

Age-related loss in attention-based modulation of tactile stimuli at early stages of somatosensory processing

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ABSTRACT

Normal aging has been linked to impairments in gating of irrelevant sensory information and neural markers of diminished cognitive processing. Whilst much of the research in this area has focussed on visual and auditory modalities it is unclear to what degree these findings apply to somatosensation. Therefore we investigated how age impacts early event-related potentials (ERPs) arising from relevant or irrelevant vibrotactile stimuli to the fingertips. Specifically, we hypothesised that older adults would demonstrate reduced attention-based modulation of tactile ERPs generated at early stages of cortical somatosensory processing. In accord with previous research we also expected to observe diminished P300 responses to attended targets and behavioural deficits. Participants received vibrotactile stimulation to the second and fifth digit on the left hand and reported target stimuli on one digit only (as instructed) with comparisons between two age groups: (1) Young adults (age range 20–39) and (2) Older adults (age range 62–89). ERP amplitudes for the P50, N70, P100, N140 and long latency positivity (LLP) were quantified for attended and non-attended trials at several electrodes (C4, CP4, CP3 and FC4). The P300 in response to attended target stimuli was measured at CPZ. There was no effect of attention on the P50 and N70 however the P100, N140 and LLP were modulated with attention. In both age groups the P100 and LLP were more positive during trials where the stimuli were attended to, whilst the N140 was enhanced for non-attended stimuli. Comparisons between groups revealed a reduction in P100 attention-based modulation for the older adults versus the young adults. This effect was due to a loss of suppression of the non-attended stimuli in older subjects. Moreover, the P300 was both slower and reduced in peak amplitude for older subjects in response to attended targets. Finally, older adults demonstrated impaired performance in terms of both reduced target detection accuracy and in reporting more false positives. Overall, present results reveal a deficit in suppressing irrelevant tactile information during an attention-demanding task which possibly relates to reduced markers of performance. Such a loss of inhibitory function is consistent with age-related change associated with a decline in executive control via prefrontal regions.

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1. Introduction

Progressive cognitive decline, indexed by decreased performance on memory and attention-related tasks is one of the major changes an individual will endure with age. Many researchers have worked to establish the neural mechanisms which bring about age-related cognitive impairment (Drag & Bieliauskas, 2010; Gazzaley & D'Esposito, 2007; MacDonald, Li, & Backman, 2009; Reuter-Lorenz & Park, 2010). Consequently, a number of models have been advanced to explain degraded performance. Traditional models include a general slowing of processing speed, an inability to inhibit

irrelevant distractive information, and a deterioration of top-down regulation via prefrontal regions (Dempster, 1992; Hasher & Zacks, 1988; Salthouse, 1996; West, 1996). Importantly, these accounts are not mutually exclusive and the contemporary view acknowledges that age-related cognitive decline stems from a complex interplay of factors.

A key to optimal cognitive function is the ability to maintain relevant data in working memory whilst preventing interference from irrelevant sources of information. A number of studies have demonstrated age-related deficits in this regard. In fact, it appears that the main disparity between young and older adults is not so much an inability to attend to task-relevant information but in a compromised ability to suppress task-irrelevant information (Reuter-Lorenz & Park, 2010). This has also been discussed by some authors in terms of increasing levels of noise in the aging brain (MacDonald et al., 2009). Any impaired filtering may result in a greater propensity to overwhelm neural processing networks (Awh

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& Vogel, 2008; McNab & Klingberg, 2008); networks such as prefrontal areas which already exhibit a lower ceiling of activation in older adults during working memory tasks (Reuter-Lorenz & Park, 2010).

An area which is critical in providing resistance to distraction is the prefrontal cortex (PFC) (Knight, Staines, Swick, & Chao, 1999). Numerous lines of evidence including animal models of selective attention (Artchakov et al., 2009; Bartus & Levere, 1977), lesion studies in humans (Chao & Knight, 1995, 1998) and imaging work (Dolcos, Miller, Kragel, Jha, & McCarthy, 2007) have established clear links between prefrontal activity, suppression of distracters and subsequent cognitive performance. Indeed, PFC acts to suppress irrelevant information early in the processing stream, including at the earliest cortical stages of sensory processing and even at the thalamus prior to cortical entry (Cao, Wang, Bai, Zhou, & Zhou, 2008; Yamaguchi & Knight, 1990; Yingling & Skinner, 1976; Zikopoulos & Barbas, 2006). Given the established role of PFC in task-related gating and cognitive performance it is essential to note that this region undergoes disproportionately greater deterioration with age compared with other brain structures (Jernigan et al., 2001; Raz et al., 1997; Resnick, Pham, Kraut, Zonderman, & Davatzikos, 2003). Thus the loss of inhibitory interference control in older adults may originate at least partly from diminished prefrontal function.

Much of the research on age-related cognitive processing has emphasised visual or auditory modalities with comparably little focus on somatosensation. Whilst there are likely many similarities in how age impacts cognitive performance driven by various sensory systems, important differences in how aging impacts visual and auditory processes have already been noted (Ceponiene, Westerfield, Torki, & Townsend, 2008). Consequently a focus on somatosensation is warranted to develop a more complete model of neurological changes associated with age. The main purpose of the current study was to investigate age-related changes in somatosensory gating during a tactile discrimination task. Furthermore, we wished to explore how these changes may relate to recent findings in our lab where transient suppression of the dorsolateral prefrontal cortex (DLPFC) was used to investigate the role of this region in attention-based sensory gating (Bolton & Staines, 2011). In our previous study, subjects performed a within-hand vibrotactile discrimination task where they were required to attend to targets on one digit, whilst ignoring distracter targets on another digit. Following the application of continuous theta burst stimulation over DLPFC, subjects demonstrated a loss of attention-based modulation over tactile evoked-potentials that were reflective of uni-modal somatosensory processing. These results supported the view that prefrontal areas regulate somatosensory signal transmission at an early cortical processing stage based upon task-relevance. Given that one explanation for age-related cognitive decline involves selective deterioration of prefrontal areas (e.g. loss of cortical volume or abnormalities in white matter), comparisons between the DLPFC-inhibited group with older adults could offer insight into the role of deficient frontal control in driving age-linked deficits, particularly in the context of somatosensory gating.

Electroencephalography (EEG) has been useful in studies on aging to reveal delayed processing of sensory information and in exposing a selective loss in suppressing distracters as they pass through various cortical centres (Dustman, Shearer, & Emmerson, 1993). In particular, event-related potentials (ERPs) following somatosensory stimulation (either electrical or mechanical) provide a useful probe into cortical processing of somatosensory information. The ensuing ERP profile offers a means of investigating both early sensory processing such as the P50 or P100 components which reflect unimodal somatosensory generators (Allison, McCarthy, Wood, & Jones, 1991; Hamalainen, Kekoni, Sams, Reinikainen, & Naatanen, 1990), and/or later more endogenous

markers such as the N140 or target-elicited P300 (Brazdil et al., 1999; Hamalainen et al., 1990; Linden, 2005). Given the sensitivity of somatosensory ERP measures to attentional manipulation (Adler, Giabbiconi, & Muller, 2009; Bolton & Staines, 2011; Eimer & Forster, 2003; Gillmeister, Sambo, & Forster, 2010; Iguchi, Hoshi, Tanosaki, Taira, & Hashimoto, 2005), they provide an ideal means of exploring age-related changes in signal processing. To date, a thorough investigation into age-related changes in attention-based modulation of somatosensory information has not been undertaken.

