (EEG) was recorded with nose reference with a sampling rate of 1000 Hz (200 Hz on-line low-pass filter, Synamp 2, Compumedics, Victoria, Australia) by 61 Ag/AgCl electrodes mounted on an elastic cap (EASYCAP, Herrsching, Germany) using a 10% arrangement (Nuwer et al., 1998). Two additional electrodes were placed at the mastoids. A bipolar setup of electrodes placed close to the outer canthi of the two eyes was used to record the horizontal electrooculogram (EOG). Vertical EOG was calculated off-line by subtracting the signal of an electrode placed under the right eye from the signal measured at Fp2. The EEG was off-line 20 Hz low-pass filtered (Kaiser-windowed sinc finite impulse response filter, beta of 4.53, 1465 coefficients, transition bandwidth 2 Hz,

stopband attenuation at least 50 dB). 1300 ms long epochs including a 200 ms long pre-tone interval corresponding to short and long tones in each condition were extracted from the filtered EEG. Epochs with a signal range exceeding 100 μ V on any channel were discarded. The remaining epochs were averaged for each participant. The average signal in the pre-tone interval was used as a reference (baseline) in the amplitude calculations.

First, ERP activity preceding tone onsets was characterized. As in previous studies using fixed inter-onset-intervals in duration- or direction discrimination tasks (e.g., Berti and Schröger, 2001; Horváth, 2014, 2016; Volosin and Horváth, 2014), the stimulus onset was preceded by a negative ERP trend. The steepness of this pre-stimulus trend was calculated as the difference of the average amplitudes measured at in the 200-150 ms and the 50-0 ms intervals preceding tone onsets in each condition. Steepness values were submitted to a mixed Group \times Condition (repeated measures, 150, 300, or 450 ms vs. 750 ms) ANOVA.

Because onset-related auditory P1 and N1 waveforms were superimposed on the ERP trend described above (which differed significantly between conditions), onset-related P1 and N1 amplitudes were characterized together by the differences in their amplitudes (i.e. peak-to-peak amplitudes). P1-N1 amplitudes were calculated as the differences of the average signals in the 20 ms long window centered at the P1 and N1 peaks, and were submitted to a Group \times Condition mixed ANOVA.

To assess offset-related ERPs in each condition, short-minus-long ERP difference waveforms were calculated. P1 and N1/N2 peaks were visually identified in the group average difference waveforms. Individual P1 and N1/N2 amplitudes were calculated as the average signals in 20 ms long intervals centered at the respective group-average peak latencies (measured at Cz) in each group. These were submitted to mixed Group \times Condition \times Electrode (T7, Cz, T8) ANOVAs. These electrodes were pre-selected because previous

experiments (Horváth, 2016) suggested that N2 and P3b may overlap the offset-related P1 and N1 at temporal electrodes to a lesser degree than at central ones. Conversely, it was expectable that potential ERP amplitude effects stemming from the overlap of these ERPs will be more pronounced at the central electrode, and will be manifested by interaction effect(s) involving the Electrode factor.

To assess whether between-group differences were present in the latencies of the ERPs observable in the difference waveforms, their peak latencies measured at Cz were analyzed by applying the jackknife procedure as described by Kiesel, et al., (2008) in mixed Group \times Condition (150, 300, or 450 ms vs. 750 ms) ANOVAs. For these calculations the jackknife-adjusted F-values (when appropriate, the size of the larger group was used), Greenhouse-Geisser epsilons if applicable, unadjusted degrees of freedom, and adjusted p-values are reported.

To assess whether the latency of the offset-related waveforms varied with reaction time, which may indicate that reaction-time sensitive components, like the N2 or P3b contribute to the waveforms, short tones followed by correct responses were sorted according to reaction time, and ERP epochs corresponding to short tones with faster-than-, and slower-than-median reaction times were averaged separately (see Horváth, 2016). Using the jackknife procedure described by Kiesel et al. (2008), the offset-related P1 (measured at T7), N1/N2 (measured at Cz), and P3b (measured at Pz) latencies were submitted to mixed Group \times Partition (faster-, or slower-than-median) \times Condition (150, 300, or 450 ms vs. 750 ms) ANOVAs. Note that in these analyses, the offset-related waveform was identified in the short tone-related ERP (because long tones did not require a response). For two jackknife means in the younger adult group, no local N1 maxima, only a shoulder could be found at Cz; in these cases, the latency at which the temporal derivative of the Cz signal (the difference of consecutive signal samples) was closest to zero was used.

3. Results

3.1 Behavioral data

Group-average reaction times and d' sensitivity scores are presented in Figure 1. The ANOVA of the reaction times (in reference to short tone-offset) showed a significant Group main effect: $F(1,39) = 16.164$, $\eta_G^2 = 0.251$, $p < 0.001$, showing that older adults responded slower than younger adults; and a Condition main effect: $F(2,78) = 21.877$, $\epsilon = 0.701$, $\eta_G^2 = 0.097$, $p < 0.001$. Following-up the Condition main effect, pair-wise t-tests (with pooled groups) showed that reaction times significantly differed between all three conditions ($t[40]$ -scores > 2.625 ; p -values < 0.013): they were the fastest in the 300 vs. 750 ms, and slowest in the 450 vs. 750 ms condition.

The ANOVA of the d' sensitivity scores showed a significant Condition main effect: $F(2,78) = 54.893$, $\epsilon = 0.907$, $\eta_G^2 = 0.275$, $p < 0.001$; and a significant Group \times Condition interaction: $F(2,78) = 3.277$, $\epsilon = 0.907$, $\eta_G^2 = 0.022$, $p = 0.048$. In both groups pair-wise t-tests showed that d' s were significantly lower in the 450 vs. 750 ms condition than in the other two ($t[20] > 4.258$ in the younger adult group for both comparisons, $t[19] > 6.985$ in the older adult group for both comparisons, p -values < 0.001 in both groups). Following-up the interaction, pair-wise, two-sample, Welch t-tests showed that the d' difference between the 150 vs. 750 ms and the 450 vs. 750 ms conditions was larger in the older than in the younger adult group ($t[38.662] = 2.197$; $p = 0.034$; none of the other comparisons showed significant differences).

3.2 ERPs

The group-average ERPs and the short-minus-long difference waveforms elicited in the younger and older adult groups are presented in Figures 2, 3 and 4. As in previous studies (e.g., Berti and Schröger, 2001; Horváth, 2014, 2016; Volosin and Horváth, 2014), tone

onsets were preceded by a negative-going ERP trend, suggesting that participants exploited the constant SOA to prepare for the tones. Tone onsets elicited the succession of P1, N1 and P2 waveforms, which were superimposed on the negative trend. P2 was followed by a sustained negativity, lasting approximately till the time-point of the potential short tone offset in each condition. This was followed by a parietal positivity, identified as a P3b.

3.2.1 ERPs – pre-stimulus interval

The steepness of the negative trend was maximal at centro-parietal sites in the group average waveforms (with maxima at CP3, CP4, and PO4 in the two groups and three conditions). To measure steepness values, CPz was selected as the electrode closest to the maxima described above. The steepness values were submitted to a Group \times Condition ANOVA, which showed a significant Condition main effect only: $F(2,78) = 4.667$, $\epsilon = 0.932$, $\eta_G^2 = 0.048$, $p = 0.014$. Following-up the Condition main effect, pair-wise t-tests (with pooled groups) showed that the negative trend was significantly less steep in the 450 vs. 750 ms than in the 150 vs. 750 ms condition ($t[40] = 2.712$; $p = 0.001$).

