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Age-related differences in auditory event-related potentials during a cued attention task

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Abstract

Objective: To determine if aging is associated with differences in attentional regulation using behavioral and event-related potential (ERP) measures.

Methods: Younger ($n = 13$; $M = 20$ years) and older ($n = 12$; $M = 76$ years) subjects performed an auditory cued attention task. Verbal cues correctly (valid) or incorrectly (invalid) predicted the ear receiving a target tone 1.5 s later, or were uninformative (neutral). Targets were either 'high' (2000 Hz) or 'low' (1000 Hz) pitch monaural tones. Subjects pressed one of 4 buttons to indicate target ear and pitch. ERPs following cues and targets (P50, N100, P200, slow waves), and negative slow potentials (CNV) between cues and targets were assessed.

Results: Cue information had significant effects on reaction time for both groups (valid < neutral < invalid). Target N100 amplitude was significantly affected by cueing in younger (invalid > valid) but not older subjects. Target slow waves were also affected by cue information (invalid > valid), and the difference was larger and lasted longer in older subjects. Slow waves following cues were significantly larger in older subjects, but the subsequent CNV amplitudes were comparable among groups.

Conclusions: When performing a cued attention task, age differences are present in transient ERPs following cues and targets.

Significance: Age differences in ERPs associated with attentional regulation support the hypothesis that attentional changes contribute to cognitive aging.

Keywords: N100; CNV; Aging; Attentional cueing

1. Introduction

Normal aging is accompanied by performance declines in many tasks that assess working memory, episodic memory, reasoning, and spatial abilities (Craik and Salthouse, 1992). A wide range of cognitive tasks share much of their age-related variance, which suggests that age-related differences are largely due to changes in basic processes that are engaged during many types of cognitive activities (Lindenberger and Baltes, 1994; McDowd and Shaw, 2000; Salthouse, 1996). Inhibitory aspects of attention have been proposed to be a basic component of cognitive aging (Hasher and Zacks, 1988), and are thought to be important for switching attention among relevant events (Hasher and Zacks, 1988; McDowd and Shaw, 2000). Attentional regulation has been conceptualized as a tradeoff between the level of engagement for expected events and the necessity to respond to important, unexpected events (Kinchla, 1992). Efficient attentional regulation is evident by high levels of performance to both expected and unexpected events.

Cued attention tasks have been used to study attentional regulation by using cues to predict a feature of an upcoming target (Posner, 1980; Posner and Cohen, 1984). The influence of attention is evident by the differential processing of targets as a function of cue information, known as cueing effects. Reaction time exhibits cueing effects with faster responses when targets are consistent with cue information (valid trials), and slower responses when targets are inconsistent with cue information (invalid trials). Intermediate reaction times are observed following uninformative cues (neutral trials) (Posner, 1980; Quinlan and Bailey, 1995; Spence and Driver, 1994; Wright et al., 1995).

Behavioral studies of cued attention and aging have reported larger cueing effects in older subjects when

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comparing absolute reaction time differences between valid and invalid targets (Curran et al., 2001; Hartley et al., 1990; Nissen and Corkin, 1985). When the differences in reaction time as a function of cueing were adjusted for overall slower reaction times in older subjects, age differences in cueing effects either increased (Hartley et al., 1990) or were no longer significant (Curran et al., 2001). Thus, cueing effects are often larger in older subjects, but the influence of overall slowing in older subjects is unclear.

In auditory cued attention tasks event-related potentials (ERPs) following target presentation show cueing effects, with the N100 component and a subsequent positive slow wave (late slow wave, LSW) exhibiting larger amplitudes for invalid, relative to valid, targets (Golob et al., 2002b; Hugdahl and Nordby, 1994; Schroger and Eimer, 1993). Amplitude modulations as a function of cueing are also present in visual ERPs beginning ~100 ms after target presentation, with larger amplitudes to valid targets in both younger (Luck, 1995; Mangun, 1995; Mangun and Hillyard, 1991) and older subjects (Curran et al., 2001). Age differences in ERP attention effects have not been studied using auditory cued attention tasks, but have been assessed using dichotic listening tasks. Younger, middle-aged, and older subjects exhibit negative slow waves and larger N100 amplitudes for stimuli presented to the attended, relative to the ignored, ear (Ford et al., 1979; Woods, 1992). When age differences are found in dichotic listening tasks they involve differences in topography (Karayandis et al., 1995) and possibly latency in the onset of attentional effects (Gaeta et al., 2003; Woods, 1992).

The purpose of the present study was to examine the effects of aging on brain activity associated with attentional regulation. ERPs were recorded from younger and older subjects performing an auditory cued attention task. ERPs during the cued attention task can be divided into 3 time periods: transient ERP components to cues (P50, N100, P200, slow waves), slow waves that develop between cues and targets (contingent negative variation (CNV)), and transient components to targets (P50, N100, P200, slow waves). Potentials at each time period were assessed as a function of cueing to examine age-related differences in the processing of cues, motor preparation and stimulus expectancy, and attention regulation following targets.

2. Methods

2.1. Subjects

Thirteen younger (M/F: 9/4; mean age = 20.1 years, range 18–22) and 12 older (M/F: 5/7; mean age = 76.4 years, range 75–79) subjects participated in the study. Younger subjects were undergraduate students from the University of California, Irvine who received course credit for their participation. Eleven older subjects were recruited from the Successful Aging Program at the University of California, Irvine Alzheimer's Disease Research Center and one older subject was recruited from a private clinical practice. All subjects were right-handed. Subjects reported they could clearly detect and comprehend the auditory stimuli, and all performed the task accurately (Section 3). The University of California, Irvine Institutional Review Board approved the experimental procedures, and all subjects signed an informed consent form.

Older subjects were given a battery of neuropsychological tests to objectively define cognitive function in several domains. Episodic memory was assessed with the WMS-III Logical Memory subtest (Wechsler, 1997a) and CERAD Word List Learning Task (Morris et al., 1989). The 30 item version of the Boston Naming test (Kaplan et al., 1983), CERAD Animal Naming (Morris et al., 1989), and Controlled Oral Word Association (FAS Fluency) (Spreen and Benton, 1977) were used to measure language ability. Executive function was tested with Trailmaking Tests A and B (Reitan, 1958), and visuospatial skills were evaluated with WAIS-III Block Design subtest (Wechsler, 1997b) and CERAD Constructional Praxis test (Morris et al., 1989).

2.2. Experimental procedures

2.2.1. Cued attention task

The experiment was conducted in an acoustically isolated, electrically shielded chamber. Subjects sat in a comfortable armchair with insert earphones in both ears and held a keypad containing 4 buttons. Subjects were instructed to maintain fixation on a point in front of them and to minimize eye-movements and blinking. The experimental session lasted approximately 30 min.

Each trial consisted of a verbal cue ('left', 'right', or 'go') followed 1.5 s later by a target tone. Targets varied along two dimensions: pitch (1000 or 2000 Hz) and location (left ear, right ear). The inter-trial interval (target onset to following cue) was 2.0 s. Subjects were instructed to listen to each cue-target pair and to press one of 4 buttons to indicate the location and pitch of the target. Stimulus-response mapping was compatible, with buttons on the left or right side corresponding to the respective ipsilateral ear, and upper and lower buttons on each side indicated 'high' and 'low' pitch tones, respectively. A set of practice trials was completed first, followed by two or 3 test blocks (100 trials/block), depending on signal-to-noise ratio of the ERPs.

Verbal cues were presented at ~50 dB nHL and lasted ~400 ms. The word left was presented monaurally to the left ear, right was presented monaurally to the right ear, and go was presented binaurally. Targets were either 1000 or 2000 Hz pure tones (70 dB SPL, 100 ms duration, 5 ms rise/fall time) presented monaurally. Subjects were encouraged to use the cues to anticipate target location. They were instructed that in most trials, left and right cues would accurately predict which ear the target tone would be

presented. The cue words left and right correctly predicted target location on 60% of the trials (valid trials) and incorrectly predicted target location on 20% of the trials (invalid trials). Note that the above cues provided only partial information regarding the upcoming stimulus location and response hand because they did not indicate if the target tone would be high or low in pitch. For 20% of the trials the cue was the word go, which did not indicate which ear the target would be presented (neutral trials). Target tones following neutral cues were equally likely to be presented to the left or right ear. Trial types were randomly distributed within a block, with the restriction that no more than 3 trials of the same type were presented consecutively. For all trial types the probabilities of target location (left, right) and target pitch (high, low) were 0.5, with 25% of the trials having each combination of location and pitch (e.g. left-high, left-low, right-high, right-low).