The present study explored the impact of age on spatial attention to tactile information at early cortical stages of somatosensory processing. Using a vibrotactile discrimination task where participants attended to stimuli delivered to one of two stimulated digits in the same hand, we investigated attention-based modulation of tactile ERP components and compared this between young and older adults. As previously mentioned, many ERP components can be modulated by attention and this has been shown even with early components representing somatosensory cortical processing (Bolton & Staines, 2011; Eimer & Forster, 2003; Schubert et al., 2008). Moreover, imaging work has shown a strong link between prefrontal activity and activity at these somatosensory processing stages (Staines, Graham, Black, & McIlroy, 2002) suggesting a prefrontal or top-down gating system based upon attention to task-relevant stimuli. Thus it seems very plausible that such prefrontal driven modulation of tactile ERP components could be susceptible to age-related deficits. We hypothesised that older adults would show diminished attention-based modulation of ERPs during a tactile discrimination task. Such disrupted modulation would be indicated by a loss in the difference between attended and unattended ERP components. Moreover, we postulated that this would most likely occur via reduced suppression of irrelevant stimuli and this effect would be evident early in the somatosensory processing stream. This would suggest reduced or absent attention-based modulation of early somatosensory processing within the cerebral cortex as a function of age. Finally, previous research investigating attention to somatosensory target stimuli revealed both slower and diminished P300 responses in older adults for attended targets possibly reflecting a relative weakening of cognitive processing (Yamaguchi & Knight, 1991). Therefore in accord with previous findings, we hypothesised that the P300 elicited in response to targets on the attended digit would be reduced in amplitude and reveal longer latencies in older subjects.

2. Methods

2.1. Participants

Twenty-five neurologically normal volunteers participated in the study after providing written informed consent. Participants were included in one of two experimental groups based upon age. Testing groups were as follows: (a) Young adults, YA (age range 20–39 years) and (b) Older adults OA (age range 62–89 years). Data from two participants were excluded due to excessive artefacts or an absence of specific ERP components. The final sample size for each group was as follows: YA ($n = 12$) and OA ($n = 11$). All experimental procedures were approved by the University of Waterloo's Office of Research Ethics. (Note: Subjects from the YA group were used in the previous publication by Bolton and Staines (2011). Thus, YA data will be repeated from prior work.)

2.2. Testing protocol

General procedures were replicated from a previous study in our lab (Bolton & Staines, 2011). Subjects were seated in a sound-attenuating booth (Industrial Acoustics, 120A, NY), facing a blank computer screen and instructed to look directly ahead throughout testing. Tactile stimuli were delivered via 2 blunt plastic probes contacting the fingertips of the second and fifth digits on the left hand depicted in Fig. 1A. These probes (approximately 1 cm diameter) were vibrated using piezo-electric actuators at a rate of 25 Hz for 125 ms during each stimulus. Vibrotactile stimulation was delivered by digitally generated waveforms converted to an analog signal (DAQCard 6024E, National Instruments, Austin, TX, USA) and then amplified (Bryston 2B-LP, Peterborough, ON, Canada). The amplitude of vibration was set so that minimal values (i.e. small amplitude targets) exceeded

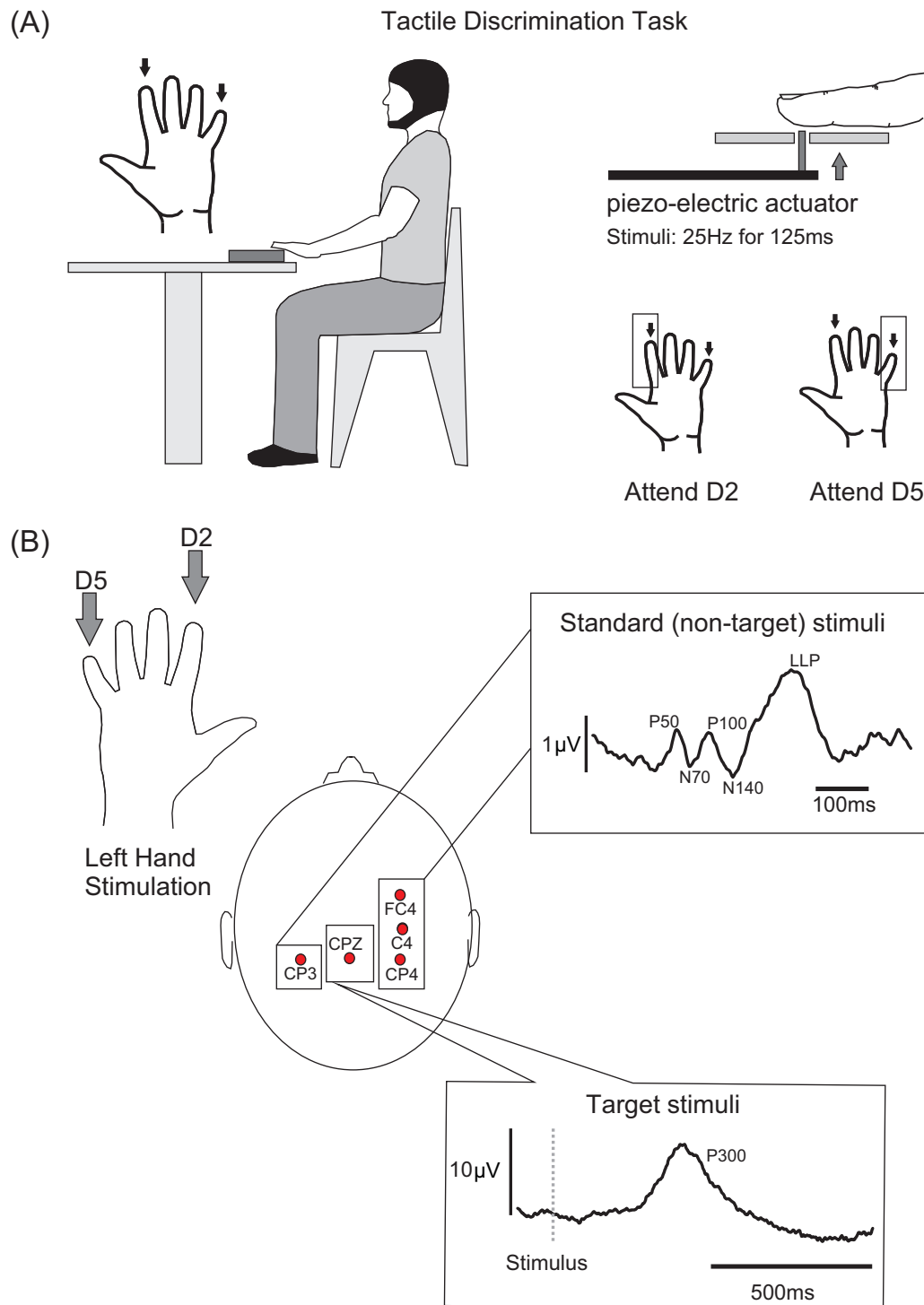


Fig. 1. (A) The experimental set-up is depicted for how subjects receive vibrotactile stimulation to D2 and D5 on the left hand. (B) The electrode location for standard (non-target) and target stimuli delivered to the left hand along with the ERP components measured at each site.

sensory threshold for all subjects. These stimuli were presented randomly to each finger (but never simultaneously) with random inter-stimulus intervals in the range of 500–1500 ms. An oddball paradigm was employed whereby 20% of the trials for each finger consisted of the deviant stimulus. These deviant stimuli represented the targets to which attention was paid and the amplitude of these targets was set at 25% the standard (non-target) amplitude. The two experimental conditions required subjects to either (a) attend to the second digit (D2) on the left hand, or (b) attend to the fifth digit (D5) on the left hand. Subjects reported target stimuli on the attended finger by pressing a button with the right hand. Subjects were instructed to gently rest their hand on the probes to ensure consistent hand pressure during testing. Headphones were worn throughout the experiment to deliver white noise

and block sound from the vibration device. Trials requiring attention to either D2 or D5 were randomly presented to subjects in 3 min blocks followed by a rest period of approximately 1 min. There were a total of 6 testing blocks with 3 blocks attending to D2 and 3 blocks attending to D5. Approximately 600 standard (non-target) stimuli were applied to each digit over the entire experiment with each testing block consisting of approximately 100 standard and 20 target stimuli.