3.2.2 ERPs – onset-related waveforms

The onset-related P1 peaked in the group average waveforms mainly at frontal, fronto-central sites (maxima at FC3, FC6, AF8, Fpz, AF4), with a mean latency of 48 ms (42-51 ms latency range) in the two groups and three conditions (because there were no physical differences between short and long tones at the onset, these were pooled). N1 peaked at fronto-central, central sites (maxima at FCz, Cz, and CPz), with a mean latency of 93 ms (91-95 ms latency range) in the two groups and three conditions. Therefore the P1-N1 amplitudes were measured as the difference of the average signal at FCz (as the electrode closest to the maxima described above) in the 38-58 ms and the 83-103 ms intervals (peak –to–peak). The P1-N1 difference amplitudes were submitted to a Group \times Condition ANOVA, which showed

a significant Group main effect: $F(1,39) = 24.055$, $\eta_G^2 = 0.362$, $p < 0.001$, showing that the amplitudes were higher in the older adult group; and a significant Condition main effect: $F(2,78) = 10.280$, $\epsilon = 0.942$, $\eta_G^2 = 0.020$, $p < 0.001$. Following-up the Condition main effect, pair-wise t-tests (with pooled groups) showed significant differences between all conditions ($t[40]$ -scores > 2.105 ; p -values < 0.042): the amplitude was highest in the 150 vs. 750 ms, and lowest in the 450 vs. 750 ms condition.

3.2.3 ERPs –offset-related activity

As in previous studies, offset-related ERP activity was characterized by a positive-negative transient waveform most readily observable at the temporal electrodes (marked by black arrows at T8 in Fig. 2 and 3), superimposed on the slow decay of the sustained ERP. As in previous studies, long tone offsets were followed by similar offset-related transient waveforms (marked by gray arrows at T8 in Fig. 2 and 3).

The group-average short-minus-long difference waveforms are contrasted in Figure 4. Previous studies showed that the offset-related waveforms are likely to be overlapped by the N2 and P3b. Based on previous experiments (Horváth, 2016) electrodes with potentially maximal (Cz) and minimal (T7 and T8) N1-N2 overlap were used in these analyses, whereas P3b was characterized by the amplitude measured at Pz. The offset-related group-average P1 and N1/N2 peak latencies measured at Cz, and P3b peak latencies measured at Pz in the short-minus-long difference waveforms of the three conditions are presented in Table 2. The topographical distributions of the ERPs (average amplitudes measured in 20 ms windows centered at these time points) are shown in Figure 5.

The Group \times Condition (150, 300, or 450 ms vs. 750 ms) \times Electrode (T7, Cz, T8) ANOVA of the offset-related P1 amplitudes (measured in 20 ms windows centered at the peak amplitudes at Cz in the group-average short-minus-long difference waveforms, Table 2)

showed a significant Condition main effect: $F(2,78) = 5.705$, $\varepsilon = 0.853$, $\eta_G^2 = 0.045$, $p = 0.007$; a significant Electrode main effect: $F(2,78) = 30.145$, $\varepsilon = 0.855$, $\eta_G^2 = 0.113$, $p < 0.001$; and a significant Condition \times Electrode interaction: $F(4,156) = 14.148$, $\varepsilon = 0.813$, $\eta_G^2 = 0.038$, $p < 0.001$. The interaction was resolved by separate one-way Condition ANOVAs (with participant groups pooled), which showed a significant effect only at Cz: $F(2,80) = 15.486$, $\varepsilon = 0.877$, $\eta_G^2 = 0.139$, $p < 0.001$; showing that the amplitude was the lowest in the 150 vs. 750 ms, and highest in the 450 vs. 750 ms condition (as indicated by pair-wise t-tests: $t[40]$ -scores > 2.067 ; p -values < 0.05). This indicates that P1 received a positive contribution at the central sites, which increased with the duration of the short tone across conditions.

The Group \times Condition \times Electrode ANOVA of the offset-related N1/N2 amplitudes showed a significant Condition main effect: $F(2,78) = 22.220$, $\varepsilon = 0.940$, $\eta_G^2 = 0.072$, $p < 0.001$; a significant Group \times Electrode interaction: $F(2,78) = 8.487$, $\varepsilon = 0.741$, $\eta_G^2 = 0.041$, $p = 0.002$; a significant Condition \times Electrode interaction: $F(4,156) = 4.850$, $\varepsilon = 0.786$, $\eta_G^2 = 0.005$, $p = 0.003$; and a significant Group \times Condition \times Electrode interaction: $F(4,156) = 2.837$, $\varepsilon = 0.786$, $\eta_G^2 = 0.003$, $p = 0.039$. Following-up the three-way interaction, separate Group \times Condition ANOVAs were conducted for the three electrode levels. For the amplitudes at Cz, a significant Group main effect: $F(1,39) = 4.755$, $\eta_G^2 = 0.096$, $p = 0.03$, showing more negative amplitudes in the older than in the younger adult group; and a significant Condition main effect: $F(2,78) = 22.425$, $\varepsilon = 0.946$, $\eta_G^2 = 0.067$, $p < 0.001$ was found. For the amplitudes at T7 and T8, only significant Condition main effects were found ($F[2,78] = 20.364$, $\varepsilon = 0.850$, $\eta_G^2 = 0.123$, $p < 0.001$; $F[2,78] = 10.877$, $\varepsilon = 0.896$, $\eta_G^2 = 0.066$, $p < 0.001$, for T7 and T8, respectively). For all three electrodes, the Condition main effect was caused by higher (more negative amplitudes) in the 150 and 300 ms vs. 750 ms conditions than in the 450 vs. 750 ms condition (as indicated by pair-wise t-tests: $t[40]$ -scores > 3.046 ; p -values < 0.008). Taken together, this indicates that N1 was enhanced for the short

duration conditions in comparison to the 450 vs. 750 ms condition; and that the monolithic N1/N2 waveform received a substantial central ERP contribution (presumably an N2) in the older adult group in comparison to the younger adults (Figure 5, middle rows).

The Group \times Condition ANOVA of the offset-related P3b amplitudes (measured at Pz) showed a significant Group main effect: $F(1,39) = 6.162$, $\eta_G^2 = 0.121$, $p = 0.017$, showing more positive amplitudes in the younger adult group; and a significant Condition main effect: $F(2,78) = 6.381$, $\epsilon = 0.993$, $\eta_G^2 = 0.020$, $p = 0.003$. The Condition main effect was followed-up by pair-wise t-tests (with pooled groups), which showed that the amplitude of the 150 vs. 750 ms condition was significantly higher (more positive) than in the other two conditions ($t[40]$ -scores > 2.093 , p -values < 0.043).

The Group \times Condition (150, 300, or 450 ms vs. 750 ms) ANOVAs of the jackknife peak latencies (measured at Cz in the short-minus-long difference waveforms; Figure 6) as described by Kiesel et al. (2008) showed no significant effects for P1 or P3b. For N1/N2, however, a significant Group main effect was present: $F(1,39) = 18.814$, $\eta_G^2 = 0.990$, $p < 0.001$, indicating longer peak latency in the older adult group. This latency shift may also reflect a substantial N2 contribution in the older adult group.

3.2.4 ERPs –the latency of the offset-related ERP activity as the function of response speed

The group-average ERPs elicited in short-tone trials with faster-, and slower-than-median responses are presented in Figure 7 and 8. Using the jackknife procedure described by Kiesel et al. (2008), the offset-related P1 (measured at T7), N1/N2 (measured at Cz), and P3b (measured at Pz) latencies were submitted to mixed Group \times Partition (faster-, or slower-than-median) \times Condition (150, 300, or 450 ms vs. 750 ms) ANOVAs. The mean jackknife latencies are presented in Figure 9. For the P1, no significant effects were found.

