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Aging and the processing of sound duration in human auditory cortex

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Abstract

Age-related declines in coding the fine temporal structure of acoustic signals is proposed to play a critical role in the speech perception difficulties commonly observed in older individuals. This hypothesis was tested by measuring auditory evoked potentials elicited by sounds of various durations in young, middle-aged and older adults. All stimuli generated N1 and P2 waves that peaked at about 104 and 200 ms post-stimulus onset. The N1 amplitude increased linearly with increases in the tonal duration in young, middle-aged, and older adults. The P2 amplitude also increased linearly with signal duration, but only in young and middle-aged adults. The results demonstrate that the N1 and P2 waves can resolve duration differences as short as 2–4 ms and that normal aging decreases the temporal resolving power for processing small differences in sound duration.

Key words: Aging; Perception; Evoked potential; Sound duration; Temporal processing; Auditory; Scene analysis

1. Introduction

Age-related declines in the ability to code the temporal properties of the speech envelope are thought to contribute to the speech perception problems often experienced by older adults (Schneider and Pichora-Fuller, 2001). Because the speech envelope is defined by energy fluctuations in the signal in which low-energy periods (gaps) are interspersed with high-energy periods of varying length, the two psychophysical measures most relevant to the processing of the speech envelope are the ability to detect a gap in a continuous sound and the ability to discriminate between two sounds on the basis of their duration. The ability to discriminate duration differences may also be important for speech perception because phonemic contrasts can be cued by differences in vowel duration (e.g. rice versus rise) (Peterson and Lehiste, 1960), or consonant transitions (e.g. weed versus bead) (Miller and Liberman, 1979).

Despite the prevalence of behavioral studies suggesting age-related declines in temporal resolution (Abel et al., 1990; Fitzgibbons and Gordon-Salant, 1994; Gordon-Salant and Fitzgibbons, 1993; Schneider and Hamstra, 1999), behavioral findings alone do not provide unequivocal evidence for deficits in the ability to distinguish differences in sound duration. Performance on psychoacoustic tasks depends on many processes, including encoding, maintenance, and manipulation of sensory information, all of which can be affected by age. Therefore, it is unclear how aging affects these various abilities required to perform the behavioral tasks. Recording of auditory evoked potentials (AEPs) provides a powerful tool for exploring the neural mechanisms underlying encoding, maintenance, and manipulation of information. In particular, the effects of age on temporal processing can be examined by comparing AEPs elicited by sounds of various durations.

Previous research in young adults has shown that the N1 wave, an AEP deflection that peaks at about 100 ms after sound onset, decreases in latency and increases in amplitude with increasing signal duration up to about

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Abbreviations: AEP, auditory evoked potential; SPL, sound pressure level

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30 ms, after which point the N1 response latency and amplitude are little affected by sound duration (Arlinger et al., 1976; Onishi and Davis, 1968; Skinner and Jones, 1968). Similarly, the magnetic counterpart of the N1 response (M1) has been shown to increase in amplitude with increasing sound duration up to a point of saturation at approximately 40 ms (Gage and Roberts, 2000). The P2 wave, which follows the N1 and peaks at about 200 ms after sound onset, also decreases in latency and increases in amplitude with increasing sound duration (Alain et al., 1997).

In the present study, we compared the effects of age on the N1 and P2 waves elicited by sounds of various durations. Participants were presented with frequent standard sounds and rare deviant sounds. The duration of the sounds varied between blocks of trials. Age-related changes in the coding of sound duration were investigated by examining how the N1 and P2 waves changed as a function of the duration of the standard sound. In the present report, we used five 2-ms increments in duration to examine in more detail the temporal resolving power of the N1 and P2 waves. Based on previous behavioral research on temporal processing (Fitzgibbons and Gordon-Salant, 1996; Schneider and Hamstra, 1999), it was hypothesized that aging would decrease the N1 and P2 amplitude growth function associated with increased sound duration. Alternatively, if the processing of sound duration is little affected by aging then the growth function of the N1 and P2 waves as a function of duration should be similar in all three age groups.