2.3. Recording and analysis

Electroencephalographic (EEG) data was recorded from 32 electrode sites according to the international 10–20 system for electrode placement and referenced

to bilateral mastoids. All channel recordings had impedance values below 5 k Ω . EEG data were amplified (20,000 $\times$), filtered (DC–200 Hz, 6 dB octave roll-off) and digitised (500 Hz, SynAmps2, Scan 4.3, Compumedics Neuroscan, Charlotte, NC) before being stored for off-line analysis.

ERPs to stimuli were averaged relative to a 100 ms pre-stimulus baseline for each attention condition. Data were band-pass filtered (1–30 Hz) and trials with artefacts (i.e. eye blinks, muscle activity) were identified by visual inspection and were excluded from further analysis. EEG analysis proceeded in two ways: First, to address the issue of sensory gating at early stages of somatosensory processing, several ERP components were evaluated at C4 and CP4 electrodes, focussing on the average amplitude for each defined ERP component over a 20 ms time window. Average amplitude windows were centred at the peaks for P50, N70, P100, N140 and long latency positivity (LLP) for each subject individually. Peaks for each component were determined within the following time windows: P50 (40–70 ms), N70 (60–90 ms), P100 (85–135 ms) N140 (125–165 ms), and LLP (180–350 ms). Early SEP components are prominent at central-parietal electrode sites contralateral to the stimulation and have been suggested to arise largely from S1 (Allison et al., 1991; Hamalainen et al., 1990), therefore C4 and CP4 electrodes were solely used to investigate the P50 and N70 components. Additional electrodes were included in the analysis for the P100 and the later components, N140 and LLP. In particular, the P100 has been suggested to arise from bilateral secondary somatosensory cortical generators (Hamalainen et al., 1990), thus the CP3 electrode was included in the P100 analysis. Furthermore, for the later components, especially during attention-demanding tasks, frontal generators reveal significant activation which adds to the continued engagement of primary sensory processing centres (Mauguiere et al., 1997; Pasternak & Greenlee, 2005). For this reason FC4 was included for the analysis of the endogenous N140 and LLP components. (Note: FC4 produced the largest amplitude later components and was therefore the focus for N140 and LLP analysis.) Only non-target stimuli (i.e. large amplitude vibrations) delivered to the second digit were analysed for this first phase (Note: Stimulation of the fifth digit did not result in consistently clear ERP components thus analysis was focussed on stimuli delivered to the second digit. This may relate to differences in the extent of cortical representation for each digit, which is comparably larger for the second versus fifth digit (Duncan & Boynton, 2007).)

Next, the P300 in response to targets on the attended second digit was evaluated at the CPZ electrode site using the peak amplitude within a time window of 200–600 ms. Whilst the P300 has been attributed to a large number of cortical generators (Brazdil, Roman, Daniel, & Rektor, 2003; Linden, 2005), peak activity for the P300 in response to somatosensory oddball target stimuli has previously been shown to be maximal at central and parietal sites (Linden, 2005), thus determining our selection of CPZ. For all somatosensory ERP data, clearly defined components and peaks were required for inclusion, for correctly responded targets only. Fig. 1B depicts the electrodes used for the study and the ERP components of interest.

A two-way, mixed model ANOVA with group (YA vs. OA) as the between-subjects factor and attention (attended vs. unattended) as the within-subjects factor was conducted on ERP amplitudes for the P50, N70, P100, N140 and LLP components. ANOVAs were calculated for each component of interest at each electrode (selected as described above) separately. Where interactions were significant, *t*-tests were used to compare the within-group difference score (attended minus unattended) between the two age groups. Independent *t*-tests were used to compare the effect of age group for each attention condition separately (OA attended versus YA attended; OA unattended versus YA unattended). The significance level was set at $p \leq 0.05$. Paired *t*-tests were used to test the hypothesis that attention would facilitate early ERP components by comparing ERP amplitudes when attention was directed to the second digit (attended) versus the fifth digit (unattended). Separate tests were conducted for each component of interest: P50 and N70 (C4 and CP4), P100 (C4, CP4 and CP3), N140 and LLP (C4, CP4 and FC4).

Behavioural performance was evaluated by determining the number of targets hit relative to the overall number of targets that were presented for each subject. This success rate was expressed as a percentage and compared between the age groups using *t*-tests. The significance level was set at $p \leq 0.05$ for all comparisons.

3. Results

3.1. Age-related effects on attention-based modulation of 'non-target' tactile ERP components

3.1.1. Amplitudes

Grand average waveforms displaying the comparison of attention-based modulation between OA and YA groups are shown in Fig. 2 for 12 electrodes and more focally at C4 and CP4 in Fig. 3 (including scalp topography at the P100 peak). This data is depicted as bar graphs for each component in Fig. 4 for the P50, N70 and P100 and in Fig. 5 for the N140 and LLP. Two-way, mixed-model ANOVAs resulted in no significant main effects with age group (C4: $F_{1,19} = 0.004$, $p = 0.949$; CP4: $F_{1,18} = 0.002$, $p = 0.968$) or attention

condition (C4: $F_{1,19} = 1.19$, $p = 0.29$; CP4: $F_{1,18} = 1.72$, $p = 0.207$) and no interactions between these factors (C4: $F_{1,19} = 0.214$, $p = 0.649$; CP4: $F_{1,18} = 0.123$, $p = 0.730$) for P50. Likewise, there were no significant main effects with age group (C4: $F_{1,17} = 0.747$, $p = 0.399$; CP4: $F_{1,16} = 0.057$, $p = 0.814$) or attention condition (C4: $F_{1,17} = 0.923$, $p = 0.35$; CP4: $F_{1,16} = 1.063$, $p = 0.318$) and no interactions between these factors (C4: $F_{1,17} = 0.504$, $p = 0.487$; CP4: $F_{1,16} = 0.002$, $p = 0.970$) for N70. There was a significant interaction between age group and attention for P100 amplitudes at both C4 ($F_{1,19} = 4.49$, $p = 0.048$) and CP4 ($F_{1,19} = 5.16$, $p = 0.035$), but this was only a trend at CP3 ($F_{1,19} = 3.79$, $p = 0.066$). Inspection of the average P100 amplitudes shown in Fig. 3 for both the OA and YA groups suggests that the interaction between age group and attention was due to a greater positivity in P100 for the unattended stimuli in the OA group. There was an effect of attention for both OA ($t_{10} = 2.11$, $p < 0.03$) and YA ($t_9 = 3.59$, $p = 0.003$) groups at C4. This effect of attention was also present at CP4 and CP3 in the YA group (CP4: $t_9 = 3.95$, $p = 0.002$; CP3: $t_9 = 3.39$, $p = 0.004$) however in the OA group this was only a trend at CP4 ($t_9 = 1.58$, $p = 0.072$) and not significantly different at CP3 ($t_9 = 0.853$, $p = 0.207$). We also directly tested the effect of age group for each of the attended conditions to further probe what produced the change in attention-based modulation (i.e. either an increase in attended values or decrease in the unattended values). There was no significant effect of age group for P100 amplitudes to attended stimuli at C4, CP4 or CP3 (C4: $t_{19} = 0.67$, $p = 0.28$; $t_{19} = 0.41$, $p = 0.35$; CP3: $t_{19} = 0.38$, $p = 0.702$). However, there was a significant difference for unattended stimuli at C4 ($t_{19} = 2.54$, $p = 0.016$) and CP3 ($t_{19} = 2.36$, $p = 0.018$), and a trend at CP4 ($t_{19} = 1.44$, $p = 0.099$) such that P100 amplitudes to unattended stimuli were more positive for the OA group.