For the N1/N2 we found a significant Group main effect: $F(1,39) = 97.827$, $\eta_G^2 = 0.998$, $p < 0.001$, showing later peaks in the older adult group; a significant Partition main effect: $F(1,39) = 9.123$, $\eta_G^2 = 0.985$, $p = 0.004$, showing later peaks for longer response times; and a significant Group \times Partition interaction: $F(1,39) = 10.276$, $\eta_G^2 = 0.949$, $p = 0.003$. Following up the interaction, a Welch two-sample t-test showed that the between-partition latency-difference was larger in the older, than in the younger adult group ($t[29.069] = 2.240$, $p = 0.033$). This result also reflects that in older adults the N1/N2 receives a substantial N2 contribution.

As in previous experiments (Horváth, 2016), ERPs in trials with faster-than-median responses were characterized by a negative shift in the ERP preceding the N1/N2 peak (indicated by shaded between-curve areas in Figure 8). Because the bifurcation of the two ERPs may start already before tone onset, the magnitude of these partition-related differences may be biased by baselining; therefore, only a simple analysis was performed to confirm the presence of these shifts: The average ERP amplitudes at Cz in the 50 ms interval preceding offsets measured in the two partitions (as in Horváth, 2016) were submitted to paired Student's t-tests in each group and condition. All comparisons showed significantly more negative amplitudes in trials with faster-than-median responses (for the older adults: $t[19]$ -scores > 3.996 , p -values < 0.001 ; for the younger adults: $t[20]$ -scores > 3.716 , p -values < 0.002).

For the P3b, a significant Group main effect was present: $F(1,39) = 13.430$, $\eta_G^2 = 0.978$, $p < 0.001$, showing that P3b peaked later for older adults. A significant Partition main effect: $F(1,39) = 21.399$, $\eta_G^2 = 0.992$, $p < 0.001$, indicated that P3b peaked later in trials with slower-than-median responses. Finally, a significant Condition main effect: $F(2,78) = 4.076$, $\epsilon = 0.709$, $\eta_G^2 = 0.976$, $p = 0.035$ was also found. Following-up the Condition main effect, pair-

wise t-tests (with pooled groups) showed that P3b peaked significantly later in the 450 vs. 750 ms condition than in the other two conditions ($t_{[40]}$ -scores > 2.225 , p -values < 0.032).

4. Discussion

4.1 Tone offset-related processing

The present study investigated age-related differences in the processing of sound offsets in a duration discrimination paradigm presenting two tones in each condition. The long tone duration was 750 ms in all three conditions, whereas short tone duration was 150, 300, or 450 ms. As in previous studies (Horváth, 2014, 2016), tone offsets were followed by a consistent positive-negative (P1-N1) waveform pattern most distinctly observable at the temporal leads in both groups, which, in combination with the fact that offset-related waveforms peaked about 50 ms later than the typical onset-related P1-N1 waveforms, may indicate that these offset-related waveforms reflected mainly the T-complex (Wolpaw and Penry, 1975) of the auditory ERP. Although the fronto-centrally peaking onset-related P1-N1 waveform was larger in the older adult group in correspondence with most previous studies (see Introduction), no significant between-group differences were found for the offset-related P1, or the temporally measured offset-related N1. These results are in agreement with the assumption that sound onset- and offset-related auditory ERPs reflect – at least in part – different aspects of sensory processing, and that these aspects may be differentially affected by aging. In terms of the ERP components, one may speculate that whereas the P1 and the supra-temporal N1 subcomponents of the late auditory ERP (which are dominant in the ERP elicited by sound onsets) are affected by age, the T-complex (which seems to dominate the offset-related waveform) is not. The lack of an age-related difference in the offset-related auditory ERP is on a par with the results of Ross et al. (2009) showing no age-related differences in offset-related magnetic fields for short duration (34-76 ms) sounds.

The offset-related N1 received a marked enhancement in the older adult group at central recording sites, which, combined with the increased latency of the negative waveform in the older adult group, suggests that N1 was overlapped by a centrally distributed N2 in the older adult group even at the shortest duration. This interpretation of the ERP pattern was also corroborated by the fact that separating slow- and fast-response trials significantly affected the latency of the central negative waveform only in the older adult group. This age-related difference in N2 elicitation may reflect a *quantitative* task-related processing difference. Because in discrimination tasks involving more similar stimuli higher N2s are elicited (Nieuwenhuis et al., 2004), the N2 difference may reflect that the discrimination task was more difficult for older than for younger adults. The behavioral data, however, does not seem to support this notion. Although older adults' responses to tone offsets were generally slower than those of younger adults, no age-related reaction time modulation was found, that is, between-group reaction time differences did not substantially change as a function of discrimination difficulty. An age-related discrimination performance loss in the d' sensitivity score was only present in the 450 vs. 700 ms condition. Because N2 was clearly present in the older adult group even in the condition with the shortest duration, it seems unlikely that the presence of N2 in older adults was caused by a task-difficulty difference.

Because N2 reflects cognitive control processes (Donkers and van Boxtel, 2004, Nieuwenhuis et al., 2003; for a summary see Folstein Van Petten, 2008), the dominance of N2 in the older adult group may also show that older adults were more reliant on cognitive control processes than younger adults in performing the task. Whereas this may be *quantitative* between-group difference, the marked N2 elicitation difference may also reflect a *qualitative* difference in the way the task was represented in the two groups. Szmalec et al. (2008) found no N2 elicited by tones in a simple detection task whereas the same tones elicited an N2 when presented in a discrimination context. In the present study, it could be

speculated that younger adults framed the task essentially as offset-detection, whereas older adults framed it as a genuine discrimination task (*a strategy-difference*). The uniform between-group reaction time difference over the conditions fits this interpretation.

This *strategy-difference* notion is somewhat reminiscent of the distinction between proactive and reactive processing strategies suggested in the context of task-switching (Braver et al., 2008), proposing that older adults rely primarily on (spared) reactive processing strategies, whereas younger adults can utilize proactive strategies as well (Jimura and Braver, 2010; Bugg, 2014). In the present context, in order to structure the task as offset detection, one would have to identify the task-relevant time periods in which only the task-relevant offset (i.e. short tone offset) could occur and perform the detection task in these, while suspending task performance in other time-intervals. This hypothetical temporal structuring can be regarded as a form of proactive control. The ERP results neither support, nor contradict this interpretation. First, preparation-related ERPs preceding the tones, and short tone offsets (see below) are expectable for both strategies. Second, the withdrawal of attention in the task-irrelevant interval could be manifested in the amplitude decrease of the task-irrelevant offset ERP, the present design, however, does not allow the assessment whether such a decrease was present. Although one could argue that the presence of the offset-related ERP for long tones (marked by gray arrows at T8 in Figure 2 and 3) shows that participants attended the tones even in task-irrelevant intervals, this is not sufficient to dispel the strategy-difference idea, because long tone-offsets elicit an offset-related transient waveform even if the tones are unattended (Horváth, 2016).

Offset-related P1 and N1/N2 amplitudes were both shifted in the positive direction across conditions with increasing short tone duration (i.e. with increasing discrimination difficulty). We speculate that this pattern was caused by an overlap from the P3b which was temporally more spread, and therefore started earlier for longer short-tone durations. Such a

temporal widening might be caused by the increasing uncertainty in the decision whether the task-relevant timepoint of the potential offset has been already reached or not. That is, for longer tones, participants are more likely to decide prematurely that the critical timepoint already passed than for shorter ones, which, on average, results in a P3b which is wider and starts earlier.

