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Prefrontal hyperactivity in older people during motor planning

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ARTICLE INFO

Article history:

Accepted 17 June 2012

Available online 23 June 2012

Keywords:

Middle-aged

Elderly

MRCP

Go/No-Go

Frontal hyperactivation

Executive function

ABSTRACT

The aim of this study was to assess the influence of age-related changes in cortical activity related to the motor preparation involved in simple- and discriminative-reaction tasks. To distinguish between age effects on motor planning and stimulus processing, both movement- and stimulus-locked event related potentials (ERPs) were investigated in 14 younger, 14 middle-aged, and 14 older adults (mean ages 24.4, 49, and 70 years, respectively). The novel results of the present study are the prefrontal over-recruitment observed in older adults in movement-related cortical potentials (MRCPs) and the differential pattern of aging effects observed at behavioral and at electrophysiological level between middle-aged and older adults. Overall, the following results were observed: (i) behavioral results confirmed the well-known slowing of responses in aging people, which were associated with optimal accuracy; (ii) the age-related differences in cortical activity underlying the generation of voluntary movements in response to external stimuli were more pronounced for the motor planning than the stimulus processing stage; (iii) the source and the time-course analysis of the over-recruitment in the older adults indicated tonic involvement of prefrontal areas regardless of task complexity; and (iv) middle-aged adults showed a 'young adult-like' behavioral speed, but an 'older adult-like' overactivation of prefrontal areas. In summary, to reach the same accuracy, older subjects prepared the action with greater anticipation and higher cost, as indexed by the earlier latency onset and larger prefrontal cortical activation.

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Introduction

Aging is associated with cognitive decline that disproportionately affects executive functions and can, in part, be explained by functional alterations and changes in neuronal morphology (see [Burke and Barnes, 2006](#) for a review). Given these changes, particularly at the level of the prefrontal cortex, it is not surprising that performance on tasks requiring information processing declines with age, causing selective behavioral impairments. Indeed, behavioral measures show a generalized delay in reaction time (RT), a slowing of movements and a loss of fine motor skills (see [Seidler et al., 2010](#) for a review); these changes, in turn, reflect age-related modifications of the underlying brain systems. Compensatory processes such as neurogenesis, recruitment of frontal areas, distribution of information processing among different areas, and bilateralization can be observed in the elderly (see [Park and Reuter-Lorenz, 2009](#) for a review).

To evaluate how behavioral slowing is generated at the brain level, neuroimaging (particularly fMRI) studies have investigated the age-related changes in functional activation during sensorimotor and cognitive performance and have found greater involvement of the prefrontal

cortex (PFC) and dorsolateral frontal cortex (DLFC) in older compared with younger adults. Further, in contrast to young adults, older people show activation of the PFC and DLFC not only in complex tasks but also in simple tasks (e.g., [Di Girolamo et al., 2001](#); [Heuninckx et al., 2008](#)). This additional activation has been interpreted as a "compensatory mechanism" that older people apply to support successful performance despite age-related declines (see [Reuter-Lorenz, 2002](#) for a review). Older people may require more computational resources to achieve accuracy levels similar to younger people and may also use additional or alternative brain areas ([Heuninckx et al., 2008](#)). These adaptive mechanisms can be considered to be in line with brain plasticity and continual brain reorganization ([Ward, 2006](#)), although these mechanisms can also be considered the expression of greater motivation and effort during the task preparation ([Falkenstein et al., 2006](#)). Alternatively, the age-related overactivation could reflect a decreased specialization or a non-selective recruitment of neural systems (i.e., dedifferentiation) that results in less efficient performance rather than compensation or irrelevance to performance (for reviews, see [Reuter-Lorenz, 2002](#); [Heuninckx et al., 2008](#); [Seidler et al., 2010](#)).

Given the low temporal resolution of neuroimaging techniques, event-related potentials (ERPs) are more suitable for investigating the timing of the neural activity underpinning motor and cognitive slowing in the elderly because ERPs allow for distinctions between the age-related changes that occur at different processing stages (i.e., perception, response selection and response generation; [Kolev et al., 2006](#)). The bulk

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of the ERP literature on aging generally shows that the slowing associated with aging might be due to delayed perceptual and cognitive processes involved in stimulus identification and response selection in parietal and frontal brain areas (Anderer et al., 1996; Iragui et al., 1993; Labyt et al., 2004; Vallesi et al., 2009; Vallesi, 2011; Wild-Wall et al., 2007; see also Rossini et al., 2007 for a review). In contrast to the aforementioned studies that focus on brain responses to stimuli (stimulus-locked ERPs), little information is available on the contribution of motor programming (movement-locked ERPs) to age-related behavioral slowing. The few and not very recent ERP studies comparing the cortical activity involved in motor planning by means of movement-related cortical potentials (MRCPs) in young and elderly subjects yielded inconsistent results. Indeed, MRCPs preceding voluntary movements in the elderly, as compared to the MRCPs of younger individuals, have been reported to be smaller in amplitude (Barrett et al., 1986), longer in latency (Ishizuka et al., 1996), or not different (Golob et al., 2005; Singh et al., 1990). More recent findings showed that the age-related RT slowing in sensorimotor tasks might originate at the motor response generation stage (about 400 ms before the response) and be attributable to a putative reduction in interhemispheric inhibition between the motor cortices via the corpus callosum (Kolev et al., 2006; Naccarato et al., 2006). Transcranial magnetic stimulation (TMS) studies showed that older adults display less excitability of intracortical inhibitory circuits than young adults (Peinemann et al., 2001) and a reduction of motor evoked potential (MEP) amplitude (Pitcher et al., 2003) that may originate from central or peripheral neural deficits (see Rossini et al., 2007 for a review). Further, some electrophysiological studies examining the lateralized readiness potential (LRP) have indicated that aging people exhibit slower motor responses than younger adults because of a functional dysregulation of executive control mechanisms involved in motor response generation in the contralateral motor cortex, and this deficit becomes progressively more evident with greater task complexity (Falkenstein et al., 2006; Yordanova et al., 2004). The latter effect is known as “the complexity effect”, which indicates that slowing is not constant across tasks but increases with task complexity (see Salthouse, 2000 for a review). Other studies have shown an increase of LRP amplitudes in older, compared to younger, adults despite a lack of difference between groups in the onset of the LRPs (Roggeveen et al., 2007; Sterr and Dean, 2008), supporting the idea that greater amplitudes might reflect more inhibitory failures.

Thus far, there are no electrophysiological correlates of the age-related increases in prefrontal activity found in fMRI studies (Davis et al., 2008; Di Girolamo et al., 2001; Heuninckx et al., 2008; Park and Reuter-Lorenz, 2009; Vallesi et al., 2010). This failure can be explained by the type of tasks used in electrophysiological investigations, the absence of recording electrodes at prefrontal locations (or neglect of the data recorded at these sites) and the time window of interest.

In the present study, to assess age-related changes in cortical activity, we used a simple and a discriminative RT task (Go/No-Go). The discriminative RT task involves more complex stimulus–response mapping, decision making, response execution or inhibition, and ERPs associated with the discriminative task clearly show the involvement of the frontal lobes (Di Russo et al., 2006). The questions addressed were twofold. First, are there age effects on the activity of frontal areas that are related to stimulus processing and/or motor preparation? According to the aforementioned fMRI evidence, we hypothesized that the older brain activates more resources than the younger brain to fulfill task requirements. The novelty of the present study is that, because of the high temporal resolution of the ERP technique and the joint investigation of both movement- and stimulus-locked ERPs, we could distinguish the relative contribution of motor preparation and stimulus processing to the pattern of age-related changes. Second, are age effects modulated by task complexity? According to the “complexity effect”, the differences between younger and older subjects in behavioral performance (Salthouse, 2000) and its underlying neural mechanisms (Falkenstein et al., 2006; Yordanova et al., 2004) should be maximized by the more

complex task. To better understand the aging trend, we did not limit the present investigation to the comparison of younger vs. older adults but considered three age classes across the adult lifespan: the twenties, the fifties and the seventies.