For the N140 there was an interaction between age and attention at FC4 ($F_{1,19} = 9.33$, $p = 0.007$) and a trend for an interaction at C4 ($F_{1,19} = 3.82$, $p = 0.066$) with no interaction at CP4 ($F_{1,21} = 0.997$, $p = 0.329$). There was however a main effect for attention at CP4 ($F_{1,21} = 7.75$, $p = 0.011$). Overall the N140 amplitudes were significantly more negative for unattended versus attended stimuli. There was a main effect for age group at C4 ($F_{1,19} = 4.59$, $p = 0.045$) and CP4 ($F_{1,21} = 7.75$, $p = 0.011$), both revealing more negative amplitudes for the YA group. Follow-up analysis on the interaction at FC4 and trend at C4 revealed a greater difference between attended and unattended stimuli for YA versus OA (FC4: $t_{19} = 3.01$, $p < 0.003$; C4: $t_{19} = 2.23$, $p < 0.033$). As with the P100, we directly compared attention conditions at FC4 and C4 to probe the change in difference score. There was no significant effect of age group for N140 amplitudes to attended stimuli at C4 ($t_{19} = 1.47$, $p = 0.11$) or FC4 ($t_{19} = 0.19$, $p = 0.871$). However, there was a significant difference across age group to unattended stimuli at C4 ($t_{19} = 3.09$, $p = 0.007$) and FC4 ($t_{19} = 2.25$, $p = 0.04$) such that N140 amplitudes were more negative for the YA group.

For the LLP no interactions were present for any electrode (FC4: $F_{1,19} = 0.493$, $p = 0.491$; C4: $F_{1,21} = 0.383$, $p = 0.543$; CP4: $F_{1,21} = 0.668$, $p = 0.423$), however there was a significant main effect of attention at all electrodes (FC4: $F_{1,21} = 6.937$, $p = 0.016$; C4: $F_{1,21} = 4.92$, $p = 0.016$; CP4: $F_{1,21} = 5.77$, $p = 0.026$). The attended amplitudes were significantly more positive than unattended amplitudes. There was also a main effect of age group at CP4 ($F_{1,21} = 6.14$, $p = 0.022$) with a trend at C4 ($F_{1,21} = 3.66$, $p = 0.07$), both showing larger amplitudes for the YA group, however there was no main effect for age group at FC4 ($F_{1,19} = 0.32$, $p = 0.578$).

3.1.2. Latencies

Two-way, mixed-model ANOVAs revealed no interactions at either electrode for the P50 latency (C4: $F_{1,19} = 0.67$, $p = 0.423$; CP4: $F_{1,18} = 0.637$, $p = 0.435$). There was a main effect for age group at both electrodes (C4: $F_{1,19} = 6.73$, $p = 0.018$; CP4: $F_{1,18} = 6.20$, $p = 0.023$) with slower peak latencies with the OA group.

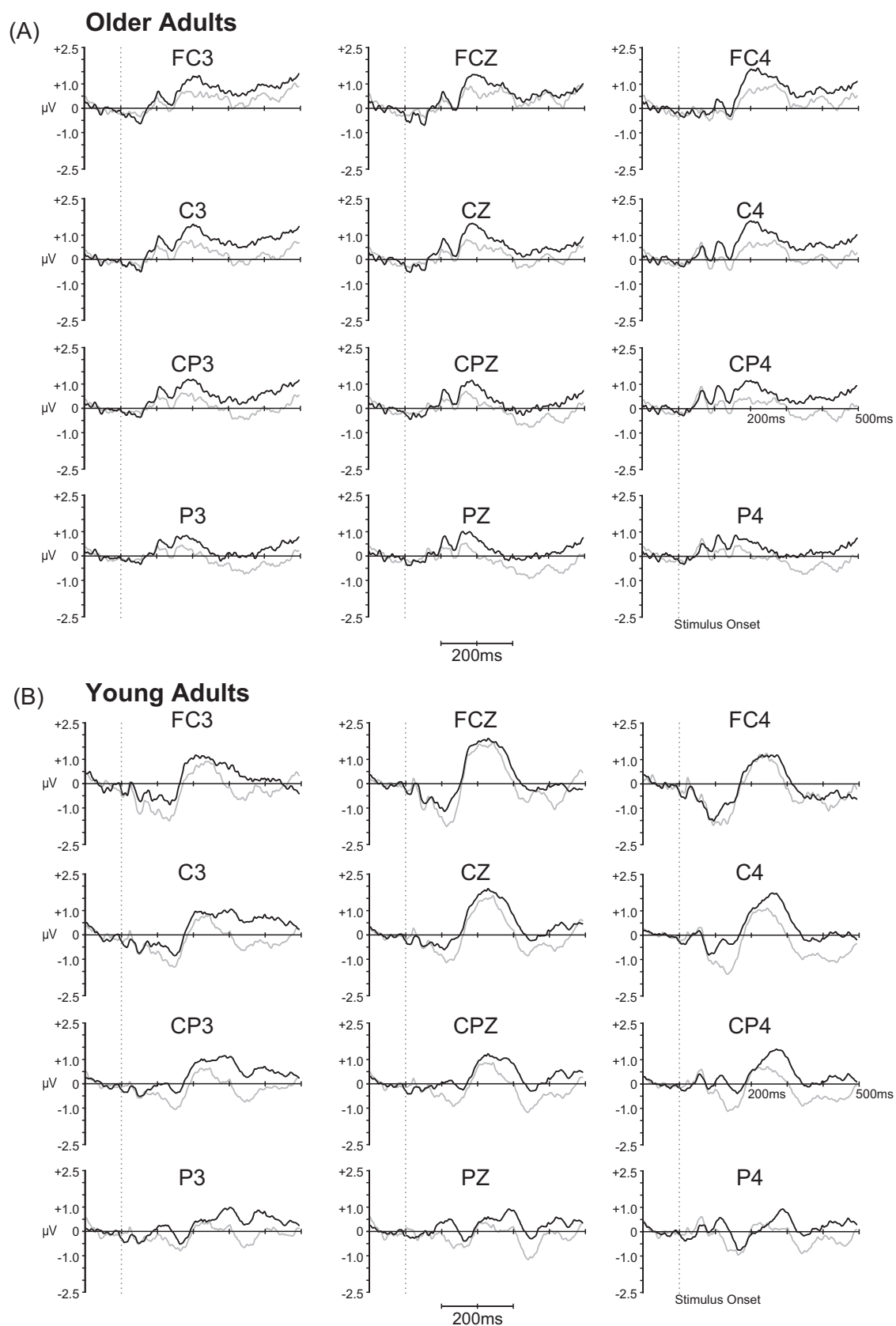


Fig. 2. Group average data is presented from both older adults (above) and young adults (below) to show the general pattern of attention-based modulation across 12 electrodes. All data are for standard (non-target) stimuli to the index finger. The dark lines represent attending to the index finger and the grey lines represent when the index finger is non-attended. All values are in microvolts.