2.2.2. Non-motor condition

To evaluate the importance of motor preparation on the CNV that developed between cues and targets, subjects also performed a version of the cued attention task that did not require a speeded response to targets (non-motor condition). The non-motor condition contained the same cue-target pairs described above, but responses were not made to each target tone. To verify that subjects were attending to the target stimuli, on 10% of the trails an auditory query (the word 'where') was presented 2.0 s after the target tone. Subjects responded to the query by pressing one of 4 buttons to indicate the location and pitch of the previous target, as described above. Two or 3 blocks of the non-motor condition, depending on ERP signal-to-noise ratio, were always given before the cued attention task to eliminate the possibility of carryover effects.

2.2.3. Control condition

A control condition was included to determine if group differences in ERPs to cues in the attention task (see Section 3) are present when cue stimuli do not predict target location. Ten younger (M/F: 1/9; mean age = 22.0 years, range 20–25) and 10 older (M/F: 2/8; mean age = 73.6 years, range 70–78) subjects were instructed to passively listen to a random sequence of the cue stimuli (monaural left and right, binaural go). The inter-stimulus interval was 2.0 s, and 120 stimuli were presented (40 presentations/cue stimulus). Younger subjects for the control condition did not participate in the attention task. Three of the 10 older subjects given the control condition also participated in the cued attention experiment, completing the control condition first, then the non-motor condition, followed by the cued attention task.

2.3. Data recording and analysis

Nine Ag/AgCl electrodes were applied to scalp sites according to the 10/20 system (F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4) in a linked mastoid configuration (Jasper, 1958). Eye movements were monitored using differential recording from electrodes placed above and below the left eye. Electrode impedances were $<5\ k\Omega$. Continuous records (DC—100 Hz, digitized at 500 Hz) of EEG and EOG were stored for further off-line analysis. The recordings were partitioned into 2.6 s epochs beginning 100 ms before cue presentation and ending 1.0 s after target presentation. Eyeblink artifacts were corrected using a vertical eye movement correction algorithm (Gratton et al., 1983). Separate ERP averages were made for each trial type (valid, invalid, neutral). Sweeps were visually inspected and were not included in the ERP average if they contained excessive DC drift, muscle artifact, or incorrect responses.

Transient ERPs in response to cues and targets (P50, N100, P200) were bandpass filtered (0.1–16 Hz, Butterworth 12 dB/oct slopes). Peak amplitudes were measured relative to a 100 ms baseline preceding the stimulus, and latencies were defined relative to stimulus onset. The P50 component was defined as the maximum positivity between 30 and 80 ms; N100 was the maximum negativity between 80 and 150 ms; P200 was defined as the maximum positivity between 150 and 250 ms. Slow wave activity following cues, targets, and between cues and targets, was analyzed after low-pass filtering (DC—16 Hz). Slow waves following cues were quantified using the mean amplitude of a 300 ms window lasting from 200 to 498 ms after cue presentation. Slow wave amplitudes of the late CNV component were measured using the mean amplitude of a 300 ms window ending at target onset. LSWs following targets were measured as the mean amplitudes of a 200 ms window lasting from 200 to 398 ms after target presentation. Three 100 ms windows (200–298, 300–398, 400–498 ms following target presentation) were used to define the time course of the LSW in greater detail.

Behavioral data included reaction time and accuracy measures. Reaction time was measured relative to target onset for correct trials. Accuracy was measured as the percent of correct responses out of all responses to target tones. The percent of trials without a response was also noted.

2.4. Statistical analysis

Behavioral and electrophysiological measures were analyzed using analysis of variance (ANOVA) with Greenhouse–Geisser correction for repeated measures when appropriate. Factors included age group (younger, older), trial type (valid, invalid, neutral), time window, and electrode site (Fz, Cz, Pz). For topographic analyses, the factors of hemisphere (left, midline, right) and anterior–posterior position (frontal, central, parietal) were used. To adjust for overall group differences in amplitude, normalized values were used in topographic analyses (McCarthy and Wood, 1985). Analyses that included the non-motor condition incorporated the factor of response

condition (motor, non-motor). Degrees of freedom prior to Greenhouse–Geisser correction are reported, and P values <0.05 were considered significant. Analyses of components following cues compared only valid and neutral trials because valid and invalid trials are not differentiated until target presentation. Analyses of components following targets compared valid and invalid trials to examine attentional regulation, and neutral trials were included as a reference for the direction of the attention effects.

3. Results

3.1. Neuropsychological testing

To characterize the cognitive profile of the older group, neuropsychological test results from 11 out of 12 older subjects are presented in Table 1. One subject that received a different battery of tests was not included in the table. All 12 older subjects performed within the normal age and education adjusted range on tests of memory, language, executive function, and visuospatial skills.

Table 1
Neuropsychological test results

	Older	Normative[a]
n	11	–
MMSE		
CERAD word list[b]	28.9 ± 0.3	27.6 ± 1.7
Sum of recall trials 1–3	22.6 ± 1.2	21.1 ± 3.7
Five minute recall	8.1 ± 0.3	7.2 ± 1.8
Thirty minute recall	7.1 ± 0.5	7.4 ± 1.8
Five minute recognition	19.9 ± 0.1	19.6 ± 0.6
Thirty minute recognition	19.5 ± 0.2	19.7 ± 0.5
WMS-III logical memory		
Immediate recall	45.7 ± 2.1	33.7 ± 9.5
Delay recall	28.8 ± 2.0	17.2 ± 7.3
Boston naming test (30 item)	28.9 ± 0.6	28.7 ± 1.7
Animal fluency	19.7 ± 1.2	18.0 ± 4.8
FAS verbal fluency	46.5 ± 4.6	42.0 ± 12.1
CERAD constructional praxis	10.6 ± 0.2	10.1 ± 1.2
WAIS-III block design[c]	13.5 ± 1.2	10.0 ± 3.0
Trailmaking test A (s)	36.0 ± 2.8	40.1 ± 14.5
Trailmaking test B (s)	79.3 ± 8.9	86.3 ± 24.1

Notes: Neuropsychological test results for 11 older subjects in this study compared to previously published normative scores for each test. Results from one older subject were not included because they completed a separate test battery. Values are mean ± SD.

[a] Normative scores from control subjects with similar age and education levels as the older subjects in this study. Citations: MMSE (Folstein et al., 1975), CERAD word list (Morris et al., 1989), WMS-III logical memory (Haaland et al., 2003), Boston naming test (Reiter, 2000), animal fluency (Morris et al., 1989), FAS verbal fluency (Tombaugh et al., 1999), CERAD constructional praxis (Morris et al., 1989), WAIS-III block design (Weschler, 1997), Trailmaking tests A and B (Tombaugh, 2004).

[b] Normative scores for 5 and 30 minutes delayed recall and recognition from >200 subjects enrolled in the successful aging Program at the University of California, Irvine Alzheimer's Disease Research Center.

[c] Age-adjusted scaled scores.