Material and methods

Participants

A total of 42 participants volunteered. They were equally distributed across the following three adult age classes: younger ($n=14$, five females, mean age 23.4 years, $SD=3.2$), middle-aged ($n=14$, three females, mean age 49.0 years, $SD=2.2$), and older adults ($n=14$, ten females, mean age 70.0 years, $SD=7.0$). All participants were healthy and without a history of neurological, psychiatric, or chronic somatic problems. The participants were taking no medication during the experimental sessions and had normal or corrected-to-normal vision. All participants were fully right-handed (Edinburgh handedness inventory; Oldfield, 1971). The older groups were recruited among friends of the authors and were employed in a wide range of professional activities (e.g., lawyer, medical doctor, technician, businessman, engineer). The younger group was recruited from the local (Roman) student population. Education levels were similar in the two older groups (years of study: 16.2 ± 2.1 years for the middle-aged group and 16.0 ± 2.9 years for the older group), and slightly lower for the young group (14.9 ± 1.6 years). Consent was obtained from all participants according to the Declaration of Helsinki after approval by the local ethical committee.

For the analysis of movement-locked ERPs, the data of all 42 participants were used. Because of the high number of artifacts in the EEG for stimulus-locked ERPs, the data from 6 participants were discarded, and a total of 36 participants were divided into the three age groups: younger ($n=12$, four females, mean age 24 years, $SD=2.6$), middle-aged ($n=12$, three females, mean age 49 years, $SD=2.4$), and older adults ($n=12$, eight females, mean age 70 years, $SD=7.2$).

Materials and task

Participants were tested individually in a sound-attenuated, dimly lit room after a 64-channel EEG cap was mounted on their scalp. Participants were seated comfortably in an armchair with their left arm relaxed and their moving (i.e., right) arm positioned palm down on a push button board so that the fingers could move freely. Visual stimuli were presented through a computer display at a distance of 114 cm. The fixation point was a yellow circle ($0.15 \times 0.15^\circ$ of visual angle) in the center of the computer monitor. Squared configurations made by vertical and horizontal bars subtending $4 \times 4^\circ$ were presented for 260 ms on a dark gray background (Fig. 1). The four configurations were displayed randomly with equal probability ($p=0.25$); Stimulus-onset asynchrony varied from 1000 to 2000 ms to avoid time prediction effects on the RTs.

In separate runs, the participants performed two tasks: a simple response task (SRT) and a discriminative response task (DRT). The order of the tasks was counterbalanced across participants. In the SRT, the participants had to press a button with their right hand as quickly as possible when any of the four configurations appeared on the screen (Go stimuli; $p=1$). In the DRT, two configurations were defined as targets, and two configurations were defined as non-targets. The participants had to press a button with their right hand when a target appeared on the screen (Go stimuli; $p=0.5$) and withhold the response when a non-target appeared (No-Go stimuli; $p=0.5$). The order of presentation was randomized within blocks. The duration of each run was 2 min with a pause interleaved (total duration of about 30 min). Five runs of SRT and ten runs of DRT allowed us to obtain 500 trials for each task.

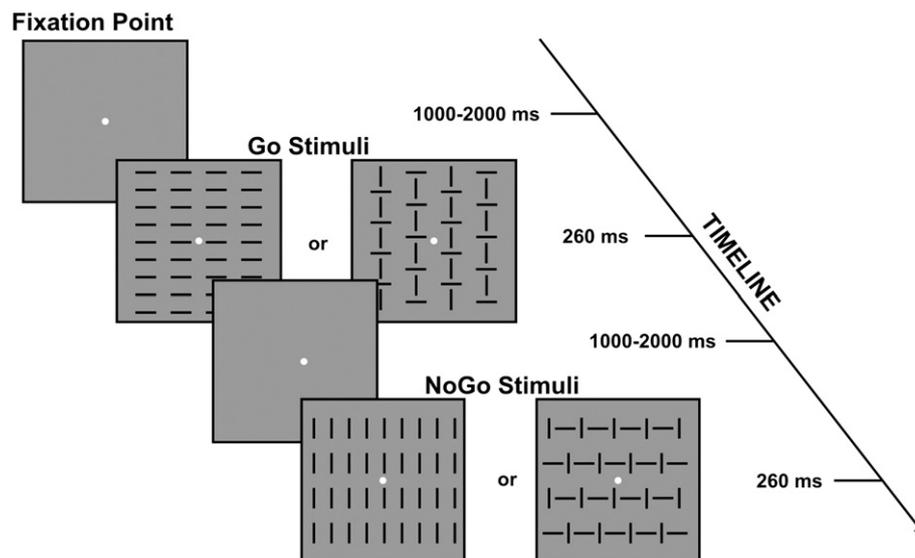


Fig. 1. Schematic illustration of the sequence of stimuli in the Go/No-Go paradigm employed in the present experiment.

Analysis of behavioral data

Median RTs for correct trials were calculated and submitted to a 3×2 mixed analysis of variance (ANOVA) design with Age (younger vs. middle-aged vs. older) as a between-subjects factor and Task (SRT vs. DRT) as a within-subjects factor. Median RTs were used because of the disproportional contribution of outliers, which are more frequent in older than younger adults, on mean RTs. Moreover, RT distributions are usually positively skewed, and the median is the appropriate measure under such conditions as long as RT differences, not absolute RTs, are relevant. To evaluate the stability of individual performances, the intra-individual RT variability was obtained using the intra-individual coefficient of variation (ICV) [ICV = standard deviation of RT/mean of RT] calculated for each subject within each task. Accuracy was measured by the percentage of omissions (i.e., missed response), anticipations (i.e., responses shorter than 150 ms or longer than 1000 ms, respectively), and false alarms (i.e., responses to No-Go stimuli in DRT). RTs, ICVs, omissions, and anticipations were submitted to a repeated-measures 3×2 ANOVA design with Age (younger vs. middle-aged vs. older) as a between-subjects factor and Task (SRT vs. DRT) as a within-subjects factor. False alarms were submitted to a one-way ANOVA with Age as a between-subjects factor. Post-hoc comparisons were conducted using the Tukey's honest significant difference (HSD) test. The overall alpha level was fixed at 0.05 after the Geisser–Greenhouse correction.

Electrophysiological recording and ERP computation

EEGs were recorded using the BrainVision™ system (BrainProducts GmbH, Munich, Germany) using 64 sensors mounted according to the 10–10 International System that were initially referenced to the left mastoid. EEGs were digitized at 250 Hz, amplified (bandpass of 0.01–80 Hz including a 50 Hz notch filter) and stored for off-line averaging. For more details, see Appendix A (Supplementary Material 1.1).