4.2 ERP reflections of the information processing sequence in the paradigm

Besides directly characterizing offset-related processing activity and its age-related differences, the results also allow a general delineation of the information processing sequence within the paradigm. The pattern of results seems to reflect the interaction of two effects, which differ in their tone duration-dependence. First, discrimination difficulty increases with increasing short/long duration ratios. Second, the constant stimulus timing patterns enable the use of tone-onset as a cue to prepare for the task-relevant time-point. Preparation efficiency follows a non-monotonous - reversed U-shaped - function, with an optimum point at a cue-target separation typically in the 150-300 ms interval (*foreperiod* effect, Bertelson, 1967; Müller-Gethmann et al., 2003). We speculate that in the present study the optimum was closer to the 300 ms onset-offset separation than to the 150 ms, which is reflected in faster reaction times in the 300 vs. 750 ms condition than in the 150 vs. 750 ms condition. The close-to-optimal preparation efficiency in the 300 vs. 750 ms condition may also have counteracted the increased difficulty in comparison to the 150 vs. 750 ms condition, which resulted in similar performance indices and similar preparatory activity as reflected in the ERPs. The drop in performance indices, and slower reaction times in the 450 vs. 750 ms condition probably reflect both the increase in discrimination difficulty, and that onsets did not allow for an efficient preparation for the task-relevant moment. The less steep negative ERP trend observed in the pre-tone interval, the lower-amplitude onset-related P1-N1, as well as the lower-amplitude offset-related N1, suggests that participants did not prepare for, and

did not direct as much attention to tone-onsets, and consequently to offsets in this condition as in the other two.

5. Conclusions

In summary, the present study found no age-related differences in sensory ERP responses to tone offsets. In older adults, however, offset-related processing was dominated by an N2 reflecting the marked involvement of cognitive control-related processing activities. Because the N2 was present regardless discrimination difficulty, it is speculated that young adults represented the task as offset-detection, whereas old adults represented the task as duration-discrimination.

6. Acknowledgements

This work was supported by the Hungarian Scientific Research Fund (OTKA K104635), and the János Bolyai Research Scholarship of the Hungarian Academy of Sciences. Conflicts of interest: none.

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Tables

	IQ (WAIS-IV)	Hearing thresholds (dB SPL)		
		500 Hz	1000 Hz	2000 Hz
Younger	106 ± 11	9 ± 5	3 ± 5	6 ± 6
Older	121 ± 15	17 ± 9	10 ± 6	17 ± 10
Welch t-test results	t(34.71) = 3.611, p < 0.001	t(29.93) = 3.502, p = 0.001	t(35.11) = 3.878 p < 0.001	t(32.14) = 4.426 p < 0.001

Table 1. Mean IQ scores and hearing thresholds (and standard deviations) in the younger and older adult groups, compared by two-sample Welch t-tests. Note that in the experiment, tone intensity was individually adjusted to 50 dB above the hearing threshold level measured with a continuous version of the tone presented in the experiment.

	Young			Old		
	150 vs. 750 ms	300 vs. 750 ms	450 vs. 750 ms	150 vs. 750 ms	300 vs. 750 ms	450 vs. 750 ms
P1	102	104	107	113	112	116
N1/N2	164	167	185	217	224	236
P3b	319	309	344	342	347	339

Table 2. Offset-related group-average P1, N1/N2 (both measured at Cz) and P3b peak latencies (measured at Pz) in the short-minus-long difference waveforms in the three conditions, in the younger and older adult groups.

Figures

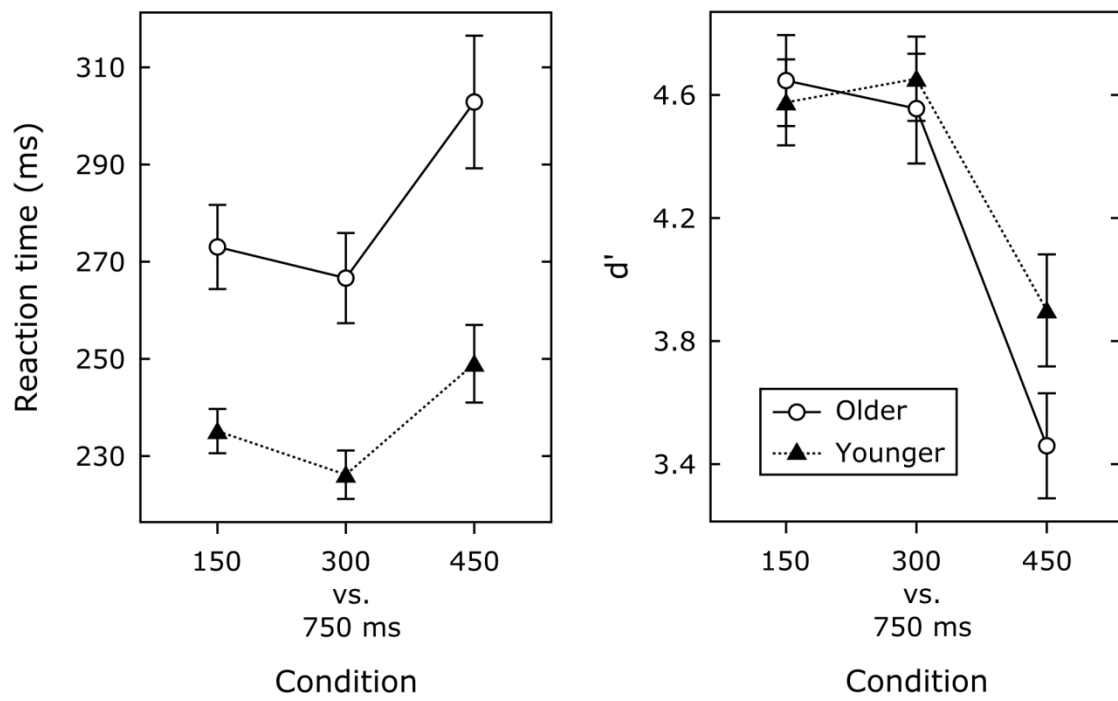


Figure 1. Group-average reaction times (left) and d' sensitivity scores (right) in the three conditions. Whiskers indicate standard errors.