2. Materials and methods

2.1. Participants

Thirty adults provided written informed consent to participate in the study. Data from one older adult were excluded because of excessive ocular contamination. Ten young (mean age = 27 years, s.d. = 4; range = 21–31; five men), 10 middle-aged (mean age = 47 years, s.d. = 7; range = 37–58; four men), and nine older (mean age = 69 years, s.d. = 5; range = 60–78; four men) adults form the final sample. All participants had pure-tone thresholds less than or equal to 30 dB HL in the range of 250–2000 Hz in the tested ear (Table 1). All but two participants were right-handed. The young adults were recruited from local colleges whereas middle-aged and older adults were recruited from the community and local volunteer groups.

2.2. Stimuli and task

Participants were presented with standard (no gap, probability 85%) and deviant (gap, probability 15%) stimuli. The present report focuses on age-related changes in processing the duration of the standard sounds. Age effects associated with processing gap stimuli are presented elsewhere (Alain et al., Submitted).

Stimuli were produced by multiplying a 2-kHz pure tone by a temporal window created by summing a series of Gaussian envelopes (standard deviation = 0.5 ms) spaced 0.5 ms apart. Two short tones marked the beginning and end of the gap. These tonal markers were created by multiplying a pure tone by an envelope consisting of the sum of six Gaussians. The 2-kHz pure tone was aligned in cosine phase with the centers of the Gaussian defining the envelope. The duration of each marker (defined as the time between the center of the first and the last Gaussians in the envelope) was 2.5 ms. The duration of the gap was defined as the time between the last Gaussian in the leading marker and the first Gaussian of the lagging marker. Gap duration ranged from 3 to 13 ms in 1-ms steps. The comparison stimulus (a tone whose duration and energy were equal to that of the two markers defining the gap) was created by filling in the missing Gaussians between the two markers. For example, the comparison stimulus (referred to here as the standard stimulus), corresponding to a 3-ms gap between two 2.5-ms markers, consisted of 17 Gaussians (standard deviation = 0.5 ms) spaced 0.5 ms apart. This produced a continuous tone whose duration (time between the first and the last of the 17 Gaussians) was 8 ms long. The amplitudes of the stimuli were adjusted so that all standard tones had the same total energy. The sound pressure level (SPL) of a continuous tone whose amplitude was equal to that of the 18-ms stimulus was 80 dB as measured by an SPL meter (Brûel and Kjær, model 2230). Stimuli were presented to the left ear through EARlink 3A insert earphones.

The inter-stimulus interval was fixed at 500 ms. Each participant was presented with five different sound durations, but within each block of trials, only one duration was presented. Young adults were presented with standard tones with durations of 8, 10, 12, 14, and 16 ms, middle-aged adults were presented with durations of 9, 11, 13, 15, and 17 ms, and older adults were presented with durations of 10, 12, 14, 16, and 18 ms. For each duration, two sequences of approximately 600 stimuli were presented to the participants. The five sound duration blocks were presented in random order across participants.

There were two different listening conditions: passive and active. In the passive listening condition, participants were instructed to ignore the auditory stimuli and to perform a concomitant visual serial-choice reaction time task. In the active listening condition, participants were asked to press, as quickly and as accurately

as possible, a button on a response box when they heard the deviant stimulus among the train of ongoing standard stimuli. For the purpose of the present report, the data from the passive and active listening conditions were collapsed together.

2.3. Electrophysiological recording and analysis

AEPs were recorded from an array of 64 tin electrodes contained within an electrode cap (Electro-Cap International). Vertical and horizontal eye movements were recorded with electrodes at the outer canthi and the superior and inferior orbit. Electrophysiological responses were amplified and filtered (bandpass 0.05–50 Hz, 250 Hz sampling rate), via NeuroScan Synamps and stored for off-line processing. During the recording, all electrodes were referenced to electrode Cz and then re-referenced to an average reference off-line at which point Cz was re-instated.