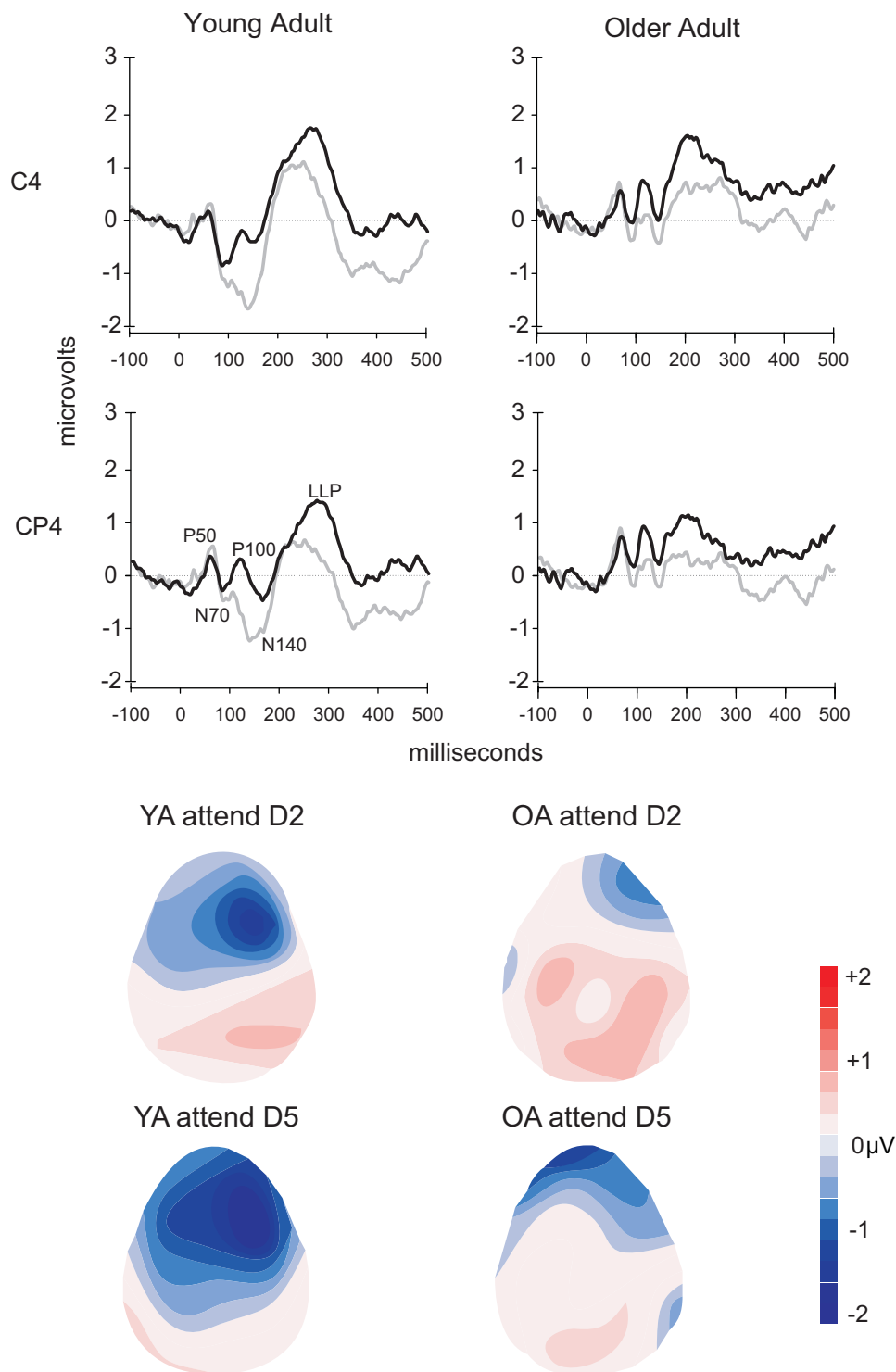


Fig. 3. Above: Group average waveforms from both young adults (YA) and older adults (OA) focussed on C4 and CP4. All data are for standard (non-target) stimuli to the index finger. The dark lines represent attending to the index finger and the grey lines represent when the index finger is non-attended. All values are in microvolts. Below: Scalp topography of group average data averaged over a 20 ms time window around the P100 peak when attending to D2 or D5 for standard stimuli on the index finger for both age groups.

Furthermore, there was a main effect of attention at CP4 ($F_{1,18} = 5.41$, $p = 0.032$) and a trend at C4 ($F_{1,19} = 4.20$, $p = 0.054$) showing slightly delayed peak latencies with unattended stimuli at P50. No interactions (C4: $F_{1,16} = 0.119$, $p = 0.734$; CP4: $F_{1,16} = 0.005$, $p = 0.945$) or main effects for attention (C4: $F_{1,16} = 2.238$, $p = 0.154$; CP4: $F_{1,16} = 1.218$, $p = 0.286$) were evident at either electrode for N70. There was a trend for a main effect of age group at CP4

($F_{1,16} = 4.08$, $p = 0.06$) showing a tendency towards slower latencies with the OA group however not for C4 ($F_{1,16} = 0.884$, $p = 0.361$).

The P100 and LLP revealed interactions at the C4 electrode (P100: $F_{1,19} = 10.83$, $p = 0.004$; LLP: $F_{1,21} = 8.67$, $p = 0.008$) and for P100 at the CP4 electrode ($F_{1,19} = 23.54$, $p < 0.001$) but not for LLP at CP4 ($F_{1,21} = 2.392$, $p = 0.137$). There were no interactions ($F_{1,19} = 3.01$, $p = 0.099$) or main effects for age

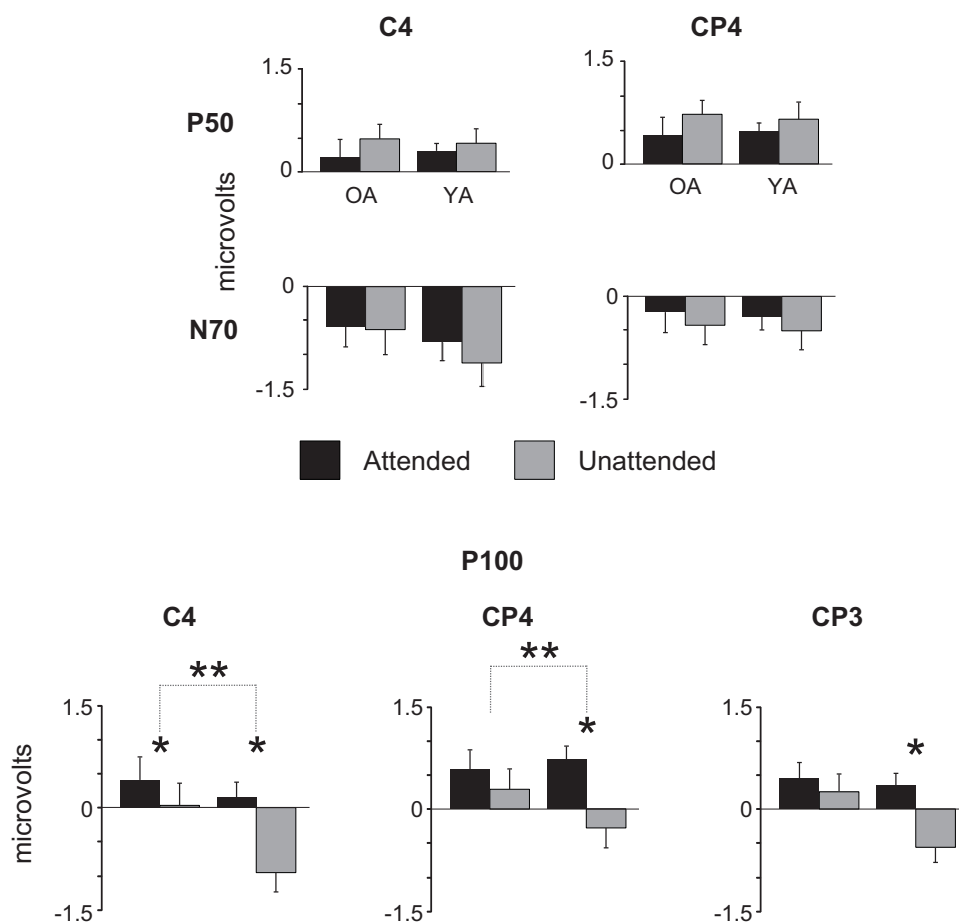


Fig. 4. Average amplitude is depicted for P50 and N70 (above) at C4 and CP4 and separately for the P100 (below) at C4, CP4 and CP3 comparing the two age groups (YA – young adults; OA – older adults). Bar graphs depict group data for average amplitude when attending to the index finger (black) or when ignoring the index finger (grey). All values are in microvolts. Asterisk (*) indicates significant main effect for attention within an age group; ** indicates significant interaction between attention and age group ($p < 0.05$).