For stimulus-locked ERPs, epochs starting 100 ms prior to stimulus onset and lasting 1100 ms were averaged. To further reduce high- and low-frequency noise, the group-averaged ERPs were band-pass filtered (0.1–30 Hz) and sorted into two categories: 1) ERPs for the go stimuli in the SRT and 2) ERPs for the go stimuli in the DRT. The first trial of each block and trials with RTs outside 150–1000 ms were discarded from further analysis. Peak amplitudes (measured with respect to the 100 ms pre-stimulus baseline) and latencies of the major ERP components were calculated for each subject in the following standard time

windows: P1: 80–150 ms; N1: 130–200 ms; P2: 180–300 ms; and P3: 250–700 ms. The N2 (180–300 ms) component was not considered because it was not evident in the studied waveforms. This component is usually clear in no-go conditions that require the participant to refrain from responding to the appearance of a non-target (Smith et al., 2010). The identification of components was also guided by their polarity and topography as previously described (Di Russo and Spinelli, 2010; Di Russo et al., 2006, 2010). The selection of electrodes used for the analyses was based on the greatest activity for a given component at the group level, and the selection of different scalp sites for the P3 in different RT tasks was also based on the topographic distribution reported in the literature (Polich, 2007) (i.e., the P1 and P2 on PO7 or PO8, the N1 on O1 or O2, the P3 in SRT on Pz and the P3 in the DRT at Cz).

For movement-locked ERPs (MRCPs), conditions (i.e., SRT and DRT) were separately segmented and averaged into non-overlapping epochs of 2000 ms (1500 ms before to 500 ms after the movement onset). The baseline was defined by the mean voltage over the initial 300 ms of the averaged epochs. To further reduce high frequency noise, the group-averaged MRCPs were low-pass filtered (i.e., Butterworth) at 15 Hz. MRCP onset latency was calculated as the first deflection larger than twice the absolute value of the baseline mean. The amplitude of the BP was measured as the mean amplitude between 900 and 600 ms before the movement in the AFz and Cz electrodes. The aforementioned time window was selected for statistical analysis because it is known to reflect BP activity (e.g., Shibasaki and Hallett, 2006) and it is not contaminated by stimulus-related artifacts. The selection of the electrodes was based on the scalp topography, which allowed us to identify the electrodes where the signal was maximal.

Statistical analysis

The data for the P1, N1 and P3 were submitted to separate mixed model ANOVAs with Age (younger vs. middle-aged vs. older) as a between-subjects factor and Task (SRT vs. DRT) as a within-subjects factor. As the P2 was present in the SRT only, it was submitted to a one-way ANOVA with Age as a between-subjects factor. The same ANOVA model was applied to the latency and amplitude of the BP identified in the MRCPs. Analyses performed on the other MRCP components (pre-movement positivity and post-movement activity) are reported in Supplementary material 1.2. Post-hoc comparisons were conducted using Tukey's HSD test. The overall alpha level was fixed at 0.05 after the Geisser–Greenhouse correction.

Furthermore, given the well-known age-related behavioral slowing (indexed by RTs; i.e., Vallesi et al., 2009) and the slowing of the cognitive processing required by the task (indexed by its electrophysiological marker, the P3 peak latency; i.e., Roggeveen et al., 2007), we explored the relationship between those variables and the BP peak latency, which we considered a sensitive index of executive functions. Thus, correlations (Pearson's *r* coefficients) were computed, separately for the SRT and the DRT tasks, between age and RT and between RT and P3 and BP latencies, with particular focus on the older group. The alpha level was fixed at $p < 0.05$ (two-tailed).

Source analysis

Estimation of dipolar sources of the MRCPs was carried out using BESA ver. 5.1.8 (MEGIS Software GmbH, Gräfelfing, Germany), which calculated the cerebral areas involved in cortical motor preparation. The employed spatio-temporal dipole analysis of BESA estimates the location, orientation and time course of multiple equivalent dipolar sources by calculating the scalp distribution, which is obtained for any given source model (forward solution). This distribution was then compared with actual MRCPs. Interactive changes in the location and orientation of dipole sources led to the minimization of residual variance (RV) between the model and the observed spatio-temporal distribution of MRCPs. The goodness of the fit of the dipole model was evaluated by measuring its RV as a percentage of the signal variance, as described by the model, and applying residual orthogonality tests (ROT; e.g., Bocker et al., 1994). The resulting individual time series for the dipole moments (the source waves) can also be submitted to an orthogonality test, which we refer to as a source wave orthogonality test (SOT; Bocker et al., 1994). All t-statistics were evaluated for significance at the 5% level. The positions of the electrodes were digitized and averaged across subjects. The 3-D coordinates for each dipole of the BESA model were determined with respect to the Talairach axes and scaled according to brain size. In these calculations, BESA utilized a realistic approximation of the head (which was based on MRIs of 24 subjects), and the radius was obtained from the group average (86 mm). To limit the number of parameters to be estimated, symmetry constraints were applied for each bilateral dipole pair in the scalp distributions that indicated bilateral foci. The possibility that dipoles would interact was reduced by selecting solutions with relatively low dipole moments with the aid of an “energy” constraint (which was weighed at 20% in the compound cost function as opposed to 80% for the RV). The optimal set of parameters was identified in an iterative manner by searching for a minimum in the compound cost function. Dipoles were fitted sequentially. Latency ranges for fitting were chosen to minimize overlap among successive, topographically distinct components. To minimize cross-talk and interactions between sources, dipoles that accounted for earlier portions of the waveform were left in place as additional dipoles were added.

Results

Behavioral data

Individual data are shown in Fig. 2; group means are shown in Table 1a. Overall, RTs were slower [$F_{(2,39)} = 12.58, p < 0.0001$] in the older adults (379 ms) than in middle-aged (338 ms) and younger (319 ms) adults, whereas no differences were found between the latter two groups. The main effect of Task was also significant [$F_{(1,39)} = 588.53, p < 0.0001$], indicating that RTs in the DRT (463 ms) were slower than those in the SRT (228 ms). The Age by Task interaction was not significant [$F_{(2,39)} > 1$], indicating that the older group was slower than the other two groups independently of the task complexity. The accuracy of the three groups was good and comparable. ICVs were not different between the groups [$F_{(2,39)} = 2.32, ns$] or tasks [$F_{(2,39)} < 1$], but the Age by Task interaction was significant [$F_{(2,39)} = 5.72, p = 0.0066$]. Post-hoc comparisons revealed a significant,

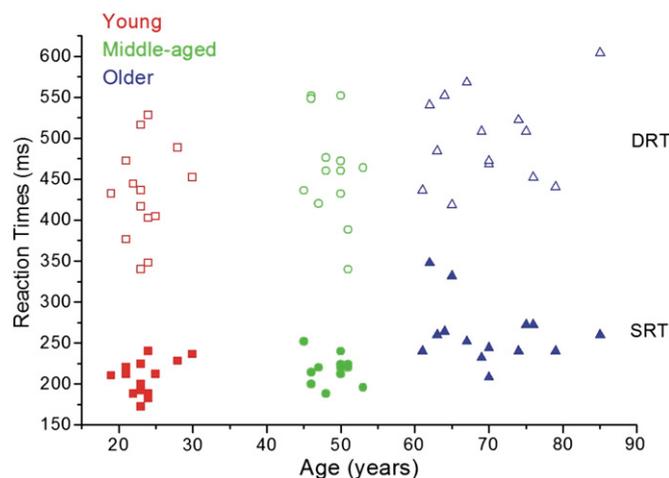


Fig. 2. Scatter plot of reaction times as a function of age. Reaction times from the SRT and the DRT are plotted on the lower (solid dots) and upper (open dots), respectively, part of the plot. The color and the shape of the dots identify each group and condition. The correlations between RTs and age in both the SRT and DRT are clearly visible, as is the lack of a “complexity effect”.