The analysis epoch included 200 ms of pre-stimulus activity and 500 ms of post-stimulus activity. Trials contaminated by excessive artifact (± 150 μV) at the electrodes not adjacent to the eyes were rejected automatically before averaging. The AEPs were then averaged separately for each site and stimulus duration. For each individual average, the ocular artifacts (e.g. blinks and lateral movements) were corrected by means of ocular source components using the Brain Electrical Source Analysis (BESA) software (Picton et al., 2000). AEPs were digitally lowpass-filtered to attenuate frequencies above 15 Hz.

AEP amplitudes and latencies were measured in selected latency regions with respect to the 200-ms prestimulus period. Peak amplitudes and latencies of the P1 (latency window 20–100 ms), N1 (60–160 ms), and P2 (140–240 ms) were obtained using automated peak detection algorithms. For each group and stimulus duration, the mean amplitude of the AEP components was obtained by using a 40-ms window centered on the group mean peak latency, relative to the mean amplitude of the 200-ms pre-stimulus activity.

The effects of stimulus duration on AEPs were analyzed on the mean responses over nine frontocentral electrodes (Fz, F1/2, FCz, FC1/2, Cz, C1/2). For each group of participants, the amplitudes and latencies of the responses were fitted as linear functions of stimulus duration. The slopes of these functions were kept constant for each dependent variable and participant group, whereas the intercept was allowed to differ among participants. More specifically, in each analysis the following regression model was fit to the same 29 participants. Let $y_{i,j,k}$ be the response of subject k in group i to stimulus j. Then:

$$y_{i,j,k} = \alpha_i x_{i,j} + \beta_k$$

where α_i is the slope of the regression line for all participants in group i ($i = 1$–3), $x_{i,j}$ is the jth duration ($j = 1$–5) used for a participant in group i, and β_k is the intercept value for participant k. Participants 1–10 were in the young group ($i = 1$), participants 11–20 were in the middle-aged group ($i = 2$), and participants 21–29 were in the older group ($i = 3$). Thus, the full model has 32 parameters: three slopes (one each for young, middle-aged, and older participants), and 29 intercept values (one for each participant). The following tests on

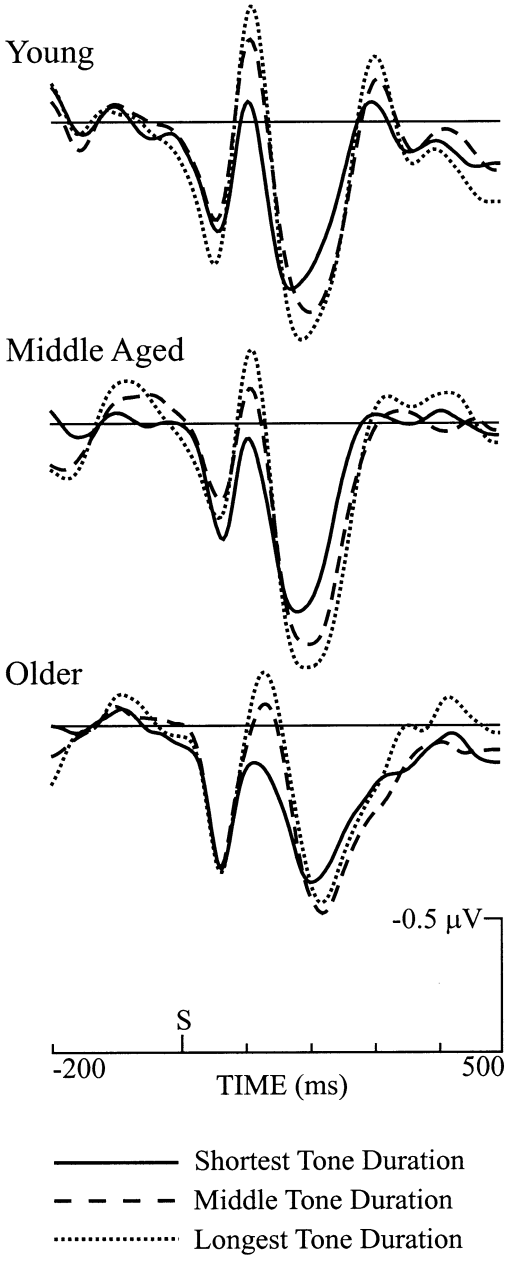

Fig. 1. Group mean event-related brain potentials for the shortest, intermediate, and longest duration stimulus in young, middle-aged, and older adults. Negativity is plotted upward. The letter 'S' in the scale indicates stimulus onset.