3.2. Behavior

Reaction time and accuracy were analyzed using 2 (group) × 3 (trial type) ANOVAs. For reaction time there were significant main effects of group [$F_{(1,23)} = 31.9; P < 0.001$] and trial type [$F_{(2,46)} = 44.1; P < 0.001$] (Fig. 1A). Reaction times were shorter in younger relative to older subjects, and for both groups reaction times were shortest for valid trials, intermediate for neutral trials, and longest for invalid trials. There was also a significant interaction between group and trial type [$F_{(2,46)} = 6.7; P < 0.01$]. In younger subjects the reaction time differences between valid vs. neutral trials (40 ms) and invalid vs. neutral trials (37 ms) were similar. In contrast, older subjects had a greater difference in reaction time between valid vs. neutral

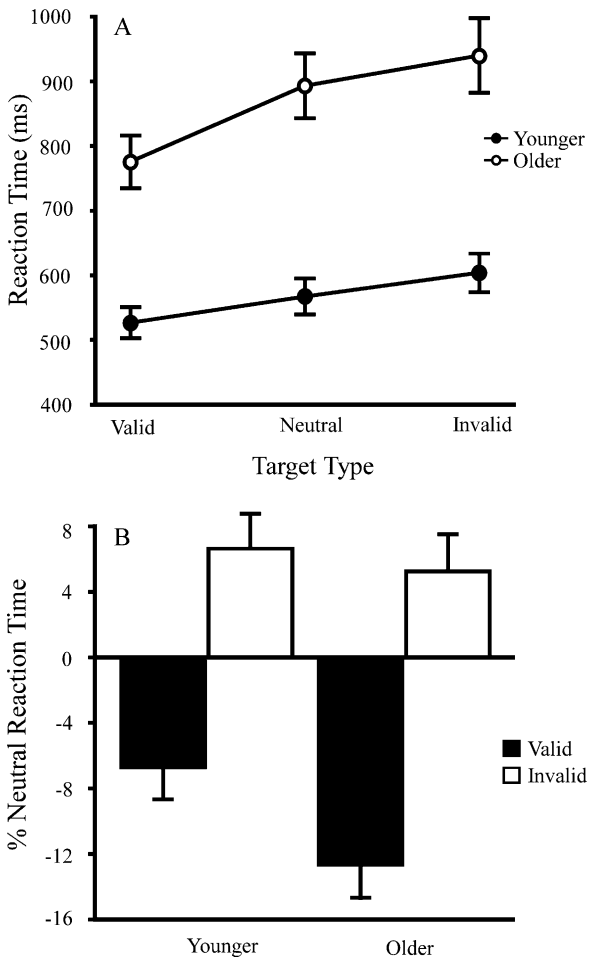

Fig. 1. Behavioral results from the cued attention task. (A) Median reaction times to valid, invalid, and neutral targets in younger and older subjects. (B) Median reaction times to valid and invalid targets expressed as a percentage of neutral reaction times for younger and older groups. Reaction time decreases (valid vs. neutral) were similar to increases (invalid vs. neutral) in younger subjects, while older subjects had larger differences between valid and neutral, compared to invalid and neutral, reaction times. Error bars represent standard error.

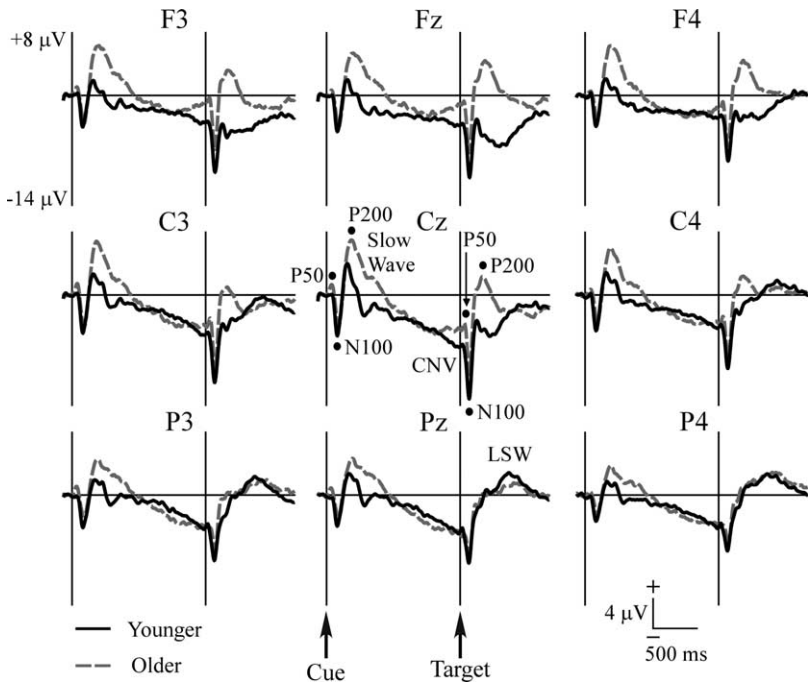

Fig. 2. Grand average potentials to valid trials for both age groups. Peak components and slow waves are labeled at Cz, except the late slow wave (LSW), which is labeled at Pz. The epoch lasts from 100 ms before cue presentation until 1.0 s after target presentation.

trials (118 ms) relative to the difference between invalid vs. neutral trials (47 ms). Group differences in cueing independent of overall reaction time were significant when reaction times to valid targets [$t_{(23)} = 2.1; P < 0.05$], but not invalid targets, were expressed as a percentage of neutrals (Fig. 1B).

For accuracy there was a significant main effect of trial type [$F_{(2,46)} = 5.7; P < 0.03$] and a significant group × trial type interaction [$F_{(2,46)} = 5.0; P < 0.04$]. Accuracy in younger subjects was comparable among all trial types (valid: 98.2 ± 0.3%, invalid: 97.5 ± 1.1%, neutral: 98.2 ± 0.6%), while older subjects were less accurate on invalid trials (90.3 ± 3.3% correct) compared with valid (96.6 ± 1.1%) and neutral (97.1 ± 1.1%) trials. For both groups most of the errors on valid (70% of errors, 78/111) and neutral (83% of errors, 29/35) trials were responses that indicated the incorrect pitch at the correct location. In contrast, for invalid trials both groups made 64% of the errors (51/77) at the incorrect location (i.e. the cued ear), but indicated the correct pitch.

3.3. Event-related potentials

Grand average potentials from valid trials in younger and older subjects are presented in Fig. 2 to show the sequence of ERP components. Cues elicited 3 components (P50, N100, and P200) followed by a slow wave. The slow wave was initially positive in polarity but became progressively more negative leading up to target presentation, consistent with the CNV. Targets elicited 3 components (P50, N100, and P200) followed by a LSW.

3.3.1. Cue ERPs

Bandpass filtered (0.1–16 Hz) grand average potentials to cues are presented in Fig. 3, and mean amplitude and latency measures are presented in Table 2. Separate 2 (group)–2 (trial type: valid, neutral) ANOVAs were performed for amplitudes and latencies at the Cz site. Because valid and invalid trials are defined only after target presentation the trial type factor included only valid and neutral trials.

P50 amplitude showed a significant main effect of group [$F_{(1,23)} = 4.6; P < 0.05$] with larger amplitudes in older subjects. There was also a significant group effect for P200 latency [$F_{(1,23)} = 6.2; P < 0.03$] with longer latencies in older compared to younger subjects. Amplitudes of the N100 [$F_{(1,23)} = 8.9; P < 0.01$] and P200 [$F_{(1,23)} = 29.7; P < 0.001$] components were significantly affected

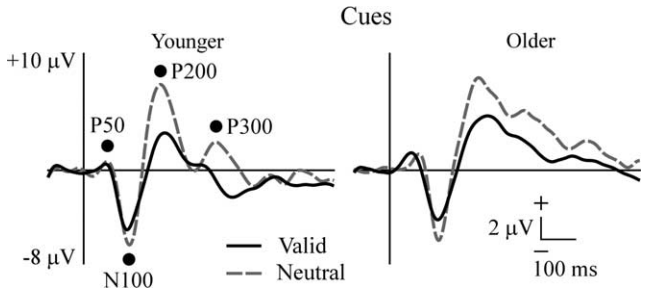

Fig. 3. Grand average potentials to valid and neutral cues for younger and older groups at Cz electrode site (0.1–16 bandpass filter). P50 amplitude and P200 latency showed significant effects of group (older > younger). N100 and P200 amplitudes had significant effects of trial type (neutral > valid). Vertical line indicates cue onset.