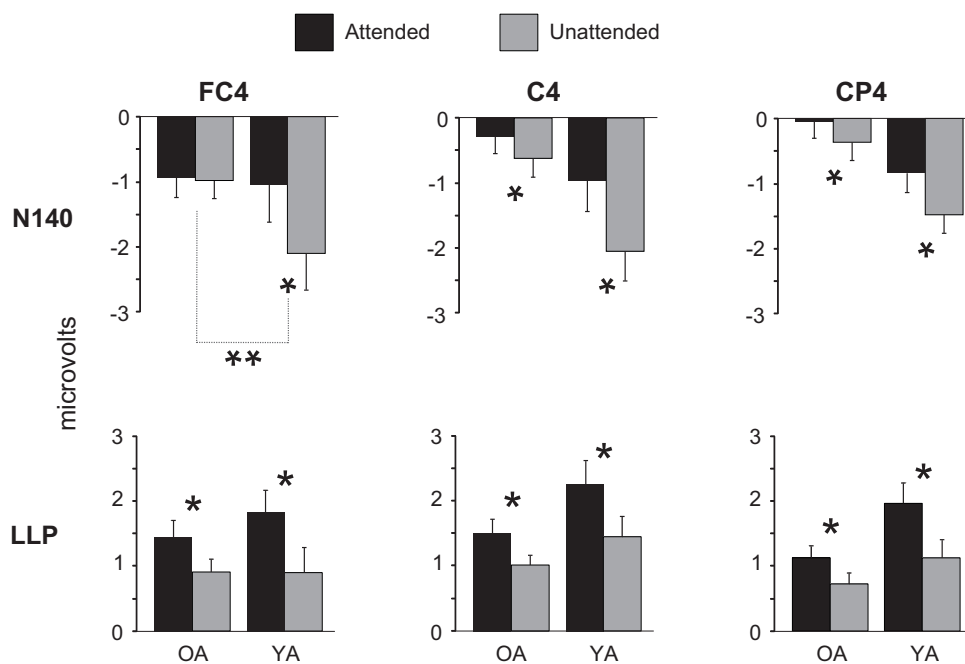


Fig. 5. Average amplitude is depicted for the N140 and LLP at FC4, C4 and CP4 comparing the two age groups (YA – young adults; OA – older adults). Bar graphs depict group data for average amplitude when attending to the index finger (black) or when ignoring the index finger (grey). All values are in microvolts. Asterisk (*) indicates significant main effect for attention within an age group ($p < 0.05$).

Table 1

Average latency (ms) for the P50, N70, P100 and N140 peaks during attended and unattended stimuli in the older adults (OA) and younger adults (YA). Standard errors are in brackets.

Group		P50		N70		P100		N140		LLP	
		D2	D5	D2	D5	D2	D5	D2	D5	D2	D5
OA	CP4	60.9 (3.0)	67.3 (2.6)	89.8 (3.2)	92.3 (2.9)	112.9 (2.2)	119.1 (3.1)	148.0 (4.4)	148.4 (3.9)	240.4 (19.3)	241.5 (12.1)
	C4	60.2 (3.7)	63.3 (2.4)	87.3 (3.0)	90.9 (2.5)	114.0 (2.7)	115.1 (3.8)	143.3 (1.9)	145.1 (3.1)	234.0 (12.5)	245.8 (10.2)
	CP3	na	na	na	na	116 (4.7)	119.3 (3.8)	na	na	na	na
	FC4	na	na	na	na	na	na	141.4 (2.6)	151.6 (4.5)	225.6 (12.4)	240.8 (14.5)
YA	CP4	55.7 (3.5)	58.3 (2.9)	84.3 (2.8)	85.4 (1.9)	120.6 (3.5)	108.8 (3.4)	157.5 (7.4)	152.0 (5.9)	267.5 (10.7)	238.8 (12.5)
	C4	49.0 (3.6)	56.8 (3.1)	86.2 (2.8)	87.6 (2.0)	120.8 (4.0)	107.6 (3.9)	150.8 (5.6)	142.8 (4.9)	265.8 (10.3)	229.7 (9.7)
	CP3	na	na	na	na	115.8 (5.3)	106.8 (4.3)	na	na	na	na
	FC4	na	na	na	na	na	na	150.2 (6.9)	144.6 (7.6)	267.6 (15.9)	238.8 (8.1)

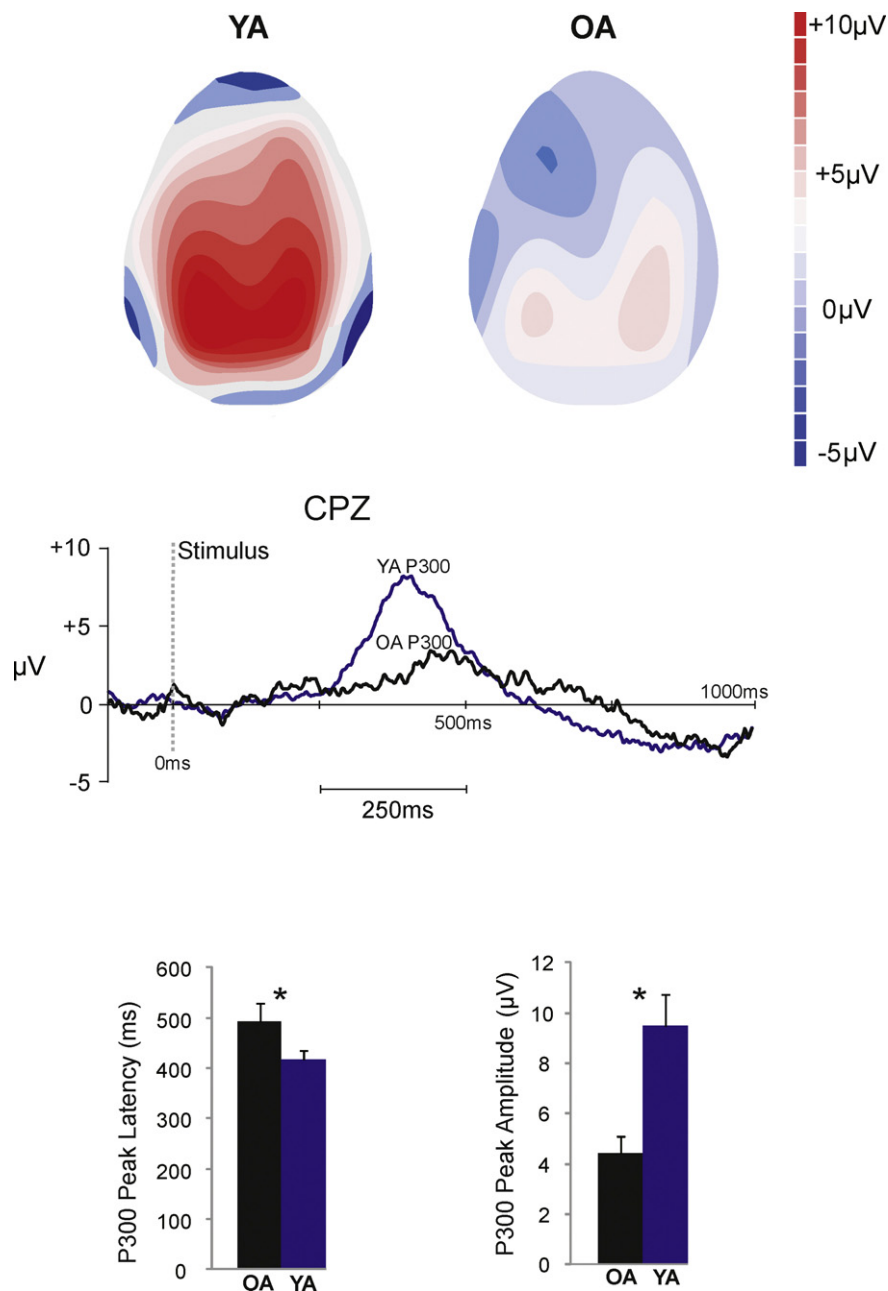


Fig. 6. Above: Scalp topography for group average data at the P300 peak for attended targets (younger adults left top corner, older adults right top corner). Below: Group average waveforms displaying the P300 in response to attended targets in both age groups. Bar graphs depict group data for average peak amplitude and latencies. All values are in microvolts. Asterisk (*) indicates significant difference ($p < 0.05$).