the slopes were conducted. First, we tested the hypothesis that $\alpha_i = 0$ for all i. If that hypothesis was rejected we tested whether $\alpha_1 = \alpha_2 = \alpha_3$. If that hypothesis was rejected we tested three sub-hypotheses ($\alpha_1 = \alpha_2$; $\alpha_1 = \alpha_3$; $\alpha_2 = \alpha_3$). Finally, with respect to the P2 data, we tested whether $\alpha_3 = 0$. We also conducted analyses of variance (ANOVA) on the individual intercepts. Specifically, we looked for group differences in intercept value.

Scalp topographies using the 61 electrodes (omitting the periocular electrodes) were also statistically analyzed after scaling the amplitudes to correct for amplitude differences between conditions and between groups (McCarthy and Wood, 1985). The measurements were subjected to within-subject and between-subject ANOVA for repeated measures with stimulus duration, group, and electrodes as factors. The original degrees of freedom for all analyses are reported throughout the paper. Type I errors associated with inhomogeneity of variance were controlled by decreasing the degrees of freedom using the Greenhouse–Geisser epsilon (ε), and the probability estimates are based on these reduced degrees of freedom.

3. Results

The interaction between sound duration and listening condition was not significant nor was the interaction between group, duration, and listening condition. Therefore, to improve signal/noise ratio, the AEPs recorded in both listening conditions were lumped together.

Fig. 1 shows the AEP waveforms elicited by the shortest, intermediate and longest stimulus durations for all three age groups. All stimuli elicited clear P1, N1, and P2 deflections, peaking respectively at approximately 65, 115, and 190 ms.

The results from the regression analyses on the effects of sound duration on AEP components amplitude and latency are illustrated in Fig. 2. We first examined the difference in N1–P2 latencies as a function of sound duration and age. The hypothesis that all slopes were zero was rejected, $F[3,113] = 16.64$, $P < 0.001$. However, the equal-slope hypothesis was not rejected, $F[2,113] = 1.61$, $P > 0.15$. The intercepts, which measured the separation between parallel function, did differ, $F[2,26] = 9.70$, $P < 0.001$. Pairwise comparisons among groups