Table 2
Event-related potentials to cues

Components		Trial type	
		Valid	Neutral
Amplitude (μV)			
P50[a]	Younger	0.7 ± 0.3	0.9 ± 0.4
	Older	1.8 ± 0.2	1.8 ± 0.6
N100[b]	Younger	−5.7 ± 0.9	−6.7 ± 0.8
	Older	−4.8 ± 0.6	−6.5 ± 1.1
P200[b]	Younger	3.8 ± 0.7	8.5 ± 1.3
	Older	5.0 ± 0.8	8.3 ± 0.8
SW window[a,b]	Younger	0.3 ± 0.8	3.4 ± 1.0
	Older	4.5 ± 0.9	8.1 ± 1.3
Latency (ms)			
P50[b]	Younger	61.6 ± 3.0	67.6 ± 3.4
	Older	63.5 ± 3.8	73.5 ± 5.7
N100	Younger	129.0 ± 5.2	125.2 ± 3.5
	Older	132.0 ± 4.8	135.2 ± 3.0
P200[a,b]	Younger	227.5 ± 5.4	211.3 ± 4.9
	Older	246.9 ± 11.3	238.2 ± 6.3

SW, slow wave.
[a] Significant main effect of group ($P < 0.05$).
[b] Significant main effect of trial type ($P < 0.05$).

by trial type (neutral > valid). Latencies of the P50 [$F_{(1,23)} = 5.3; P < 0.04$] (neutral > valid) and P200 [$F_{(1,23)} = 6.6; P < 0.02$] (valid > neutral) also showed significant main effects of trial type.

Grand average ERPs had notable group differences in a positive slow wave beginning ~200 ms after cue presentation that persisted for at least 500 ms (Fig. 4). Younger subjects had a positive component with a peak latency of ~300 ms (P300) that was superimposed at the beginning of the slow wave, but only 3 older subjects had a similar positive peak. Identifiable peaks were most prominent in neutral trials, suggesting the low-probability binaural cue evoked a P300, which has been shown to decreases in amplitude with age (Knight, 1987). Because many older subjects did not have a measurable P300, slow wave activity following cue presentation was quantified by calculating mean amplitudes during a 300 ms time window that encompassed group differences in the grand average ERPs (200–498 ms after cue presentation) (Fig. 4).

Slow wave amplitudes were analyzed using a 2 (group) × 2 (trial type: valid, neutral) × 3 (hemisphere: left, midline, right) × 3 (anterior–posterior: frontal, central, parietal) ANOVA. There was a significant main effect of group [$F_{(1,23)} = 16.5; P < 0.01$], with older subjects having more positive slow wave values than younger subjects. A significant effect of trial type [$F_{(1,23)} = 55.9; P < 0.001$] indicated larger amplitudes for neutral compared to valid trials, and a significant effect of anterior–posterior position [$F_{(2,46)} = 5.7; P < 0.02$] showed slow wave amplitudes were largest at fronto-central sites and decreased at parietal sites. There was a group × anterior–posterior position

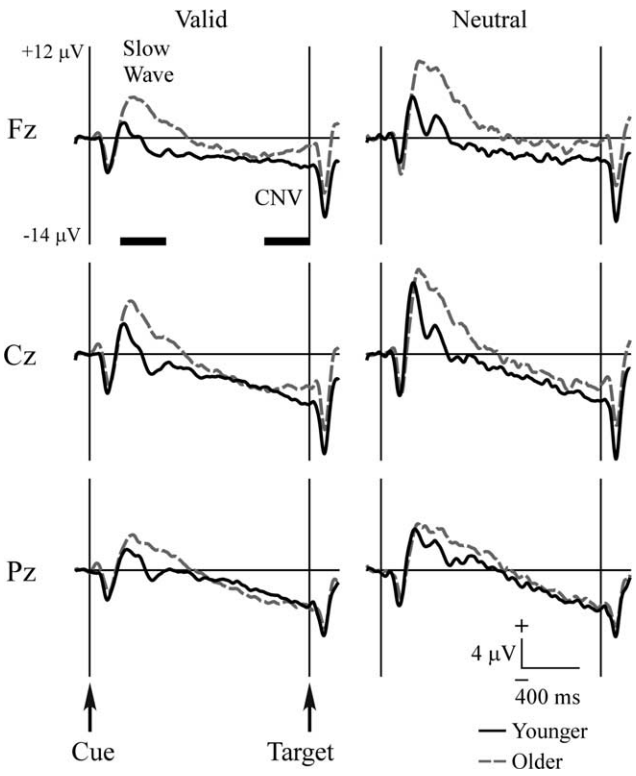

Fig. 4. Grand average potentials between cues and targets at midline electrode sites (DC—16 Hz). Grand average potentials to valid and neutral cues are presented for younger and older subjects. Slow waves following cues were significantly larger in older vs. younger subjects, but CNV amplitudes were similar across groups. Horizontal black bars indicate the window measures taken 200–498 ms after the cue to quantify the slow wave, and −298–0 ms before the target to measure the CNV. Vertical black lines indicate cue and target onset.

interaction [$F_{(2,46)} = 7.3; P < 0.01$], with the largest amplitude difference between groups at fronto-central sites and smaller differences at parietal sites (see Fig. 4). The group × anterior–posterior position interaction was also significant in a separate ANOVA conducted using normalized values [$F_{(2,46)} = 6.3; P < 0.02$]. Valid cues had similar amplitudes across sites, but neutral cues had smaller amplitudes at right vs. midline and left hemisphere sites as seen by a significant trial type × hemisphere interaction [$F_{(2,46)} = 6.1; P < 0.02$].

In summary, group differences were most evident during slow wave activity from 200 to 500 ms after cue presentation. Older subjects had significantly more positive amplitudes at frontal and central sites but were similar to younger subjects at parietal sites. Slow wave amplitudes following neutral cues were more positive than valid cues in both groups. Group differences in transient ERPs were observed for P50 amplitude (older > younger) and P200 latency (older > younger).

3.3.2. Slow potentials between cue and target (CNV)

Grand averages of slow potentials between cues and targets are shown in Fig. 4. Mean CNV amplitudes

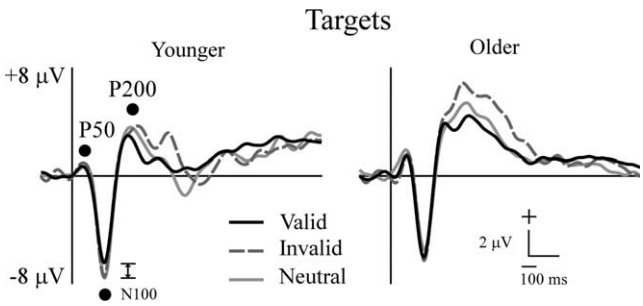

Fig. 5. Grand average potentials comparing valid, invalid, and neutral targets for both age groups at Cz electrode site (0.1–16 Hz bandpass filter). N100 amplitude was smaller for valid vs. invalid and neutral targets in younger subjects (see arrows), but older subjects showed no differences across trial types. Vertical line indicates target onset.

(−298 to 0 ms before target presentation) were assessed using a 2 (group) × 2 (trial type: valid, neutral) × 3 (electrode site: Fz, Cz, Pz) ANOVA. There were no significant main effects or interactions involving group or trial type. A significant effect of electrode site [$F_{(2,46)} = 16.3; P < 0.001$] showed larger amplitudes at Cz and Pz compared to Fz. When an ANOVA of all 9 sites was conducted with the additional factors of anterior–posterior position and hemisphere, the results were similar with larger amplitudes at midline vs. lateral sites, but there were no significant group effects (data not shown).

3.3.3. Target ERPs: P50, N100, P200

Grand average potentials to valid, invalid, and neutral targets at the Cz site are presented in Fig. 5, and amplitude and latency measures are shown in Table 3. Separate 2 (group) × 3 (trial type) ANOVAs were performed to assess component amplitudes and latencies at the Cz site. Additional analyses compared only valid and invalid trial types.