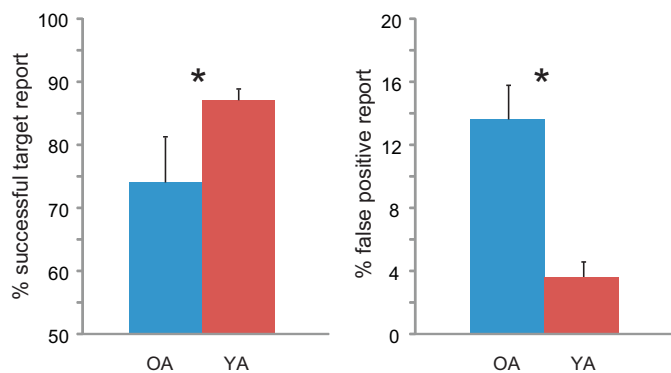


Fig. 7. Percentage of index finger targets correctly reported whilst attending to the index finger (left) and percentage of false positives (right). Each bar represents the group average data for each age group. Asterisk (*) indicates a significant difference ($p < 0.05$).

($F_{1,19} = 1.396$, $p = 0.252$) or attention ($F_{1,19} = 0.656$, $p = 0.428$) at CP3 for the P100. For the LLP component, there was no interaction at the FC4 electrode ($F_{1,18} = 3.188$, $p = 0.091$) and no main effects for age ($F_{1,18} = 2.118$, $p = 0.163$) or attention ($F_{1,18} = 0.305$, $p = 0.588$). Follow-up comparisons showed delayed peak latencies for attended stimuli relative to unattended stimuli in the YA group for the C4 electrode (P100: $t_{19} = 4.26$, $p = 0.002$; LLP: $t_{21} = 4.24$, $p = 0.004$) and CP4 electrode (P100: $t_{19} = 6.41$, $p < 0.001$). From visual inspection of the waveforms it is apparent that the delay is a consequence of the significantly greater peak amplitudes for attended versus unattended stimuli in the YA group versus the OA group. For the N140, no interactions were present at C4 or CP4 (C4: $F_{1,19} = 2.01$, $p = 0.173$; CP4: $F_{1,21} = 1.287$, $p = 0.269$). Similarly, no main effects for age (C4: $F_{1,19} = 0.024$, $p = 0.88$; CP4: $F_{1,21} = 1.403$, $p = 0.249$) or attention (C4: $F_{1,19} = 0.599$, $p = 0.449$; CP4: $F_{1,19} = 1.098$, $p = 0.307$) were revealed at N140. However there was an interaction at FC4 for N140 latency ($F_{1,18} = 7.504$, $p = 0.013$) due to a delayed peak latency for unattended stimuli in the OA group ($t_{19} = 3.81$, $p = 0.013$). All latencies are presented in Table 1.

3.2. Age-related changes in P300: target detection

The P300 ERPs generated in response to attended targets are displayed as group averaged waveforms in Fig. 6, showing the comparison of age groups. Between-group comparisons revealed a faster peak onset ($t_{17} = 4.82$, $p = 0.032$) and a larger peak amplitude ($t_{17} = 2.95$, $p = 0.001$) in the YA versus the OA group at CPZ.

3.3. Behavioural performance

t-Test comparison revealed a lower success rate (i.e. accurate target detection) for OA (73.9%) versus YA (87.1%) subjects ($t_{22} = 2.87$, $p = 0.042$). Comparison of false positive rates (reporting distractor targets on the unattended digit) revealed a significantly greater number of false positives for the OA (13.6%) versus YA (3.6%) age group ($t_{22} = 5.96$, $p = 0.0002$). Behavioural performance data is presented in bar graphs, Fig. 7.

4. Discussion

Neurologically intact, older adults showed diminished attention-based modulation of somatosensory ERPs during a tactile discrimination task when compared with younger adults. Several ERP components were modulated based upon attention in both age groups however the degree of this modulation differed. Most strikingly, non-attended stimuli resulted in greater P100 amplitudes for older adults compared with younger adults. Present

data revealed a loss of attention-based modulation of somatosensory ERPs as a function of age and the impact at P100 would indicate this loss was evident at early cortical stages of somatosensory processing. As expected from previous research, the P300 in response to attended tactile targets was both slower and reduced in amplitude for the older subjects. Moreover, we noted impaired behavioural performance in the older versus younger adults. Combined, our results show impaired sensory-gating, diminished neural markers of target recognition, and performance deficits in a tactile discrimination task amid distraction for older adults. Such a loss in the ability to filter out irrelevant somatosensory input with age is consistent with findings across visual (Gazzaley et al., 2008) and auditory modalities (Chao & Knight, 1997). These results add to a growing understanding of mechanisms underlying cognitive decline with normal aging.

4.1. Changes in attention-based modulation of tactile ERPs with age

As hypothesised, attention-based modulation of somatosensory signals during a tactile discrimination task was diminished in older adults compared with young adults. Moreover, this altered modulation pattern was due to reduced suppression of non-attended (i.e. task-irrelevant) stimuli, at least for the P100. The deficient capacity for older adults to suppress irrelevant sensory information during attention-demanding tasks is consistent with previous findings in visual-based (Gazzaley et al., 2008) and auditory-based (Chao & Knight, 1997) attention tasks. In fact, the selective deficit in suppressing irrelevant information without influencing the enhancement of attended information has also been noted (Gazzaley et al., 2008). Overall, our current results support the idea that activation or enhancement effects of attention are preserved in older adults whilst inhibition is selectively impaired (Dempster, 1992; Hasher & Zacks, 1988; Reuter-Lorenz & Park, 2010).

The present tactile discrimination paradigm did not drive modulation onto the earliest measured components (P50 and N70) in either age group. Consequently our study was unable to expose any possible age-related changes in attention-based modulation at the most primary cortical processing stage. It is possible that the present sample size was inadequate to detect differences between attended and unattended waveforms, particularly given the relatively small amplitude of the P50 and N70. However, an absence of modulation at these very early stages is common throughout the tactile ERP literature. In fact, Schubert et al. (2008) acknowledged that the P50 modulation displayed in their study was rare and they argued that it was the pronounced difficulty of their task which uniquely drove modulation onto this early component (Schubert et al., 2008). It was noteworthy that the onset of these components were delayed in the older adults, which likely reflects a general slowing of early sensory processing with age regardless of attention. Such a delay in early ERP components has been found across various sensory modalities (Salthouse, 1996) and this remains true even when adjusting for sensory threshold differences with age (Dustman et al., 1993). Conversely, the loss of modulation at the P100, a component likely generated by bilateral secondary somatosensory cortices (Hamalainen et al., 1990), indicates impaired top-down modulation of early somatosensory processing in the older adults. Such results match with an age-related deficit in suppressing irrelevant visual stimuli approximately 100 ms into the visual processing stream during a visual attention task (Gazzaley et al., 2008). Likewise, auditory-evoked potentials arising from distracter tones, notably those components reflecting passage of the auditory signal into the primary auditory cortex, have been shown to be larger in older subjects (Chao & Knight, 1997). As stated previously, the current view holds that there is an age-related loss of top-down modulation (via frontal

regions as discussed later) over suppressing the irrelevant inputs and this effect is often apparent early in the cortical processing chain.