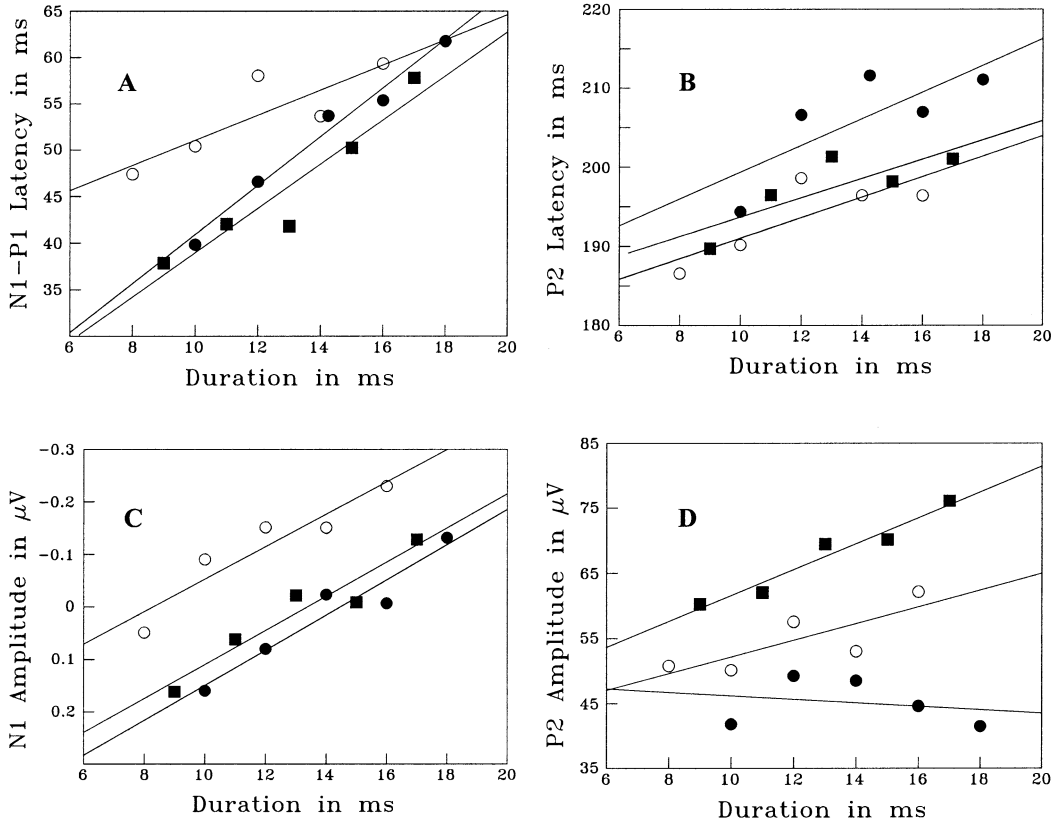

Fig. 2. Young adults (open circles), middle-aged adults (square), and older adults (filled circle). Top left panel shows the N1–P2 latency difference (the latency difference at 14 ms for the older adults has been laterally displaced so that it does not overlap with that for younger adults). Top right panel shows the effects of age on P2 latency. Lower left panel shows the effects of age on N1 amplitude. Lower right panel shows the effects of age on P2 amplitude. The N1 and P2 amplitudes reflect the group mean voltage measured at nine frontocentral sites (see Section 2 for details).