N100 amplitude had a significant effect of trial type when comparing valid and invalid trials [$F_{(1,23)} = 5.2; P < 0.04$] (see Fig. 5). The group × trial type interaction did not attain significance, however, the majority of younger subjects (10/13) had larger N100 amplitudes for invalid vs. valid trials. In contrast, older subjects were nearly evenly divided between larger (7/12) or smaller (5/12) N100 amplitudes for invalid relative to valid trials. *T* Tests comparing trial types within each group showed a significant difference in the younger [$t_{(12)} = 2.2; P < 0.05$] but not older group. N100 latency also showed a significant effect of trial type [$F_{(2,46)} = 4.2; P < 0.03$] (valid = invalid < neutral).

Analysis of P200 amplitude revealed a significant main effect of trial type [$F_{(2,46)} = 7.6; P < 0.01$]. In both groups, amplitudes were smallest following validly cued targets, largest for invalidly cued targets, and intermediate for neutral targets. When only valid and invalid trials were examined there was also a significant effect of trial type [$F_{(1,23)} = 22.3; P < 0.001$], with smaller amplitudes for valid relative to invalid trials. Thus, both groups exhibited a cueing effect on P200 amplitude (valid < neutral < invalid), but only younger subjects showed earlier cueing effects on N100 amplitude. There were no significant effects for P50 amplitude or latency.

Table 3
Event-related potentials to targets

Component		Trial type		
		Valid	Neutral	Invalid
Amplitude (μV)				
P50	Younger	0.7 ± 0.3	1.2 ± 0.6	1.2 ± 0.6
	Older	1.8 ± 0.4	2.4 ± 0.4	2.1 ± 0.5
N100[a]	Younger	−6.9 ± 0.9	−7.9 ± 1.2	−8.0 ± 1.1
	Older	−6.4 ± 0.6	−6.0 ± 0.7	−6.6 ± 0.7
P200[a,b]	Younger	3.2 ± 0.6	4.0 ± 0.8	4.8 ± 0.6
	Older	4.9 ± 0.7	5.9 ± 0.8	6.7 ± 1.1
Latency (ms)				
P50[a,c]	Younger	40.9 ± 2.9	45.8 ± 3.9	45.4 ± 3.7
	Older	50.0 ± 2.4	48.9 ± 3.6	53.1 ± 2.9
N100[c]	Younger	100.1 ± 2.3	101.7 ± 1.9	99.2 ± 2.0
	Older	102.5 ± 2.2	106.5 ± 2.8	104.9 ± 1.9
P200	Younger	174.0 ± 4.3	176.6 ± 4.4	184.9 ± 8.1
	Older	190.1 ± 10.3	198.2 ± 10.1	192.3 ± 10.8

Notes: separate analysis included 3 trial types (valid, neutral, invalid) or two trial types (valid, invalid). For analysis with 3 trial types.

[a] Significant main effect of trial type ($P < 0.05$).

[b] Significant main effect of trial type ($P < 0.05$). For analysis with two trial types.

[c] Significant main effect of group ($P < 0.05$).

3.3.4. Target ERPs: late slow wave

Grand averages to targets (DC—16 Hz) are presented in Figs. 6 and 7. LSW amplitude differences between valid and invalid trials were larger and lasted longer in the older compared to the younger group. In the younger group, invalid targets were more positive than valid targets from ~200 to 400 ms, which was followed by a slight reversal (valid > invalid) at fronto-central sites. In the older group, amplitudes to invalid targets were more positive than valid targets from ~200 to 800 ms. Group differences in LSW amplitude are not attributable to differences in pre-stimulus baseline levels because CNV amplitudes before targets were not significantly different between groups.

Initial analysis of the LSW used one time window (200–398 ms) during the time period that both groups exhibited cueing effects in the grand average ERPs (Figs. 6 and 7). A 2 (group) × 2 (trial type: valid, invalid) × 3 (electrode site: Fz, Cz, Pz) ANOVA had a significant main effect of group [$F_{(1,23)} = 8.9; P < 0.01$] with more positive slow wave amplitudes for older compared to younger subjects. A significant effect of trial type [$F_{(1,23)} = 57.9; P < 0.001$] showed cueing effects on the LSW, with more positive amplitudes following invalid targets relative to validly cued targets. Significant group × trial type [$F_{(1,23)} = 9.0; P < 0.01$] and trial type × electrode site [$F_{(2,46)} = 19.3; P < 0.001$] interactions indicated that

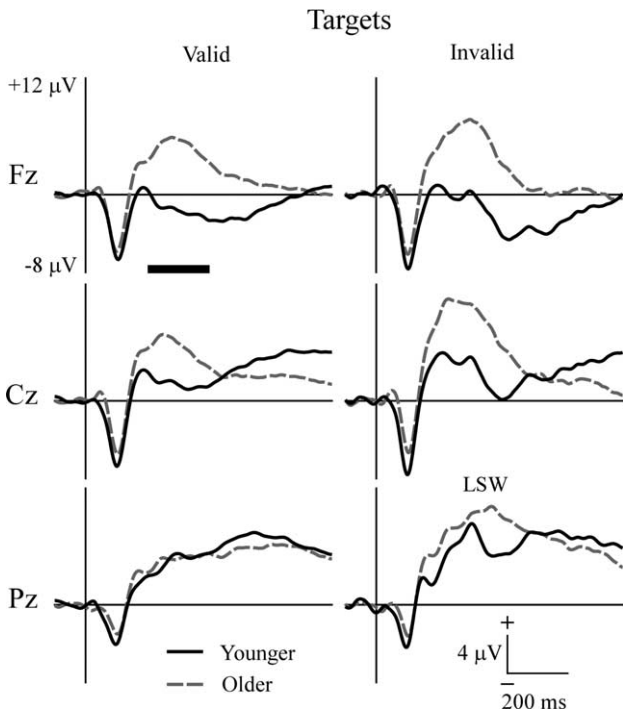

Fig. 6. Grand average potentials to targets at midline sites (DC—16 Hz). Group differences in the late slow wave (LSW) following targets were most prominent at Fz and Cz for both valid and invalid trial types, with similar amplitudes across groups at Pz site. Horizontal black bar indicates the LSW window measure from 200 to 398 ms after the target. Vertical line indicates target onset.

the cueing effects were larger in the older compared to the younger group (Fig. 7, see left), and largest at Pz relative to Cz and Fz sites. A significant effect of electrode site [$F_{(2,46)} = 26.6; P < 0.001$] showed that LSW amplitude increased from Fz to Pz sites.

Group differences in topography were further assessed with a 2 (group) × 2 (trial type: valid, invalid) × 3 (hemisphere: left, midline, right) × 3 (anterior–posterior: frontal, central, parietal) ANOVA using normalized values. There were significant effects of anterior–posterior position [$F_{(2,46)} = 39.5; P < 0.001$] and a group × anterior–posterior interaction [$F_{(2,46)} = 11.4; P < 0.01$]. Normalized amplitudes were largest at parietal sites, and group differences were largest at frontal sites. Significant effects of hemisphere [$F_{(2,46)} = 11.1; P < 0.001$] and a group × hemisphere interaction [$F_{(2,46)} = 3.6; P < 0.05$] indicated larger amplitudes at midline vs. lateral sites, and larger right hemisphere amplitudes in younger vs. older subjects.

To define the time course of the LSW in greater detail mean amplitudes at the Pz site were quantified using 3 adjacent 100 ms time windows (200–298, 300–398, 400–498 ms) that spanned the duration of the trial type difference in older subjects, which lasted longer than younger subjects in the grand average ERPs (Fig. 8). A 2 (group) × 3 (trial type) × 3 (time window) ANOVA showed a significant effect of trial type [$F_{(2,46)} = 19.6; P < 0.001$] and a significant group × trial type interaction [$F_{(2,46)} = 6.8; P < 0.01$]. The effect of cueing (invalid > valid = neutral) was evident in the LSW amplitude, and amplitude differences between valid and invalid targets were larger in older relative to younger subjects. There was a significant trial type × time window interaction [$F_{(4,92)} = 5.2; P < 0.01$] with amplitudes for valid trials increasing across the time windows in younger, and to a lesser degree older, subjects. Invalid targets showed an increase followed by a decrease, especially in older subjects, and neutral trials had similar amplitudes across time windows. A separate ANOVA comparing only valid and invalid trials had a significant group × trial type × time window interaction [$F_{(2,46)} = 3.6; P < 0.04$] indicating that the cueing effect was larger and lasted longer in older subjects. This effect is illustrated by constructing grand average difference waves for each group, where potentials from valid trials were subtracted from invalid trials (Fig. 7, right column).