“U” shaped ICV difference between the age groups ($ps < 0.01$) that was limited to the DRT; the younger and older subjects had higher ICVs (0.279 and 0.189, respectively) than the middle-aged subjects (0.152). Accuracy was not significantly different between Ages or Tasks for either omissions [$F_{(2,39)} = 1.25, ns$] or anticipations [$F_{(2,39)} = 1.05, ns$]. The percentage of false alarms showed an incremental trend from younger to older adults, but this effect was not significant [$F_{(2,39)} = 1.875, ns$].

Stimulus-locked ERPs

Fig. 3 illustrates the ERP components at relevant sensors: the top panel refers to the SRT, and the bottom panel refers to the DRT. The earliest component (P1) began at about 70 ms and peaked at about 110 ms on the bilateral parietal-occipital sensors (PO7 and PO8). The N1 peaked at about 160 ms at the bilateral occipital sites (O1 and O2). As Fig. 3 shows, neither the latency [$F_{(2,33)} = 2.91, ns$] nor the amplitude [$F_{(2,33)} < 1$] of the P1 component differed significantly between the groups. Likewise, neither the latency nor the amplitude of the N1 component differed between groups [latency: $F_{(2,33)} < 1$; amplitude: $F_{(2,33)} = 1.83, ns$]. However, strong differences were found for the P1 and the N1 in both latency [P1: $F_{(1,33)} = 8.07, p = 0.076$; N1: $F_{(1,33)} = 8.58, p < 0.0061$] and amplitude [P1: $F_{(1,33)} = 8.38, p = 0.0067$; N1: $F_{(1,33)} = 30.61, p < 0.0001$] as a function of the task complexity. The P1 amplitude was larger and its latency was longer in the SRT than in the DRT (amplitude: 5.26 vs. 4.50 μV ; latency: 125 vs. 118 ms). Conversely, the N1 amplitude was larger and its latency was longer in the DRT than in the SRT (amplitude: -2.98 vs. $-0.71 \mu V$; latency: 188 vs. 170 ms). For both the P1 and N1 components, there was no significant Age by Task interaction for amplitude [$F_{(2,33)} < 1$] or latency [$F_{(2,33)} < 1$].

The P2 component was detectable only in the SRT (see the upper part of Fig. 3) and did not differ between groups in latency [$F_{(2,33)} < 1$]; the amplitude showed a marginally significant linear increase as a function

Table 1
Reaction time and P3 latency across age groups and tasks.

| Age groups | a) Reaction time Mean (SD) [ms] | | b) P3 latency Mean (SD) [ms] | |
|-------------|------------------------------------|------------|---------------------------------|------------|
| | SRT | DRT | SRT | DRT |
| Younger | 207 (21.0) | 432 (56.9) | 305 (48.3) | 479 (53.3) |
| Middle-aged | 217 (17.4) | 459 (61.0) | 354 (42.5) | 559 (82.8) |
| Older | 261 (37.4) | 498 (54.8) | 404 (36.6) | 619 (98.3) |

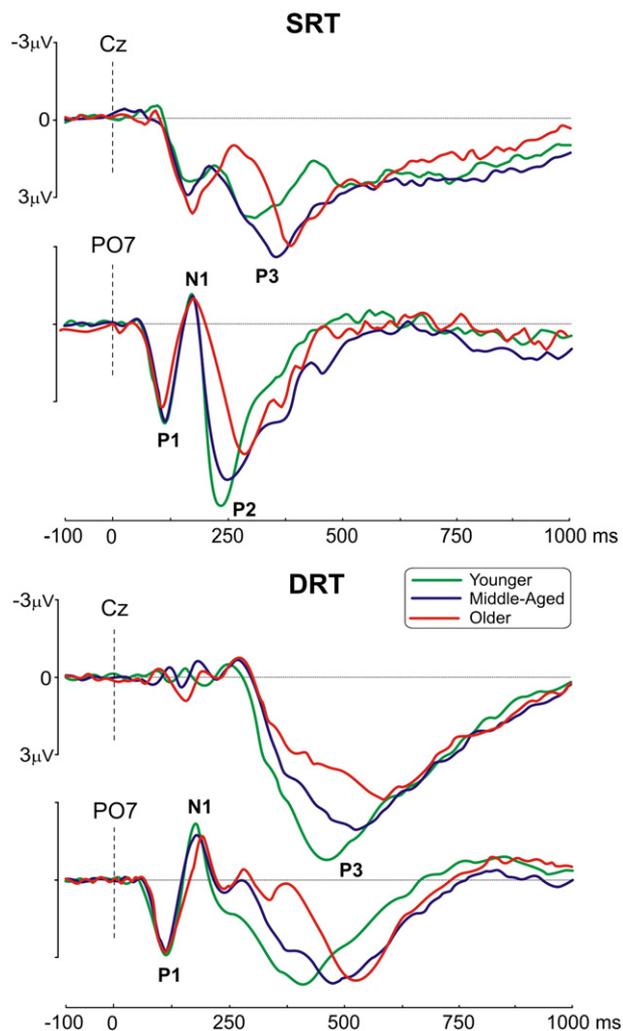


Fig. 3. Grand average of the stimulus-related ERPs for the SRT and the DRT on the top and the bottom panel, respectively. The traces from the three age groups are superimposed. The vertical dashed line indicates the visual stimulus onset. The P1, N1 and P2 components are more evident on lateral parieto-occipital sites. The P3 component is more evident on medial central sites.

of age [$F_{(2,33)} = 3.18, p = 0.0512$]. Fig. 3 also shows the typical P3 component with a central distribution that was reliably elicited in both the SRT and the DRT. Table 1b shows group means of the P3 latency, which, as expected, showed a significant effect of age [$F_{(2,33)} = 18.51, p < 0.0001$]. Post-hoc analysis indicated that all three groups significantly differed from each other, with the longest, intermediate and shortest P3 latencies in older (512 ms), middle-aged (457 ms) and younger (392 ms) subjects, respectively. Moreover, the main effect of task complexity was significant [$F_{(1,33)} = 188.86, p < 0.0001$], indicating that the P3 latency in the DRT (552 ms) was longer than in the SRT (354 ms). However, the Age by Task interaction was not significant [$F_{(2,33)} < 1$]. Regarding P3 amplitude, there was a non-significant decremental trend with increasing age (9.7, 9.3 and 7.8 μV for younger, middle-aged and older subjects, respectively) [$F_{(2,33)} = 1.96, ns$] and a marginally significant effect of task complexity [$F_{(1,33)} = 4.11, p = 0.0506$], with larger P3 amplitudes in the more complex DRT than in the less complex SRT. The Age by Task interaction was not significant [$F_{(2,33)} < 1$].

Movement-related cortical potentials

Waveform description

Fig. 4 shows the grand average MRCP waveforms from the medial prefrontal (AFz; top panel) and central (Cz; bottom panel) sensors

plotted for the three groups. Time zero corresponds to the movement onset (response). The vertical bars on each plot show the timing of the stimulus onset, and their thicknesses represent the standard deviation of the RTs for each group. The light-red bars refer to the SRT condition, and the gray bars refer to the DRT condition. The traces from both experimental conditions are superimposed: SRT (red traces) and DRT (black traces).