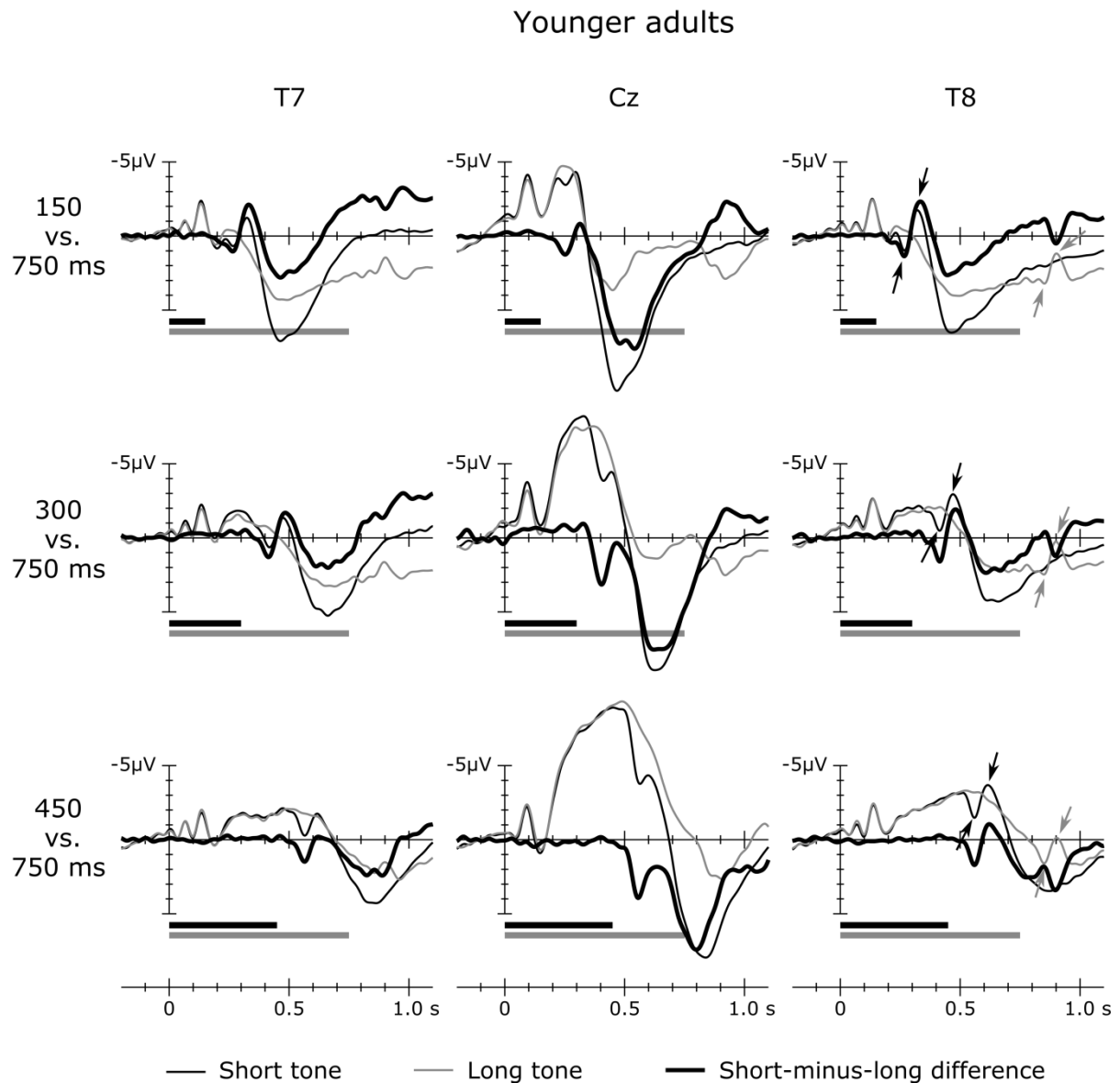


Figure 2. Group-average ERPs elicited at the T7 (left), Cz (middle), and T8 (right) electrodes for the short (thin black curves) and long tones (thin gray curves) in the three conditions (each presented in a single row) in the younger adult group, and the corresponding short-minus-long difference waveforms (thick black curves). Tone durations are represented as black (short) and gray (long) bars under the horizontal axes. Black and gray arrows indicate the offset-related P1 and N1 waveforms at the T8 electrode for the short and the long tones respectively.

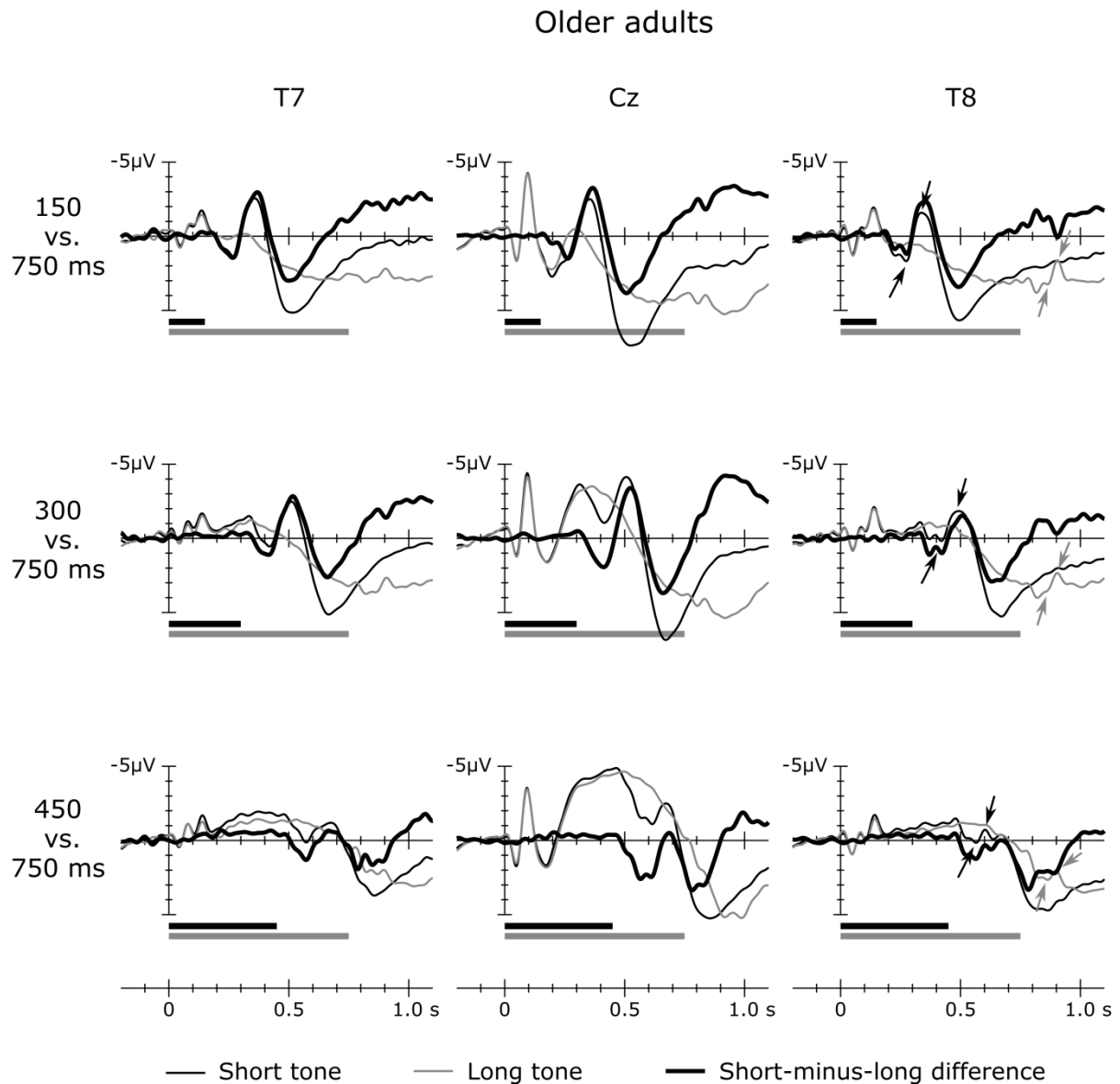


Figure 3. Group-average ERPs elicited at the T7 (left), Cz (middle), and T8 (right) electrodes for the short (thin black curves) and long tones (thin gray curves) in the three conditions (each presented in a single row) in the older adult group, and the corresponding short-minus-long difference waveforms (thick black curves). Tone durations are represented as black (short) and gray (long) bars under the horizontal axes. Black and gray arrows indicate the offset-related P1 and N1 waveforms at the T8 electrode for the short and the long tones respectively.