In summary, LSW amplitude was more positive in older compared to younger subjects. Group differences were maximal at frontal sites, less pronounced at central sites, and not apparent at parietal sites. Invalid trials were more positive than neutral and valid trials, with a significantly greater difference between valid and invalid trials in the older subjects. The duration of the cueing effect also lasted significantly longer in older relative to younger subjects.

3.4. Motor vs. non-motor conditions

The CNV likely reflects a combination of motor preparation and stimulus expectancy (i.e. working memory for cue information and timing of stimulus onset) (Brunia, 1999). To determine if group differences in CNV amplitudes would be evident in the absence of motor preparation subjects performed a non-motor version of the cued attention task. Grand average ERPs from both response conditions (motor, non-motor) are shown in Fig. 9. Mean CNV amplitudes from −298 to 0 ms before target onset were analyzed with a 2 (group) × 2 (response condition) × 2 (trial type: valid, neutral) × 3 (electrode site: Fz, Cz, Pz) ANOVA. There was a significant main effect of response condition [$F_{(1,23)} = 27.8; P < 0.001$] with amplitudes in the motor condition (-3.8 ± 0.5 μV) more negative than the non-motor condition (-1.2 ± 0.3 μV). A nonsignificant group × response condition interaction showed that amplitude differences between the motor and non-motor condition were similar for both groups. There was a significant group × trial type interaction [$F_{(1,23)} = 8.1; P < 0.01$] indicating similar amplitudes among cue types in younger subjects, but more negative CNV amplitudes following valid vs. neutral cues in older subjects. For both groups, the differences between motor and non-motor conditions were largest at Cz and Pz sites, and smallest at Fz, as shown by a significant response condition × electrode site interaction [$F_{(2,46)} = 5.9; P < 0.01$].

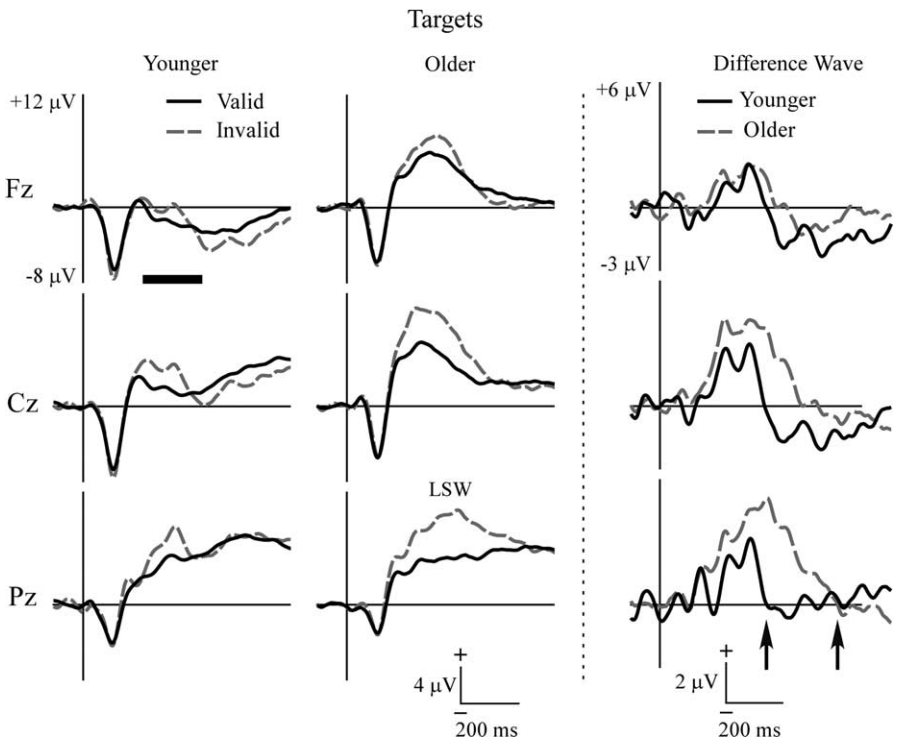

Fig. 7. Grand average potentials to valid and invalid targets for younger (left column) and older (middle column) groups. Differences in late slow wave (LSW) amplitude between trial types were significantly larger for older compared to younger subjects, and were largest at Pz and Cz sites. To illustrate this effect, difference waves were constructed by subtracting grand averages of valid trials from invalid trials for each group (right column). Arrows indicate the difference waveform returns to baseline faster in younger compared to older subjects and the overall amplitude difference was significantly larger in older subjects. Horizontal black bar indicates the LSW window measure from 200 to 398 ms after the target. Vertical line indicates target onset.

3.5. Cue ERPs: control condition

The purpose of the control condition was to determine if group differences in slow wave activity following cues are present when subjects listen to cue stimuli without performing the cued attention task. For the purpose of comparing the control condition with the cued attention task ERPs to the word go were labeled 'neutral' trials and ERPs to the words left and right were labeled 'valid' trials. Potentials elicited by cue words in the control condition are shown in Fig. 10.

Transient ERPs were analyzed using separate 2 (group) × 2 (trial type: valid, neutral) ANOVAs for component amplitudes and latencies at the Cz site. P50 amplitude had a significant main effect of group [$F_{(1,18)} = 7.3; P < 0.02$] with larger amplitudes in older vs. younger subjects (2.7 ± 0.4 vs. 1.3 ± 0.4 μV). A significant group effect for P200 latency [$F_{(1,18)} = 25.5; P < 0.001$] showed longer latencies in older (253.7 ± 5.8 ms) compared to younger (212.6 ± 5.8 ms) subjects. P200 amplitude also had a significant effect of trial type [$F_{(1,18)} = 22.8; P < 0.001$], with larger amplitudes for neutral (8.1 ± 1.0 μV) compared to valid trials (4.8 ± 0.6 μV).

Mean slow wave amplitude (200–498 ms after cue word) was analyzed with a 2 (group) × 2 (trial type: valid, neutral) × 3 (electrode site: Fz, Cz, Pz) ANOVA. There was a main effect of group [$F_{(1,18)} = 15.8; P < 0.01$] with larger amplitudes in older (5.5 ± 0.7 μV) compared to younger (1.7 ± 0.7 μV) subjects. Significant effects of electrode site [$F_{(2,36)} = 9.6; P < 0.01$] and a group × electrode site interaction [$F_{(2,36)} = 6.3; P < 0.02$] showed the slow wave amplitudes were largest at Cz and Pz compared to Fz, and the group difference was largest at Fz and Cz compared to Pz (see Fig. 10). A significant main effect of trial type [$F_{(1,18)} = 21.7; P < 0.001$] indicated larger amplitudes

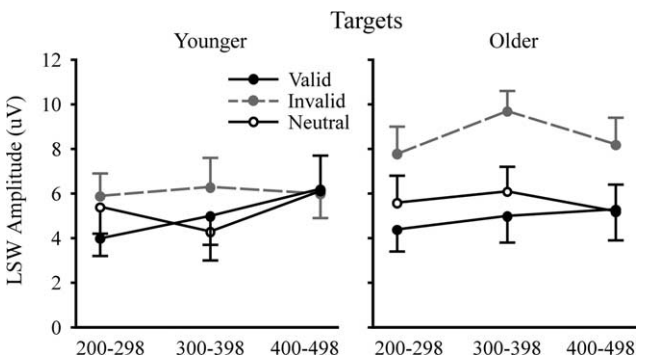

Fig. 8. Mean amplitude measures of the late slow wave across 3 time windows (200–298, 300–398, 400–498 ms) are shown comparing valid, invalid, and neutral trial types for both age groups (Pz electrode site). Significant effects of cueing (invalid > valid = neutral) were larger and lasted longer in older compared to younger subjects. Error bars represent standard error.