In the younger group, the MRCPs were characterized by a gentle pre-movement negative deflection that began at Cz 850 ms and 1040 ms before the response for the SRT and DRT, respectively, and that peaked on the same site 150 ms (SRT) and 350 ms (DRT) before the response. This activity resembled the well-known readiness potential or *Bereitschaftspotential* (BP) component that is typically observed in MRCP studies (see Shibasaki and Hallett, 2006 for a review). The activity at Cz also showed two positive peaks, one that was concomitant with the response and another about 150 ms afterwards. At AFz, no activity was detected until -350 ms during the SRT, and activity began 600 ms earlier in the DRT. This negative wave peaked at -100 and -380 ms for the SRT and DRT, respectively, and displayed a positive peak about 50 ms prior to the response, a negative peak 100 ms later and an additional positive peak (that overlapped to Cz) about 150 ms after the response. In the middle-aged and older groups, the BP over the central sensors resembled that of younger adults, whereas the prefrontal activity, especially in the SRT, began much earlier and was larger than that of their younger counterparts. Concomitant with and after the response, the aforementioned positive and negative components were also detected. All these activities, which were prominent at the medial prefrontal and central sensors, were strongly affected by both age and task complexity. Because the spatio-temporal scalp topography of these waveforms peaked at medial prefrontal and central sites, we selected the AFz and Cz electrodes for statistical analyses.

Effects of age and task complexity

Only the results concerning the BP are reported. The analyses of the waveform concomitant with and following the movement onset could be biased by the possible overlap of stimulus-locked and response-locked ERPs. However, we have analyzed these data, and the results are presented in Appendix A (Supplementary Results 2.1.1. and 2.1.2).

ANOVAs performed on the onset latency of the BP showed significant effects of Age effect at both the AFz and Cz sites [$F_{(2,39)} = 35.84$ and $F_{(2,39)} = 13.12$, respectively; $ps < 0.0001$]. Post-hoc comparisons showed that the activity onset was earlier in older (AFz = -1240 ms, Cz = -1100 ms; $p < 0.0001$) and middle-aged (AFz = -1125 ms, Cz = -1040 ms; $p < 0.01$) subjects than in younger subjects (AFz = -650 ms, Cz = -960 ms). Further, the Task effect was significant at both the AFz and Cz sites [$F_{(2,39)} = 5.09, p = 0.0109$], and the activity began earlier in the DRT (AFz = -1115 ms, Cz = -1100 ms) than in the SRT (AFz = -910 ms, Cz = -1000 ms). Significant Age \times Task interactions were found at AFz [$F_{(2,39)} = 4.84, p = 0.0132$] and Cz [$F_{(2,39)} = 4.00, p = 0.0263$]. Post-hoc comparisons showed a Task effect over the prefrontal site in younger and middle-aged ($ps < 0.0001$) subjects but not in older adults, indicating that the BP started later in the SRT for the younger groups, whereas it maintained its temporal profile in the older group. Further, younger and middle-aged subjects had different onsets of the BP in the DRT only, and the onsets of the middle-age subjects were closer to those of the older group. For Cz, post-hoc comparisons showed an effect of Task in all groups ($ps < 0.0001$). Furthermore, the groups showed similar BP onset in the DRT, whereas the younger and middle-aged subjects differed ($ps < 0.0001$) from the older subjects in BP onset during the SRT only.

ANOVAs on the BP amplitude at AFz showed a significant main effect of Age [$F_{(2,39)} = 10.36, p = 0.0002$] and larger mean amplitudes for older ($-2.42 \mu\text{V}$) than younger ($-0.47 \mu\text{V}$; $p = 0.0001$) and middle-aged adults ($-0.95 \mu\text{V}$; $p = 0.0004$); the latter two groups did not differ

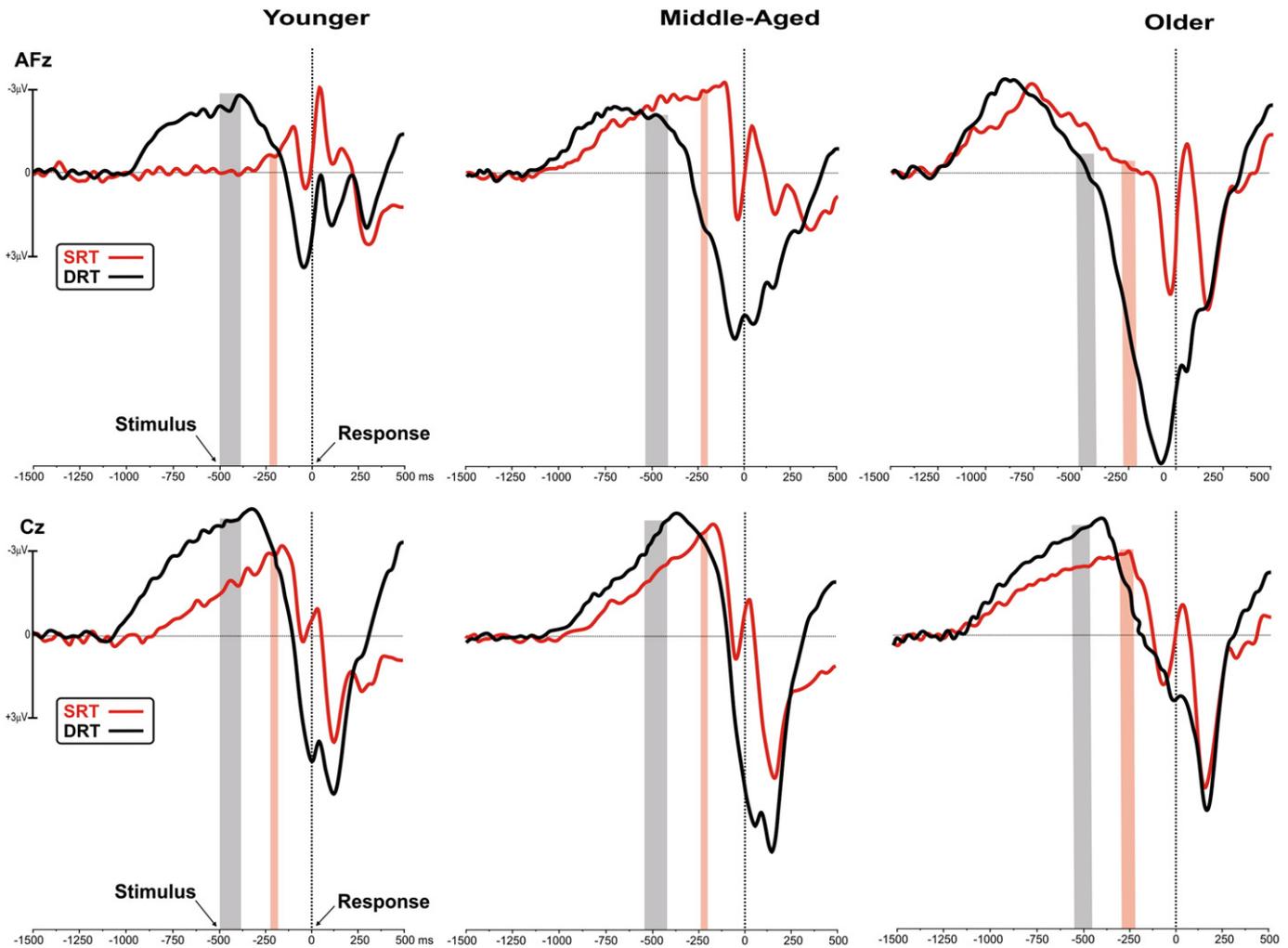


Fig. 4. Grand average of the motor-related ERPs from sensors over the medial prefrontal (AFz) and sensorimotor (Cz) cortices are shown on the upper and lower parts of the figure, respectively. The traces for the two tasks are superimposed for each group according to the task. The dashed line indicates the response time, as indicated by key press. The vertical bars on each plot show the timing of the stimulus presentation, and their thickness refers to the standard deviation of the RTs measured in each group. The light-red bars refer to the SRT condition, and the gray bars refer to the DRT condition. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