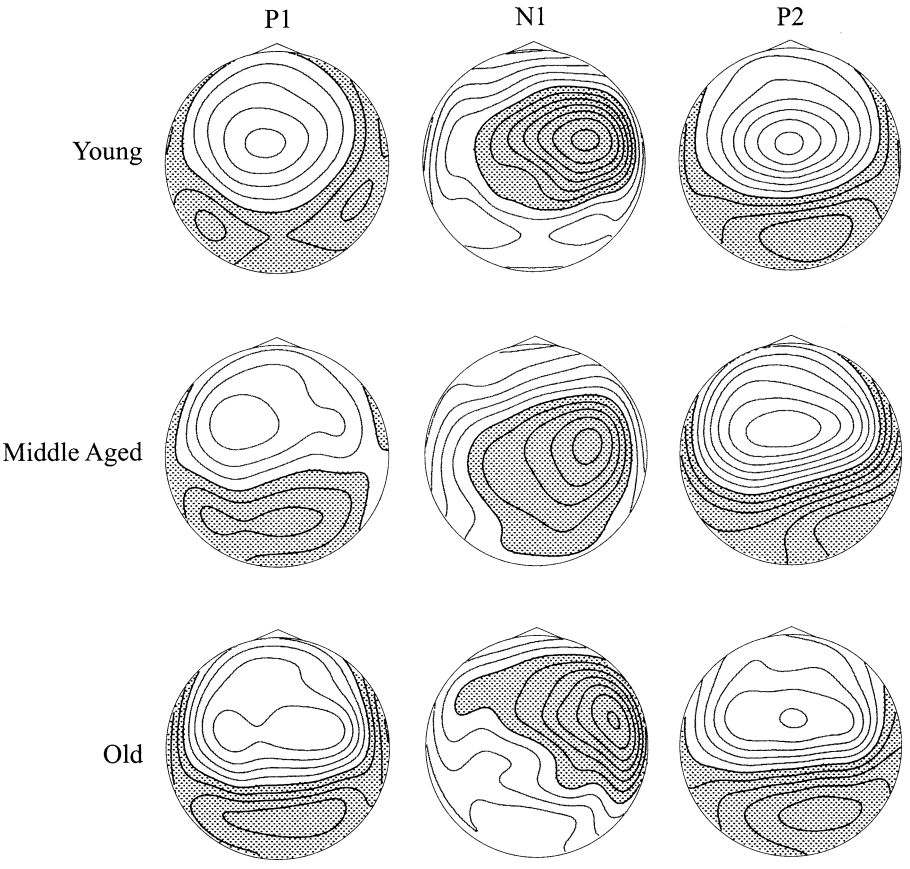

Fig. 3. Contour maps of P1, N1, and P2 in young, middle-aged and older adults for the longest-stimulus duration. Shaded areas indicate negativity. Contour spacing equals 0.1 μV.

found significant differences only between young and middle-aged participants.

For the P2 latencies, all slopes differed significantly from zero, $F[3,113] = 9.02$, $P < 0.001$. The slope was comparable in all three age groups, $F[2,113] = 0.28$, $P > 0.5$. No group differences in intercepts were found, $F[2,26] = 0.20$, $P > 0.5$.

For the N1 amplitudes, the hypothesis that all slopes were zero was rejected, $F[3,113] = 24.11$, $P < 0.001$. The slopes in young, middle-aged and older adults were comparable, $F[2,113] = 0.04$, $P > 0.5$. No group differences in intercepts were found, $F[2,26] = 1.96$, $P > 0.15$.

For the P2 amplitudes, the hypothesis that all slopes were zero was rejected, $F[3,113] = 4.37$, $P < 0.006$. In contrast with the N1 amplitude, the hypothesis that all slopes were equal was marginally rejected, $F[2,113] = 2.88$, $P < 0.06$. While the young and middle-aged adults showed increased P2 amplitude with increased sound duration, the slope for older subjects did not differ significantly from zero, $F[1,113] = 0.15$, $P > 0.5$. No group differences in intercepts were found, $F[2,26] = 0.18$, $P > 0.5$.

To determine whether age differences in the slopes of the functions relating P2 amplitude to stimulus duration might be related to high-frequency hearing loss, we regressed these slopes against a linear combination of the hearing levels at 2, 4, and 8 kHz. Specifically, using the method of least squares, we determined the best-fitting coefficients (α_0, α_2, α_4, and α_8) in the prediction equation:

Table 1
Group mean audiometric thresholds (and standard error) in dB in young, middle-aged and older participants

	Frequency				
Groups:	250	500	1000	2000	4000
Young	3.0 (2.0)	5.0 (1.9)	2.5 (1.5)	0.5 (2.1)	6.0 (3.1)
Middle-aged	7.0 (2.0)	8.5 (1.9)	7.5 (1.5)	7.5 (2.1)	10.5 (3.1)
Older	13.3 (2.1)	16.6 (2.0)	16.1 (1.6)	16.1 (2.2)	20.0 (3.2)

$$s_{P2}(i) = \alpha_0 + \alpha_2 h_2(i) + \alpha_4 h_4(i) + \alpha_8 h_8(i)$$

where $s_{P2}(i)$ is the slope of the function relating P2 amplitude to signal duration for subject i, and $h_2(i)$, $h_4(i)$, and $h_8(i)$ are the hearing levels for subject i at 2, 4, and 8 kHz, respectively. The null hypothesis that $\alpha_2 = \alpha_4 = \alpha_8 = 0$ could not be rejected, $F[3,25] = 1.217$, MSE = 0.000867, $P > 0.3$. Therefore, there is no evidence that age differences in the slopes of the functions relating P2 amplitude to stimulus duration are related to the degree of high-frequency hearing loss in these participants.

Fig. 3 shows the contour maps illustrating the amplitude distribution of the P1, N1 and P2 waves in all three age groups. The P1, N1 and P2 deflections were maximal over the right fronto-central scalp sites (i.e. contralateral to the ear of stimulation). The P1 and N1 amplitude distributions tended to be more lateralized in older than in middle-aged or young adults but the difference failed to reach significance, $F[60,1560] < 1.49$ in both cases.