Short-minus-long difference waveforms

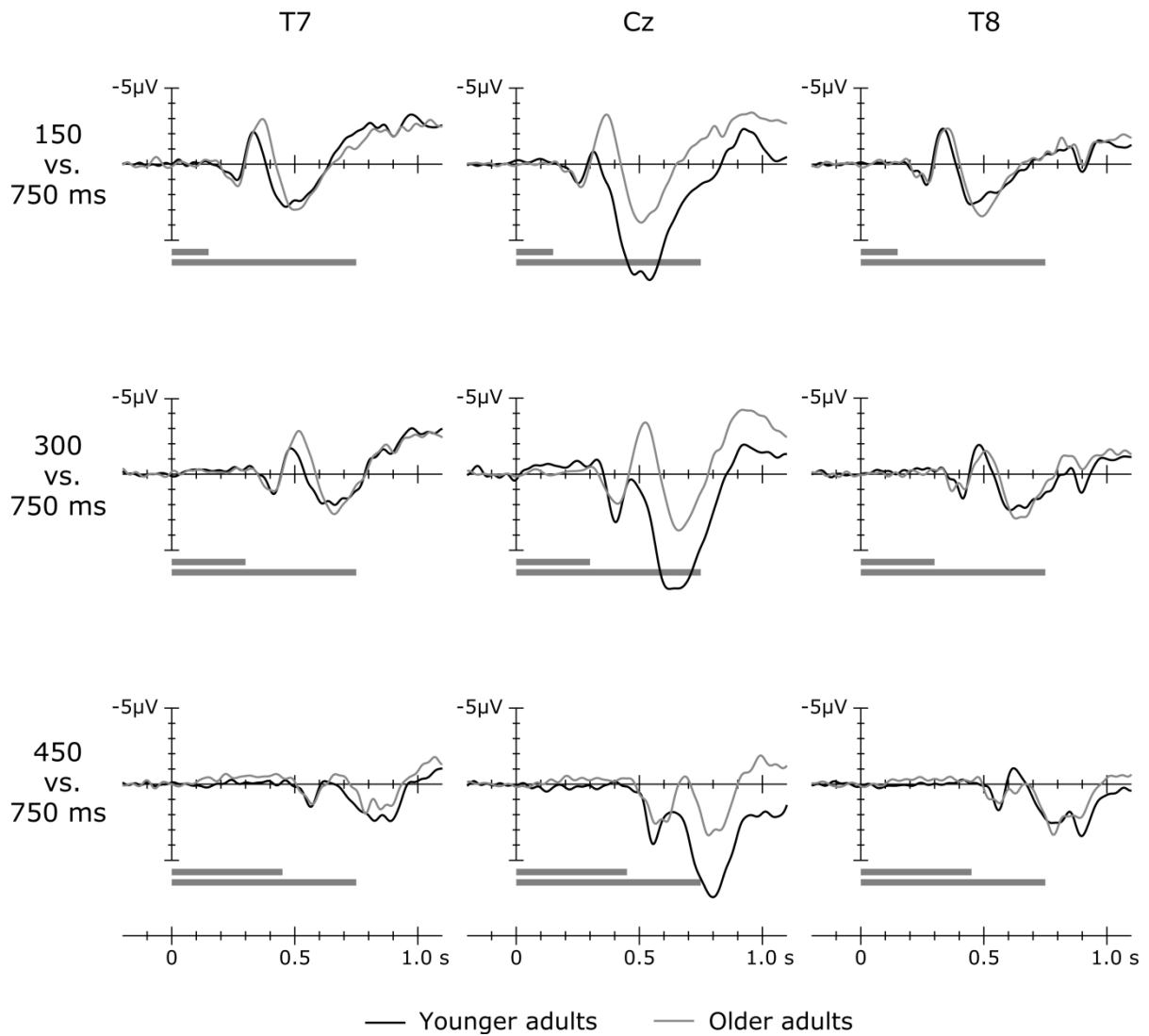


Figure 4. Group-average short-minus-long difference waveforms elicited at the T7 (left), Cz (middle), and T8 (right) electrodes in the younger adult (black curves) and older adult group (gray curves) in the three conditions (each presented in a single row). Tone durations in the given conditions are represented as gray bars under the horizontal axes.

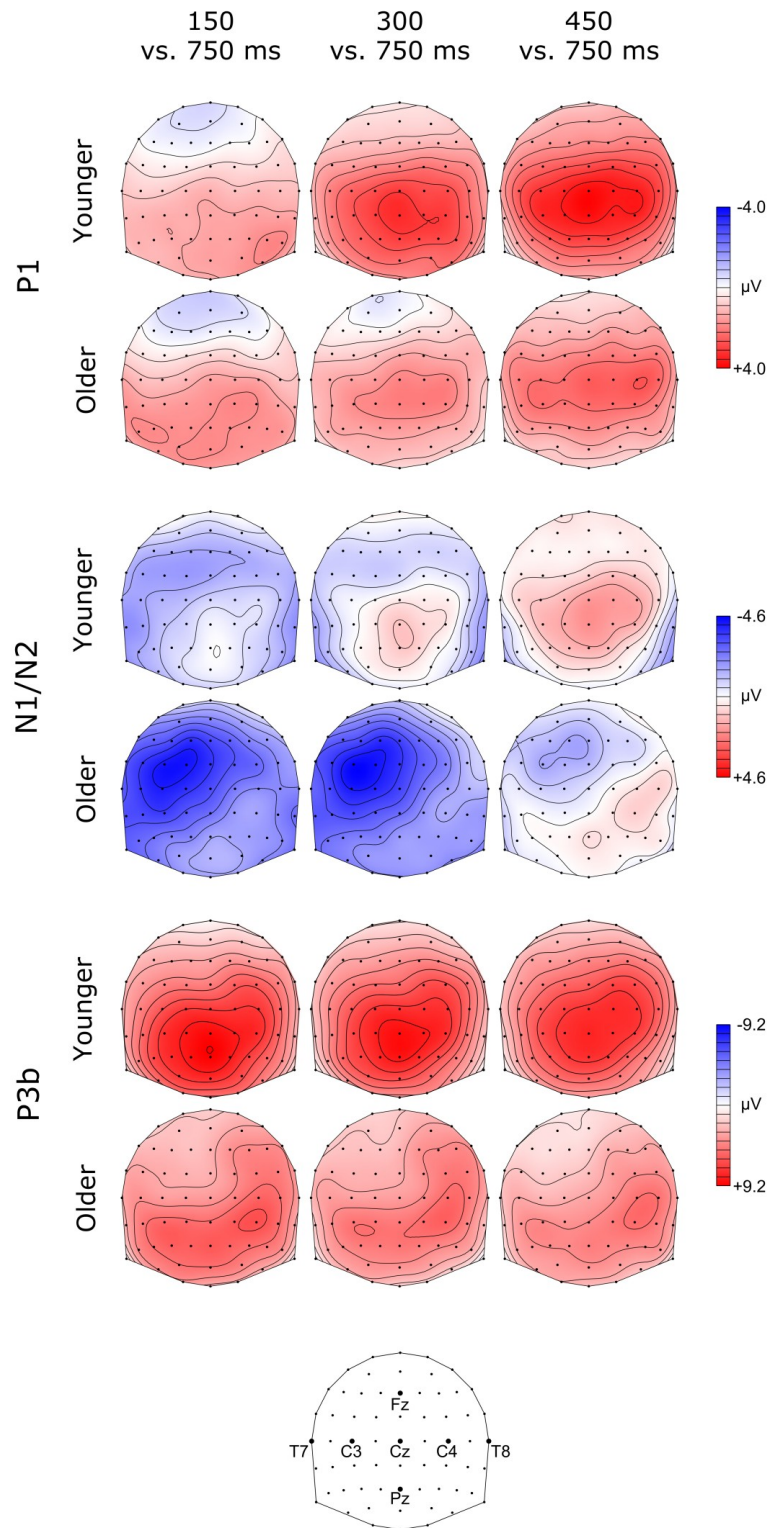


Figure 5. Group-average offset-related topographical ERP distributions (average amplitudes measured in the short-minus-long difference waveforms, in 20 ms windows centered at the peak latencies described in Table 2) for the two groups in the three conditions for the P1, N1/N2, and P3b time ranges.