from each other. There was also a strong effect of Task [$F_{(1,39)} = 20.88$, $p < 0.0001$] with larger amplitudes in the DRT ($-1.93 \mu\text{V}$) than in the SRT ($-0.62 \mu\text{V}$). However, no significant interaction was found [$F_{(2,39)} < 1$]. At Cz, we found a similar pattern of main effects for Age [$F_{(2,39)} = 3.52$, $p < 0.0393$] and Task [$F_{(1,39)} = 35.28$, $p < 0.0001$] with larger mean amplitudes ($ps < 0.001$) in older ($-2.37 \mu\text{V}$) than younger ($-1.78 \mu\text{V}$) and middle-aged ($-1.20 \mu\text{V}$) subjects, and larger amplitudes in the DRT ($-2.46 \mu\text{V}$) than in the SRT ($-1.10 \mu\text{V}$). Furthermore, a significant interaction was found [$F_{(2,39)} = 6.41$, $p = 0.0039$]. Post-hoc comparisons showed a significant ($p = 0.0031$) difference between tasks only in the younger group. Table 2 summarizes the group mean amplitudes.

An analysis of the BP peak latency at AFz showed a main effect of Age [$F_{(2,39)} = 147.39$, $p < 0.0001$] and longer latencies in younger (-263 ms) than middle-aged (-283 ms) and older adults (-730 ms , $ps < 0.0001$). Moreover, there was a main effect of Task [$F_{(1,39)} = 142.60$, $p < 0.0001$], and the latency in the SRT (-308 ms) was longer than that in the DRT (-542 ms). The Age \times Task interaction was also significant [$F_{(2,39)} = 8.55$, $p = 0.0008$]. Post-hoc comparisons showed differences between tasks in all age classes. Furthermore, younger and middle-aged subjects differed from the older group in both the SRT and the DRT ($ps < 0.001$). An analysis of the BP peak latency at Cz showed main effects of Age [$F_{(2,39)} = 24.29$, $p < 0.0001$] and Task

[$F_{(1,39)} = 21.57$, $p < 0.0001$] and shorter latencies in older subjects (-536 ms) than both middle-aged (-271 ms) and younger (-245 ms ; $p < 0.0001$) subjects. Latencies were also shorter in the SRT (-277 ms) than in the DRT (-425 ms).

Scalp topography

To visualize the voltage topography of the ERP components, spline-interpolated 3-D maps were constructed using BESA 2000 software (MEGIS Software GmbH, Gräfelfing, Germany). The topographic distribution of the MRCPs in the three age groups is shown in Fig. 5a for the SRT and Fig. 5b for the DRT. As shown in the first line of Fig. 5a, which refers to the time window from -900 to -600 , the scalp distribution of the early negative activity in the older group was focused on the prefrontal cortex (PFC) of the right hemisphere, whereas the topography of the middle-aged group was more posterior. In the younger group, no activity was observed in this time window. Later, the scalp topography of the BP peak ($-150/-220 \text{ ms}$; second line) was widely distributed in medial central-parietal areas in all three groups. After the BP, a positive wave in the PFC peaked at $30-60 \text{ ms}$ before the movement (third line). This activity was particularly evident in older participants and smaller in younger participants. Finally, at about $100-170 \text{ ms}$ after the beginning of the movement, a focal positive distribution over the medial anterior regions can be observed (fourth line). This activity was more

Table 2
Group mean amplitude on AFz and Cz.

| Age Groups | AFz amplitude Mean (SD) [μ V] | | Cz amplitude Mean (SD) [μ V] | |
|-------------|---------------------------------------|-------------|--------------------------------------|-------------|
| | SRT | DRT | SRT | DRT |
| Younger | -0.13 (1.2) | -1.17 (2.2) | -0.54 (2.2) | -3.03 (1.1) |
| Middle-aged | -0.47 (1.3) | -1.53 (1.5) | -0.69 (0.8) | -1.71 (1.3) |
| Older | -1.74 (1.2) | -3.10 (1.1) | -2.09 (1.1) | -2.66 (1.3) |

posterior in younger and middle-aged (peaking at Cz) participants, and it was more anterior and showed two foci of activity over both medial frontal and prefrontal regions in older participants.

Fig. 5b shows the scalp topography in the DRT. The older participants showed a large negative activity focused on the right medial PFC at the beginning of the averaged epochs (-900/-600 ms; first line). This activity was less pronounced in the middle-aged group and absent in the younger group. Later, the BP scalp topography peaked in medial central-parietal areas in all three groups (between -350 and -400 ms; second line). Right before the movement onset (between -45 and -80 ms; third line), the topography changed polarity and showed a positive activity in medial prefrontal regions; this positive activity was strongest in older groups and more posterior in the younger group. Similar to the SRT, a positive distribution was focused over the central-frontal regions in all groups (100–170 ms, fourth line). At the

same latency, another positive focus of activity was present over the PFC in older participants only.

Source localization

Considering the similar spatio-temporal structure of the MRCPs between age groups and tasks (compare Figs. 5a and b) and the typical low signal to noise ratio of these kinds of potentials, an initial general model was calculated averaging data across all groups and tasks, as shown in Fig. 6a. This general model suggested that the MRCPs are produced by a minimum of three neural structures, namely, the bilateral prefrontal cortex (PFC), the left supplementary motor area (SMA) and the primary motor area (M1). Fig. 6a shows the localization and the orientation of these cortical sources on both a 3-D realistic brain template (top) and on an axial plane sketched below. To explain the prefrontal activity, a first source was fit using a pair of mirror dipoles in the interval between -900 and -600 ms and was localized in the PFC within the medial frontal gyrus in Brodmann area 10 (Talairach coordinates $\pm 17, 48, 6$). To account for the central BP activity, a second source was fit using a single dipole in the interval between -600 and -150 ms and was localized in the medial frontal gyrus within Brodmann area 6 in the left SMA (Talairach coordinates -10, -9, 63). A third source was fit using a single dipole in the interval between -100 and +100 ms and was localized in the pre-central gyrus within Brodmann area 6 in M1 (Talairach coordinates -25, -22, 60). This model accounted for the MRCPs in the interval from -900 to +100 ms, leaving a RV of 3.5%. At residual orthogonality