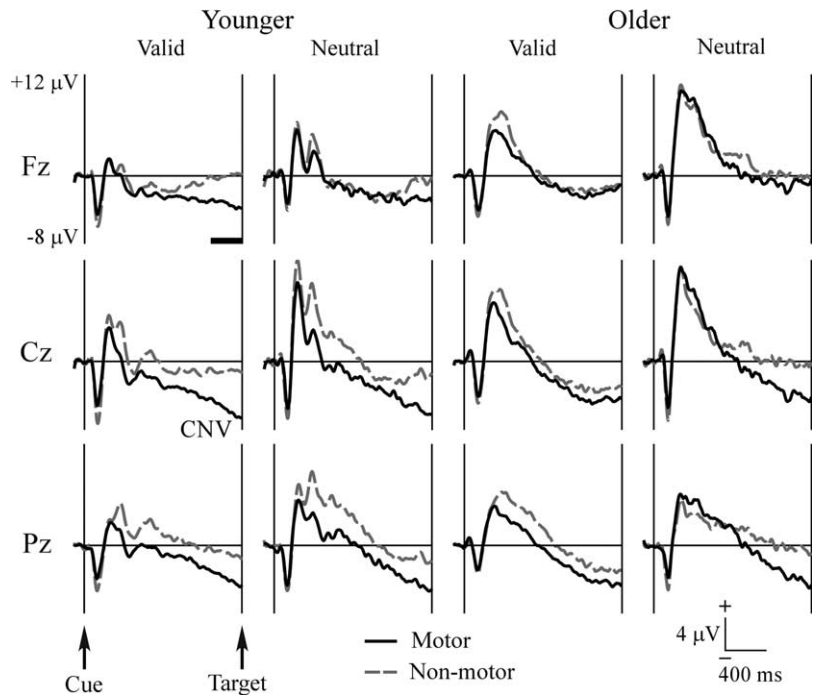

Fig. 9. Grand average potentials in motor and non-motor conditions of the cued attention task at midline electrode sites (DC—16 Hz). The CNV was significantly smaller in the non-motor vs. motor condition, but there were no significant group effects. Horizontal black bar indicates the 300 ms window measure for the CNV. Left and right vertical lines indicate cue and target presentation, respectively.

following neutral ($4.5 \pm 0.5\ \mu V$) vs. valid cues ($2.8 \pm 0.5\ \mu V$), which may reflect neutral trials having increased positivity from the P300 peak in younger subjects.

To compare potentials at the time period of the CNV in the attention and control tasks (1200–1500 ms window after cue word presentation), each combination of group (younger, older) and condition (attention, control) was treated as a between-subjects factor. A 4 (group/condition) × 2 (trial type: valid, neutral) × 3 (electrode: Fz, Cz, Pz) ANOVA had a significant main effect of group/condition $[F_{(1,41)} = 12.4; P < 0.001]$. Follow-up analyses included separate 2 (group) × 2 (trial type) × 3 (electrode) ANOVAs conducted for the attention and control conditions. There were no significant group differences and no group × trial type interactions in either condition. Conversely, separate 2 (condition: attention, control) × 2 (trial type) × 3 (electrode) ANOVAs for the younger and older groups showed significantly more negative potentials in the attention vs. control condition for younger $[F_{(1,241)} = 11.9; P < 0.01]$ and older subjects $[F_{(1,20)} = 33.5; P < 0.001]$.

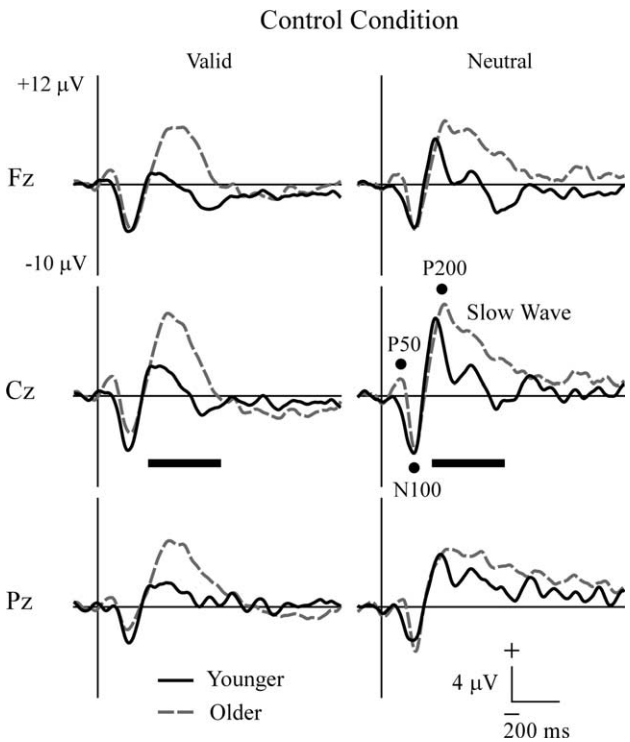

Fig. 10. Grand average potentials during the control condition at midline electrode sites (DC—16 Hz). Group differences in slow wave amplitude were found for both valid (left and right) and neutral (go) cue words. Horizontal black bar indicates the 300 ms window measure used to quantify slow wave amplitude. Vertical line indicates stimulus onset.

4. Discussion

In the present study a cued attention paradigm was employed to examine age-related changes in attentional regulation. Reaction time showed similar cueing effects for both younger and older subjects (valid < neutral < invalid). Group differences were observed in ERPs

following cue (slow wave) and target (N100; LSW) presentation, but were not evident during the CNV between cues and targets. Slow potentials following cues showed group differences (older > younger) in both the cued attention and control condition. Target N100 amplitudes were modulated by trial type (invalid > valid) in younger, but not older, subjects. Relative to younger subjects, differences in LSW amplitude between valid and invalid targets were larger and lasted longer in older subjects. Results suggest that transient neural responses to cue words and the modulation of attention following expected versus unexpected targets are affected during aging, whereas sustained potentials associated with motor preparation and stimulus expectancy are preserved.

4.1. Behavioral results

As in previous cued attention studies, both groups showed cueing effects (Posner, 1980; Hartley et al., 1990; Golob et al., 2002a). Reaction times were shortest for valid trials, intermediate for neutral trials, and longest for invalid trials. Relative to neutral cue information, valid cueing decreased reaction time by the same amount that invalid cueing increased reaction time (~7%) for the younger group. In contrast, the older group had more than a two-fold decrease in reaction time for valid vs. neutral cueing (13%) compared to the increase for invalid vs. neutral cueing (5%). Older subjects also had lower accuracy on invalid (90%) vs. neutral and valid (~97%) trials compared to younger subjects (~98%). Greater reaction time decreases on valid vs. neutral trials and reduced accuracy on invalid trials suggest older subjects may have relied more on cue information to facilitate responding, compared to younger subjects. Speed accuracy trade-offs cannot explain the behavioral results in the older group because subjects were both fastest and most accurate on valid trials. Consistent with previous cued attention studies, overall reaction time measures were longer for older compared to younger subjects (Hartley et al., 1990; Greenwood et al., 1993; Brodeur and Enns, 1997).

Attentional inhibition has been proposed as an important aspect of cognitive aging (Hasher and Zacks, 1988; Zacks and Hasher, 1997). This theory is relevant to the cued attention task if responses to invalid trials are assumed to reflect inhibitory processes. On a trial-by-trial basis cue information provides an expectation of target location that subsequently influences the response to the target. On invalid trials the 'prepotent' response (i.e. to a target at the cued location) must be overridden to execute a correct response to the target at the uncued location. Age differences in inhibiting prepotent responses have been observed in other tasks (Greenwood, 2000; West and Alain, 2000). Thus, if inhibitory deficits are expressed by incorrect responses to invalid trials, then the behavioral results provide partial support for age-related inhibitory deficits in attentional regulation. However, this conclusion is tentative because previous visual cued attention studies report no significant age differences in accuracy (Curran et al., 2001; Hartley et al., 1990; Nissen and Corkin, 1985). There were also no significant age differences in reaction time to correct invalid targets, as a percent of neutrals (Curran et al., 2001; Hartley et al., 1990; Nissen and Corkin, 1985) as predicted by deficient inhibition of the incorrectly cued location.