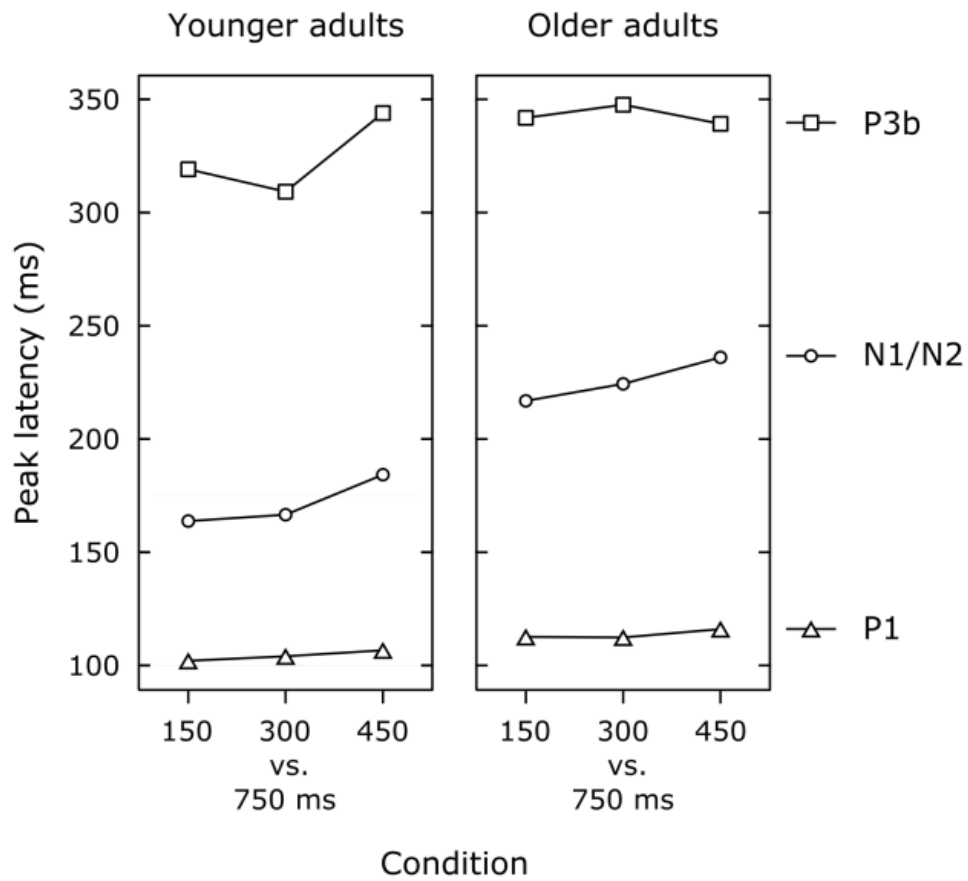


Figure 6. Group-mean jackknife peak latencies of the offset-related P1, N1/N2, and P3b measured at Cz in the short-minus-long difference waveforms in the three conditions.

Younger adults

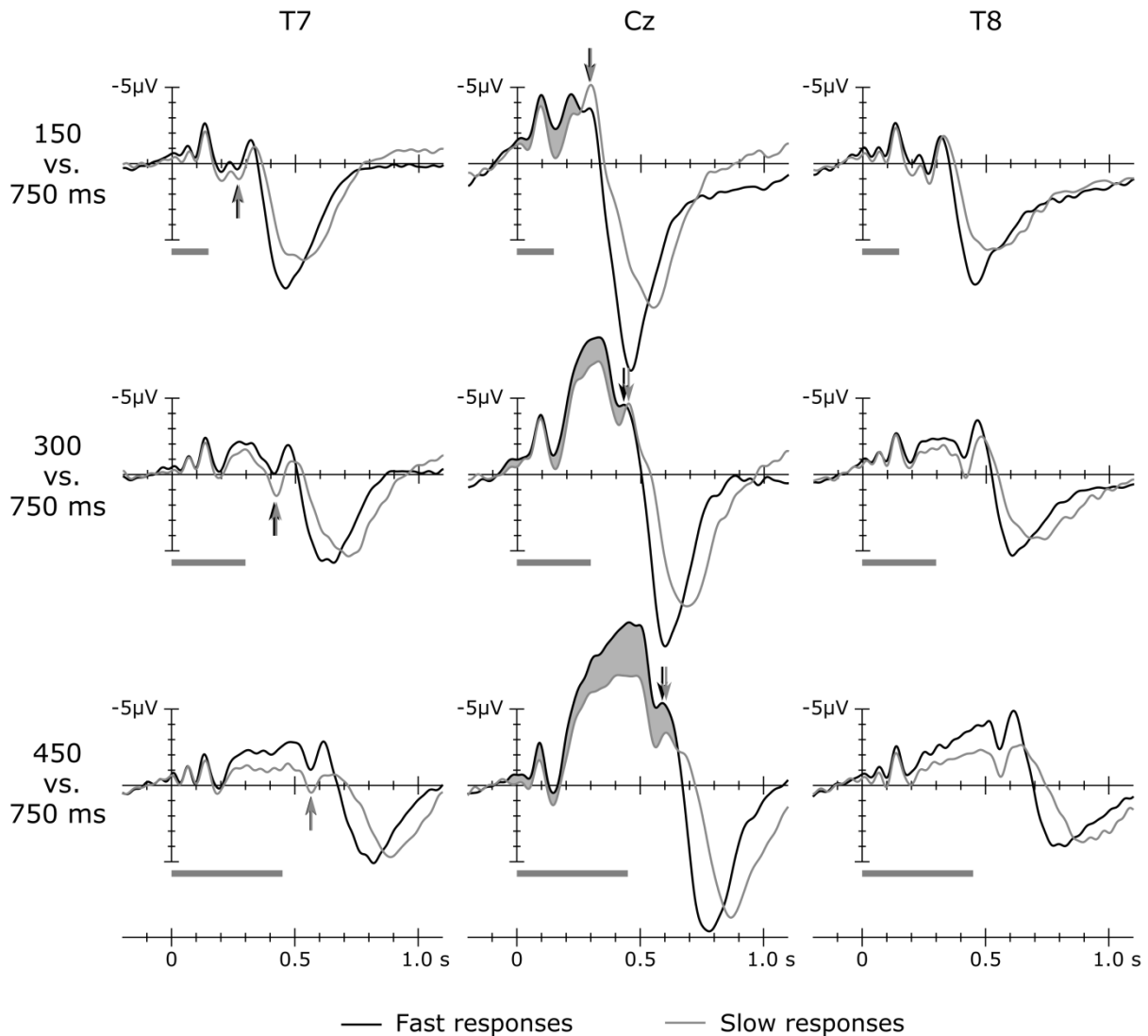


Figure 7. Group-average ERPs elicited by short tones in trials with below-median (black curves) and above-median reaction times (gray curves) at the T7 (left), Cz (middle), and T8 (right) electrodes, in the three conditions (each presented in a single row) in the younger adult group. Short tone durations in the given conditions are represented as gray bars under the horizontal axes. Offset-related P1 peak latencies are indicated by arrows with colors corresponding to the curves at T7, offset-related N1/N2s peak latencies are indicated by arrows with colors corresponding to the curves at Cz. The light gray shading between the two curves at Cz highlight a sustained difference in ERP activity preceding the offset-related waveforms.