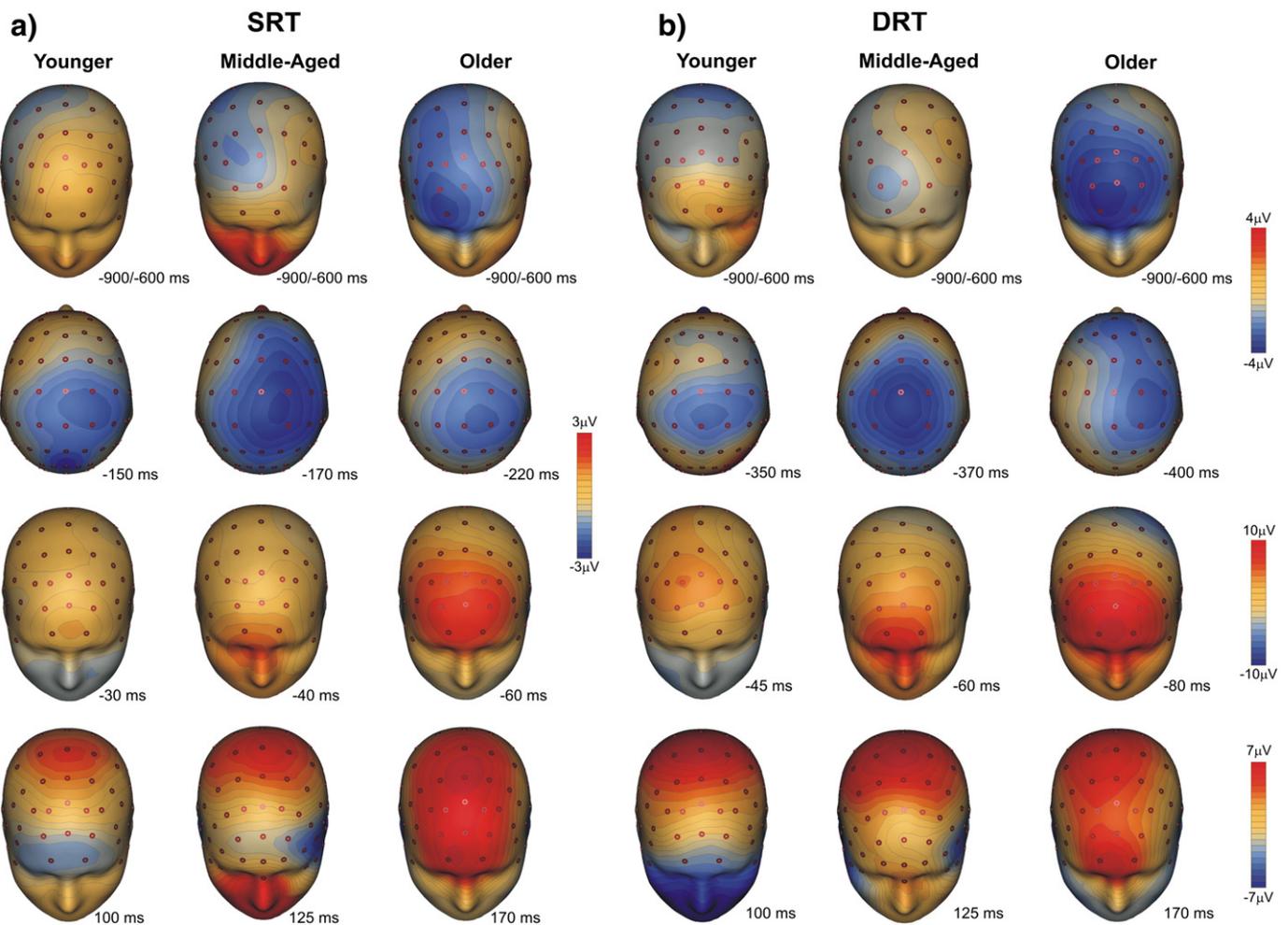
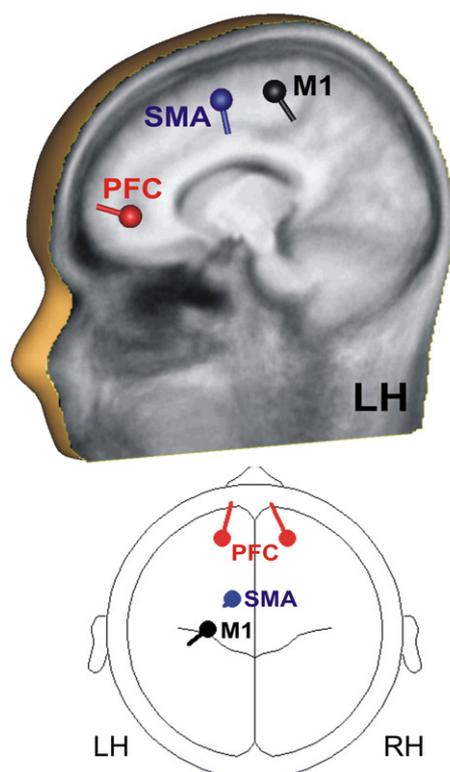


Fig. 5. Scalp topography of the grand average MRCPs across the different groups for the SRT (a) and the DRT (b). The maps are decomposed into four relevant time windows aligned from the top to the bottom.

a) Sources Localization



b) Sources Time-Course

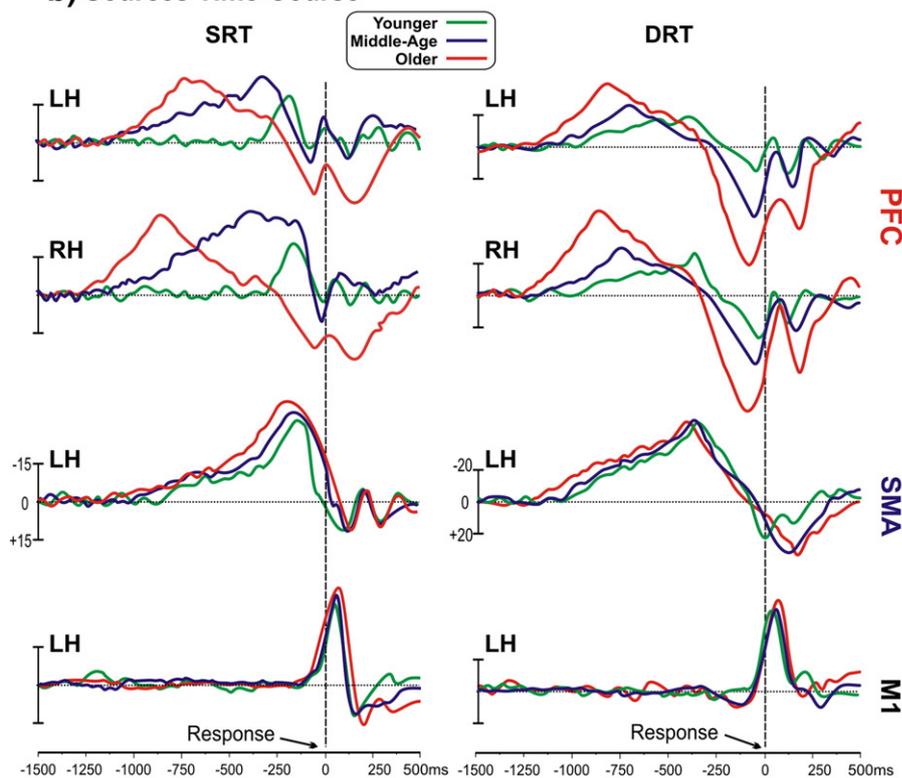


Fig. 6. (a) Source model of the MRCP components projected on a realistic model of the brain. Cortical sources were found in the bilateral frontal gyri, left SMA, and left M1. (b) Time-course of the cortical sources modeled for the SRT (left) and the DRT (right). The traces from the groups are superimposed for each cortical source.

tests, no channel pointed to a significant residual signal, which indicated that there was no failure in any channel associated with the model.

Fig. 6b shows the time course of the aforementioned sources modeled separately for each task and group. The rationale of this analysis was to seed the source location on sites found through the general model and to compare the time-course of common sources between Ages and Tasks. For the SRT, the bilateral source in the PFC showed age differences. In older adults, this source started at about -1200 ms and peaked at about -800 ms. In middle-aged adults, the onset was about -1100 ms and peaked at -370 ms. In younger adults, this prefrontal activity was not present until about -300 ms and peaked at -180 ms. After these peaks, the prefrontal activity in the older adults slowly decreased, showing a positive peak at -60 ms; afterwards, we found a more negative peak during the response, followed by a positive peak at 160 ms. In middle-aged and younger adults, the prefrontal peaks were quickly followed by positive activities, which peaked at about -40 ms. Concomitantly with the response, these activities inverted their polarity, and afterwards, only small activities were found. The source in the left SMA (contralateral to the hand used) started its activity 1100 , 1000 and 840 ms before the response in older, middle-aged, and younger participants, respectively. This premotor activity peaked at -215 , -170 and -150 ms in older, middle-aged and younger, respectively. The source in the left M1 started its activity about 100 ms before the response in all groups and peaked about 60 ms after the movement onset.