4.2. Attentional cueing and target ERPs

4.2.1. N100 and P200

Consistent with previous studies, N100 amplitudes in younger subjects are smaller to valid compared to invalid targets (Golob et al., 2002b; Hugdahl and Nordby, 1994). The effect of cueing on N100 amplitude in younger subjects may reflect benefits of valid cueing because N100 amplitudes were similar for invalid and neutral targets (Table 3). Because the N100 is mostly generated by secondary auditory cortical areas (Liegeois-Chauvel et al., 1994; Naatanen and Picton, 1987; Picton et al., 1999), cueing effects in younger subjects suggest the auditory cortex is involved in attentional regulation (Hillyard et al., 1973; Naatanen, 1990). N100 differences between valid and invalid trials cannot be attributed to having the cue and target presented to the same (valid) vs. different (invalid) ear because studies using paired auditory stimuli reported no change in N100 amplitude as a function of cue type (Butler, 1972; Schroger and Eimer, 1996; Tata et al., 2001). Instead, these studies report ERP differences between valid and invalid targets ~200 ms after stimulus presentation, after the occurrence of the N100, a result in agreement with the LSW findings in the current study.

In contrast to the younger group, older subjects did not exhibit differences in N100 amplitude as a function of cueing. Age differences in attention modulation of N100 are not present in dichotic listening studies where stimuli are presented to both ears and subjects attend to one target feature (i.e. location), although there were trends toward smaller N100 amplitude increases in older subjects (Ford et al., 1979; Gaeta et al., 2003, Exp. 1). The role of inhibitory processes is an important difference between dichotic listening and cued attention paradigms (Golob et al., 2002b). Dichotic listening tasks may not engage inhibitory processes because target stimuli are only presented at expected locations. However, during cued attention tasks responses to cued locations are thought to be inhibited when targets are presented at unexpected locations. We speculate that inhibitory processes in cued attention, but not dichotic listening, tasks may contribute to the age differences in N100 amplitude found in the present study. Another explanation for the age difference in the cued attention task may relate to correct responses being defined by a conjunction of location and pitch information. Dichotic listening tasks where subjects attend to one of 4 possible combinations of ear and pitch (high vs. low) do show

age differences in attentional modulation of ERPs (~100–400 ms after stimulus) (Gaeta et al., 2003, Exp. 2).

Cueing effects are also evident for target P200 amplitudes (Golob et al., 2002b), which were largest to invalid targets, intermediate to neutral targets, and smallest to valid targets in both groups. P200 amplitudes revealed greater differentiation between cue types relative to N100 amplitudes, with neutrally cued target amplitude approximately intermediate between valid and invalid targets. P200 amplitude measures could have been influenced by the overlapping LSW even though bandpass filtering was used to attenuate slow shifts.

4.2.2. Late slow wave (LSW)

LSW amplitude differences between valid and invalid trials are significantly larger and last longer in older compared to younger subjects. In the younger group, cueing effects on LSW amplitude replicated findings from previous auditory attention studies (Golob et al., 2002b; Ofek and Pratt, 2004; Schroger and Eimer, 1996); invalid targets are more positive than valid targets lasting from ~200to 400 ms, followed by a small reversal (valid > invalid) at fronto-central sites (Fig. 7, see left). The older group exhibited similar cueing effects on LSW amplitude (invalid > valid), but they lasted from ~200 to 800 ms and did not include the reversal seen in younger subjects.

The influence of cueing on LSW amplitude is thought to indicate attentional regulation of target processing induced by cue information (Golob et al., 2002b; Schroger and Eimer, 1996). Functional neuroimaging studies report that attention tasks activate a network that includes posterior parietal cortex, frontal cortex, and modality specific regions (Corbetta et al., 2002; Coull and Nobre, 1998; Nobre, 2001; Pugh et al., 1996). Activation differences between valid and invalid trials have been observed in the intraparietal sulcus and temporoparietal cortical junction (Corbetta et al., 2000; Nobre, 2001). Although source analysis was not performed in this study, topographic results indicate that the LSW is maximal at parietal sites. In addition, behavioral studies report prolonged reaction times to invalid, but not valid, trials in humans having lesions of parietal association cortex (Posner and Petersen, 1990; Posner et al., 1984). Taken together, the neuroimaging studies, LSW topography, and lesion results are consistent with the proposal that attention related activity in posterior parietal cortex contributes to the LSW. Amplitude modulations of the LSW are not due to the cue and target being presented to the same (valid) vs. different (invalid) ear because cueing effects on LSW amplitude are not observed when subjects are instructed to ignore the stimuli (Schroger and Eimer, 1996, Exp. 3).

4.3. Potentials to cues

Transient potentials to cues exhibit similar effects of age in both the cued attention task and passive listening control condition. Older subjects have more positive P50 and slow wave amplitudes, and longer P200 latencies compared to younger subjects. Similar slow wave amplitudes in the attention and control conditions suggest that age-related differences are not attributable to attention-related task demands. The group differences may relate to processing the complex acoustic cue stimuli because comparable slow waves are not observed when using pure tone stimuli (Iragui et al., 1993; Anderer et al., 1996; Golob et al., 2001). Semantic information conveyed by the cues may not account for slow wave differences because age differences have been found to visual word and non-word stimuli (Karayandis et al., 1993; Swick and Knight, 1997).

4.4. Potentials between cues and targets

The CNV is a sustained potential that develops during the interval between two task-relevant stimuli, with the second stimulus usually requiring a motor response (Brunia, 1999; Walter et al., 1964). The late CNV occurs just before the second stimulus and is generated by a network of cortical and subcortical structures (Gemba et al., 1990; Hamano et al., 1997; Ikeda et al., 1997). This study measured the late CNV during two conditions to assess the effect of age on motor preparation and stimulus expectancy (motor condition) compared with stimulus expectancy alone (non-motor condition). Similar to previous studies, late CNV amplitude was not significantly different between groups in either response condition (Dirnberger et al., 2000; Tecce et al., 1982), although older subjects had slightly smaller amplitude differences between motor and non-motor conditions for valid trials (see Fig. 9). Other studies have reported somewhat smaller CNV amplitudes for older subjects (Loveless and Stanford, 1974; Michalewski et al., 1980). Recent findings indicate that substantial modulations in CNV amplitudes are observed in the oldest–old (Golob et al., 2004). Both groups had larger CNV amplitudes in the motor condition relative to the non-motor condition suggesting that CNV amplitude increases associated with motor preparation do not change with age.

In the cued attention task age differences are present in slow wave activity ~200–500 ms after cue presentation, but there are no age differences in the amplitude of the immediately following CNV. In the control condition age differences are also seen in slow wave activity that returns to baseline (~500 ms) and does not develop into a CNV. In the cued attention task, after the time when the cue slow wave returns to baseline in the control condition (~500 ms), amplitudes of slow potentials for both groups are comparable. Taken together, these results suggest that two components (slow wave following cue, late CNV) are active between cue and target presentation. The slow wave following cues, but not the CNV, exhibit age-related differences.

4.5. Summary

ERP measures corresponding to 3 distinct time periods during an auditory cued attention task revealed age-related differences in transient potentials to cue and target stimuli, but not for sustained potentials between cues and targets. Group differences in slow waves following cues in the attention and control conditions suggest that older subjects process cue words differently than younger subjects. Late CNV amplitudes are similar for both groups in the motor and non-motor response conditions, indicating motor preparation and stimulus expectancy are unaffected by aging. N100 and LSW amplitudes following targets revealed group differences in the modulation of attention to expected and unexpected stimuli. Age-related differences in ERPs associated with attentional regulation are compatible with the hypothesis that attentional processes are modified and may contribute to cognitive aging.

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