Older adults

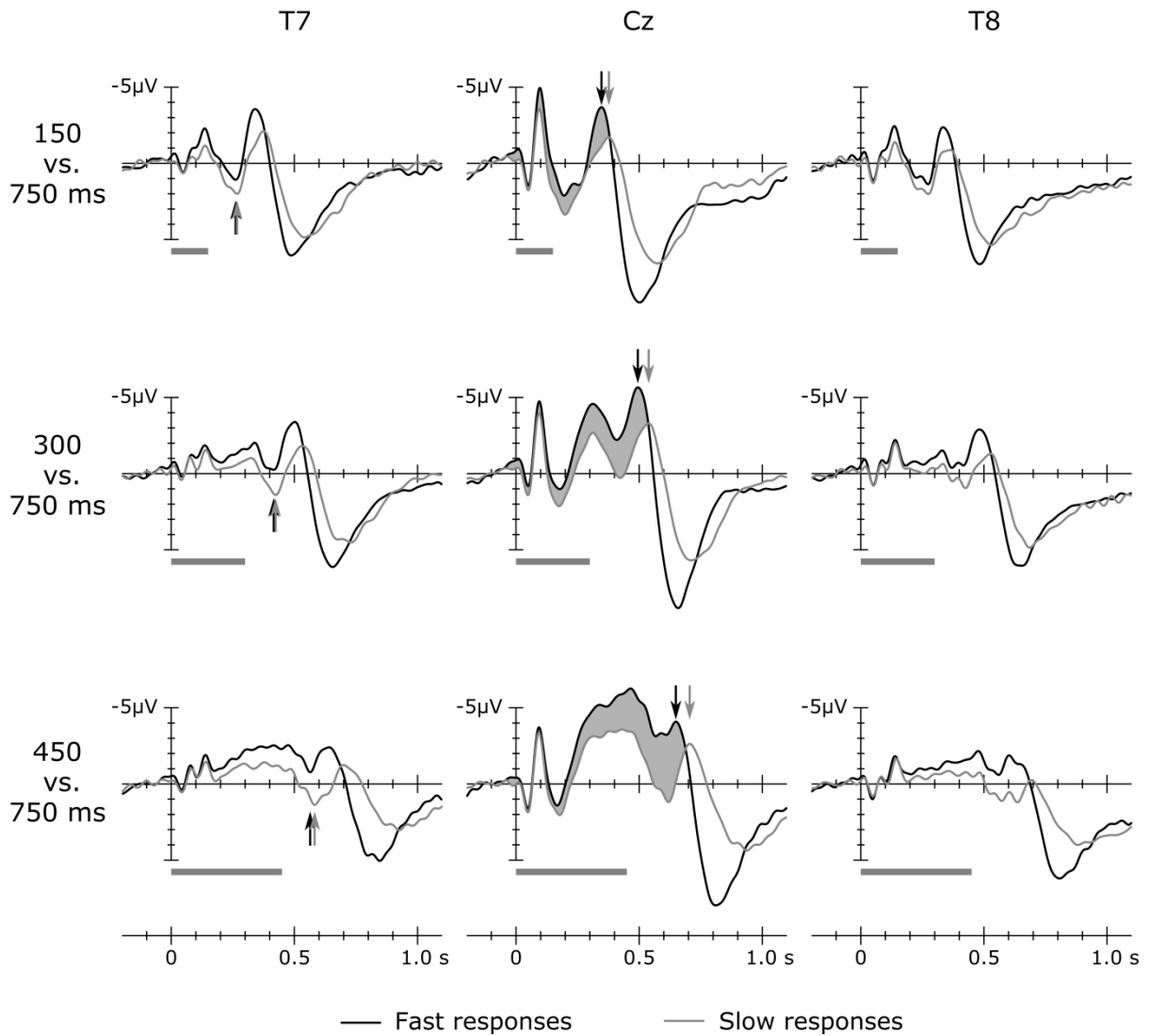


Figure 8. Group-average ERPs elicited by short tones in trials with below-median (black curves) and above-median reaction times (gray curves) at T7 (left), Cz (middle), and T8 (right) electrodes, in the three conditions (each presented in a single row) in the older adult group. Short tone durations in the given conditions are represented as gray bars under the horizontal axes. Offset-related P1 peak latencies are indicated by arrows with colors corresponding to the curves at T7, offset-related N1/N2s latencies are indicated by arrows with colors corresponding to the curves at Cz. The light gray shading between the two curves at Cz highlight a sustained difference in ERP activity preceding the offset-related waveforms.

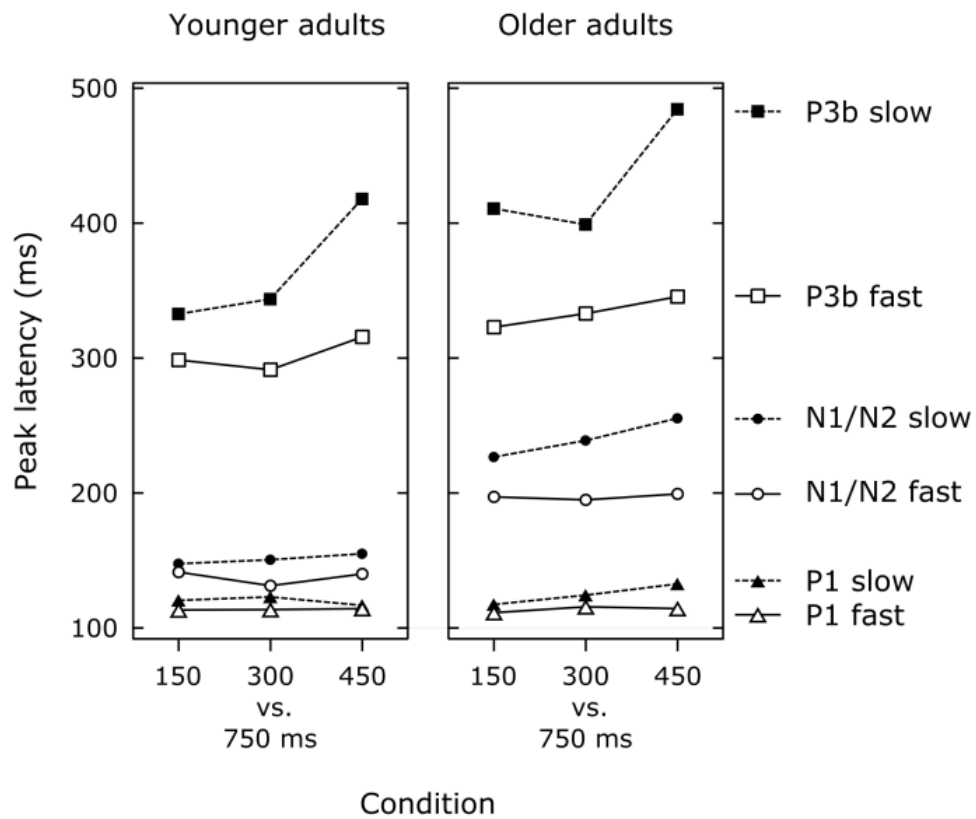


Figure 9. Group-mean jackknife peak latencies for the offset-related P1, N1/N2, and P3b, elicited by short tones in trials with faster-than-, and slower-than-median reaction times in the younger (left) and older adult groups (right), in the three conditions.