Altered task-related modulation was also noted for the N140 in older adults and once again the difference between attended and unattended stimuli was more pronounced in younger adults. However this time it was the unattended stimuli that resulted in larger N140 amplitudes. Unlike the P100 which reflects unimodal processing, the N140 represents a much more abstract level of sensory processing. Consequently, making direct links to how attention influences this component is somewhat tenuous. Nevertheless, our result may relate to findings by Adler et al. (2009) where the N140 was greatest for distracter tactile stimuli presented to the unattended finger but only when subjects were engaged in a relatively easy discrimination task using the attended finger (Adler et al., 2009). The authors suggested that under low cognitive load the distracter stimuli pulled attention toward that body location and they proposed that increased task difficulty nullified this effect. Thus, it is possible that present age-related differences in N140 modulation may reflect a cognitive load disparity for the two age groups when performing the present task. This idea would certainly be consistent with the lower performance noted for older adults in the current study.

Although the capacity for sensory filtering based on attention was clearly lost at the P100 and N140 in older adults, this reduced sensory gating effect was not found for the LLP. Several broadly distributed neural generators produce the LLP (Hamalainen et al., 1990; Michie, Bearpark, Crawford, & Glue, 1987) therefore it is possible that this component may be more resistant to deterioration. An alternative (or supplemental) account for this result is that the later processing stages could reflect a strategic shift by older adults towards increased cognitive effort via frontal networks (Velanova, Lustig, Jacoby, & Buckner, 2007). A similar observation was made by Gazzaley et al. (2008) who demonstrated that the loss of attention-related sensory gating using VEPs was largely limited to very early visual cortical processing stages and that later, more endogenously influenced stages were unaffected by age-related decline (Gazzaley et al., 2008). Therefore, multiple neural generators engaged farther along the processing stream possibly allow later ERP components to be more robust in resisting degradation with age.

4.2. Neural mechanisms underlying diminished attention-based modulation

Overall our findings support the proposition that at least one of the major changes in brain function with normal aging is a general loss of inhibitory control and that this effect is evident at early stages of sensory processing. The fact that older adults exhibited a much higher rate of reporting false positives would suggest that a consequence of failing to inhibit irrelevant stimuli is greater susceptibility to distraction. Such susceptibility is reminiscent of a prefrontal deficit in gating out distracters. As previously noted several lines of evidence indicate that prefrontal regions are extremely important in regulating this inhibitory control (Knight et al., 1999) and that a disproportionate deterioration of this brain region with age underlies the loss of attention-based modulation (Jernigan et al., 2001; Raz et al., 1997; Resnick et al., 2003). Therefore, it seems likely that the age-related decline with inhibitory control and performance from our study reflects diminished prefrontal function.

Whilst the present study did not offer a direct means of measuring prefrontal activity there is some indication that our results relate to prefrontal deficits. Most notably is the fact that in a previous study we explored attention-based modulation of tactile ERPs using the exact same paradigm but instead focussed our comparison on young adult subjects following TMS-induced inhibition of

the DLPFC (Bolton & Staines, 2011). For that study we applied continuous theta burst stimulation over the right DLPFC to temporarily suppress focal cortical excitability during the same tactile discrimination task. Research with both monkeys (Shindy, Posley, & Fuster, 1994) and humans (Stoekel et al., 2003) has indicated an important role for the DLPFC during sequential somatosensory discrimination tasks which has been attributed to maintaining somatosensory target information in memory whilst monitoring the ongoing stream of incoming stimuli. Our previous results revealed that following suppression of DLPFC, subjects demonstrated a loss of the normal attention-based modulation at the P100, similar to present findings with older adults. Notably, the loss of modulation was due to a loss of suppression of the non-attended (distracter) stimuli. Thus the combination of cTBS data with present results, both using the same tactile discrimination paradigm, supports the notion that impaired prefrontal regulation is underlying at least some of the changes in the older adult group.

An important point to consider is that older adults were less accurate at detecting targets suggesting they found the task more difficult. Given the importance of PFC in coping with greater cognitive demand along with a prefrontal role in suppressing irrelevant information it is possible that impaired sensory gating in our study may reflect a greater cognitive load. Previous work has shown that when young adults were taxed with a higher cognitive workload their ability to suppress distracter information resembled inhibitory deficits noted in older subjects (Zanto & Gazzaley, 2009). Thus at least part of our observed loss of attention-based modulation may simply reflect heightened work demands on prefrontal areas. Alternatively, this overload may be a consequence of impaired suppression of irrelevant information which leads to a higher downstream workload for cognitive resources. Overall our study cannot dissociate between these possibilities but it should be recognised that at least some of the impaired suppression may be due to the fact that the PFC is already preoccupied with a harder task, possibly embellishing any age-related deterioration.

4.3. Neural correlates of target recognition and behavioural performance

As expected from previous ERP studies employing oddball target detection tasks, older adults produced slower P300 components of lower amplitude in response to targets when compared with younger adults. The P300 offers a neural marker of cognitive processing and is elicited during tasks demanding sustained attention to target stimuli, and this component is particularly pronounced when infrequent targets are embedded within a background of more frequently occurring standard and distracter stimuli (Linden, 2005; Polich, 2007). This component can be driven by various sensory modalities and has been linked to performance on several neuropsychological tests (Walhovd & Fjell, 2003). Given the large number of neural generators that contribute to this response (Linden, 2005; Polich, 2007) it is unclear precisely why the P300 is diminished with age beyond a general decline in brain function. It likely stems from a complex interaction of impaired connectivity between distributed neural regions which coalesce to serve this larger goal of stimulus comparison and target recognition. Of note, a decrease in P300 peak amplitude has been related to an increase in working memory load during a visual attention task (Morgan, Klein, Boehm, Shapiro, & Linden, 2008). Interestingly, Yamaguchi and Knight (1991) demonstrated slower and reduced amplitude P300 responses for somatosensory targets in an attention-based task despite similar performance between age groups (Yamaguchi & Knight, 1991). However, their use of a relatively easy task (i.e. target detection accuracy close to 100% for both groups) may have limited the ability to detect behavioural differences. Thus the P300 can provide a glimpse of more subtle underlying deficits even when

overt performance is unaffected. If the P300 does offer some gauge of processing capacity, our present performance drop in the older adults may reflect a behavioural consequence of diminished capacity.

4.4. Summary and conclusions

In accord with a number of recent studies, our findings indicate a collection of age-related changes that in combination likely contribute to impaired cognitive performance. Delays in both early signal transmission through somatosensory areas as well as delays in higher order information processing indices like the P300 support the notion that processing speed is compromised with age. Furthermore, our findings clearly reveal a loss of attention-based modulation of tactile information at an early stage of cortical processing in older adults compared with young adults. Importantly, the fact that this lost modulation was due to a deficit in suppression of the irrelevant information indicates impaired inhibitory control. Combined with previous work in our lab where transient inhibition of DLPFC resulted in a similar pattern of attenuated modulation this deficit in inhibitory control is likely a consequence of declining prefrontal function with age. These findings are highly consistent with age-related deficits noted for attention and memory-demanding tasks using visual and auditory modalities whereby a decline in executive control via prefrontal centres results in a deficit in filtering out irrelevant information. Thus our results on sustained spatial attention to tactile oddball targets, particularly in the midst of distraction, builds upon an emerging framework of mechanisms underlying age-related cognitive decline.

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