3.1. Audiometric threshold

Table 1 summarizes the audiometric thresholds for young, middle-aged and older participants. ANOVA with age group as a between-subjects factor and frequency (i.e. 250, 500, 1000, 2000, and 4000 Hz) as a within-subjects factor yielded a main effect of group, $F[2,26] = 22.34$, $P < 0.001$, all pairwise comparison at $P < 0.02$. Young adults had the lowest thresholds, middle-aged were intermediate, and older adults had the highest audiometric thresholds. The group–frequency interaction was not significant.

4. Discussion

Disturbance in the auditory temporal processing abilities of the elderly has been proposed as an explanation for age-related declines in speech perception or discrimination. Yet, there has been little attempt until now to assess the effects of age on the neural events underlying the processing of short-duration sounds. Recording of auditory evoked responses to sounds of various durations offers a means to assess fine neural coding of sound duration. In all three age groups, the N1 wave increased linearly in amplitude with increasing sound duration. More importantly, the growth function was identical in all three age groups, with the N1 amplitude resolving durational differences on the order of 2–4 ms. The growth of the N1 amplitude with increases in stimulus duration cannot be attributed to changes in stimulus energy because all stimuli were identical in terms of total energy.

In contrast to the N1 data, only young and middle-aged adults showed increases in P2 amplitude with signal duration. In older adults, the P2 amplitude was not significantly affected by increasing tonal duration. This age difference in the slope of the function relating P2 amplitude to stimulus duration was not related to the degree of high-frequency hearing loss in these participants. Our results suggest that encoding of sound duration, as indexed by the P2 wave, is impaired in older adults. The fact that the N1 amplitude growth function was comparable in all three age groups may indicate that some preliminary encoding of sound duration is resistant to the aging process, but that subsequent analysis of duration, as indexed by the P2 wave, may be impoverished in older adults. This finding provides neurophysiological evidence for age-related declines in processing short-duration sounds. The fact that young and middle-aged adults show comparable N1 and P2 growth functions suggests that age-related declines in the precise encoding of sound duration takes place after the fifth decade of life.

The present finding has a number of implications for our current understanding of the mechanism responsible for the age-related decline in behavioral measures of temporal resolution and duration discrimination. As mentioned in the introduction, performance on psychoacoustic tasks depends on both bottom-up and top-down controlled processes. Given that in most tasks participants are required to compare two successively presented sounds, the poor performance often observed in older adults could be attributed to difficulties in the comparison process in addition to difficulty in coding sound duration. Evidence from electrophysiological studies suggests that older adults have difficulties registering stimulus deviance in a stream of standard stimuli, as evidenced by a decrease in mismatch negativity amplitude (e.g. Alain and Woods, 1999; Bertoli et al., 2002). The internal comparison of acoustic information may become less precise and less efficient with aging. In the present study, we found that age affected the processing of sound duration even when no manipulation or comparison with an internal representation was required, suggesting that age-related declines in behavioral measures of temporal resolution and duration discrimination may reflect impairment in encoding. The AEP amplitude distributions were comparable in all three age groups, suggesting minimal structural and/or functional reorganization of the AEP generators with aging.

The N1 and P2 amplitudes increased with increasing sound duration. This finding is consistent with previous reports using pure tones (Alain et al., 1997), noise bursts (Joutsiniemi et al., 1989; Onishi and Davis, 1968), or trains of click stimuli (Forss et al., 1993). The present study extends previous work by showing

that the N1 and P2 amplitudes can resolve durational differences on the order of 2–4 ms. The resolving power of the N1 and P2 responses approximates the gap detection threshold in young and older adults (Schneider and Hamstra, 1999), as well as the temporal integration function observed for signal durations of 10 ms (Abel, 1972) or less (Oxenham et al., 1997).

5. Conclusion

The main finding of this study is that the processing of sound duration as indexed by auditory evoked responses is impaired by the aging process. Age-related differences previously demonstrated in tasks requiring participants to detect a gap or judge stimulus duration may be related to difficulties extracting fine temporal information as well as other factors such as the maintenance and manipulation of acoustic information.

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