For the DRT, the activity in the PFC was larger in older, smaller in younger and intermediate in middle-aged participants. The following age-related temporal differences were detectable: in older adults, the activity started about -1200 and peaked at about -850 ms; in middle-aged adults, it started at -1100 ms and peaked at about -740 ms; in younger adults, it started at -970 ms and peaked at

about -380 ms. After these early peaks, the prefrontal activities inverted their polarities toward a positive peak, followed by a more negative peak, and a positive peak again just after the response. These peaks were similar in latency between hemispheres, and the former positive peak was earlier in older (-90 ms) adults than middle-aged (-60 ms) and younger (-45 ms) adults. The activities of all groups became more negative concomitant with the response, but after the response, the PFC source peaked again at 170 , 150 and 115 ms in older, middle-aged, and younger adults, respectively. Overall, the amplitudes were larger in the older group than the younger groups. The source in the left SMA started its activity at -1200 , -1040 , and -1020 ms and peaked at -410 , -375 , and -350 ms in the older, middle-aged and younger groups, respectively. The M1 source started its activity about 100 ms before, and peaked about 80 ms after, the response in all groups.

Together, these models accounted for the MRCPs in the interval from -900 to $+100$ ms, leaving a RV $<4.1\%$. At the source wave orthogonality test, the sources failed to reach significance over the whole interval of the fit; this result indicates that the dipole moments do not show systematic cross-talk in the time courses.

Correlation analysis

Confirming the literature, RTs (see Fig. 2) were positively correlated with age ($r = 0.60$, $p < 0.0001$ and $r = 0.49$, $p = 0.0110$ for the SRT and the DRT, respectively) and P3 latency ($r = 0.49$, $p = 0.0030$ in the SRT only). Furthermore, for the SRT, RTs were negatively correlated with the BP peak latencies at both AFz and Cz ($r = -0.69$, $p < 0.0001$ and $r = -0.65$, $p < 0.0001$ respectively), which, in turn, were negatively correlated with the P3 latency ($r = -0.59$, $p < 0.0001$ and $r = -0.51$, $p = 0.0012$ at AFz and Cz, respectively). For the DRT, RTs were negatively correlated with the BP peak latency at AFz ($r = -0.47$, $p = 0.0030$), replicating the result observed for the SRT. RTs were positively

correlated with the BP peak amplitude (at Cz; $r = -0.32$, $p = 0.0410$), and the P3 latency was negatively correlated with the BP peak amplitude (at AFz; $r = -0.35$, $p = 0.0420$).

Discussion

The present study evaluated the influence of age on brain activity related to motor planning and stimulus processing. On the basis of the neuroimaging data (Heuninckx et al., 2008), we hypothesized that the brains, especially frontal areas, of older people activate more resources than those of younger adults to accomplish task requirements. On the whole, the joint examination of stimulus-locked and movement-locked brain electrophysiology together with the behavioral data of younger, middle-aged, and older adults allowed shedding light into how effectively the aging brain compensates dysfunctional age-related changes. The behavioral results confirmed the well-known slowing of processing with aging (Kolev et al., 2006; Vallesi et al., 2009; Yordanova et al., 2004), associated with comparable levels of accuracy across age classes. More important, we identified several age-related differences in the cortical activity that underlies the generation of voluntary movements in response to external stimuli. These differences were more evident in the response planning stage than the stimulus processing stage; movement-locked ERPs revealed large differences between older and younger persons, while differences for stimulus-locked ERPs were comparatively smaller. In any case, the slowing of stimulus processing by aging was correlated with long-lasting motor preparation and slow reaction times regardless of task complexity.

The novel result of the present study is the presence of an appreciable age-related brain slowing of motor planning not only in a relatively complex RT task (i.e., the DRT), but also in a very easy task (i.e., the SRT). The onset of the MRCPs in older adults was much earlier than previously reported in aging studies (Barrett et al., 1986; Falkenstein et al., 2006; Golob et al., 2005; Ishizuka et al., 1996; Kolev et al., 2006; Naccarato et al., 2006; Singh et al., 1990; Yordanova et al., 2004). Further, we found a large prefrontal involvement that has not been shown by earlier MRCP studies. These differences might be due to the discriminative reaction task employed in the present study; other studies have used choice reaction tasks (Falkenstein et al., 2006; Yordanova et al., 2004), voluntary self-paced movement (Barrett et al., 1986; Singh et al., 1990) or externally triggered response according to the paradigm of contingent negative variation (Golob et al., 2005). Further, the present task required fast and accurate responses every 1–2 s, whereas previous studies have required slower response rates. More important, in the DRT both motor execution and inhibition were required, and the equal ratio of Go and No-Go trials produced maximal response uncertainty. These features make the present task more demanding than previously used tasks and produced MRCPs that started earlier and showed different involvements of the frontal lobes in younger and older subjects in terms of motor preparation and execution. Furthermore, some studies did not provide evidence of prefrontal over-activity in older adults because they either did not record from prefrontal electrodes (Barrett et al., 1986; Golob et al., 2005) or did not consider these data in their analyses (see Fig. 4a in Yordanova et al., 2004).

The time-course of the source analysis for the SRT clearly shows that the beginning of bilateral activity in the PFC depends on age; PFC activity started very early in the older adults (1100 ms before movement), later in middle-aged adults (900 ms), and much later in younger adults (300 ms). For the DRT, the pattern of age-related effects was the same, but the differences between middle-aged and older adults were less pronounced. The scalp topography results showed an early negative activity in the PFC starting more than 1 s before the response; this activity was larger in older adults than in middle-aged adults and absent in younger adults. Before the response, a strong positive activity was found in prefrontal areas of

older adults (–60 ms and –80 ms, in the SRT and the DRT, respectively) that was less pronounced and delayed in middle-aged adults (–40 ms and –60 ms in the SRT and the DRT, respectively). On the other hand, in younger adults, the same activity was localized in more posterior areas, and its peak was closer to the beginning of the movement (–30 ms and –45 ms in the SRT and the DRT, respectively). Overall, age-related effects on prefrontal activity were macroscopic, with both onset time and amplitude increasing with age. Older adults need to activate the PFC even to accomplish very easy tasks, whereas younger adults are able to spare cortical resources during the same tasks. Only when the RT task was more complex (i.e., the DRT) did younger adults show prefrontal activity involvement that started about 1 s before the initiation of movement and reached the same amplitude as that observed in the older groups; this result suggests that executive control processes were required in the DRT for the younger adults. Thus, the processing selected to accomplish the DRT was qualitatively similar for younger and older subjects. In the case of the DRT, the differences were quantitative: to reach the same accuracy (anticipation and commission errors were comparable), older subjects prepared the action with larger anticipation and higher cost, as indexed by the earlier latency onset and larger prefrontal cortical activation. The substantial changes in the polarity of the PFC activity in the time window between 1 s before and 200 ms after the movement might be related to its top-down supervision role (Norman and Shallice, 1986), which controls response selection during the motor preparation. In the present study, the large PFC negativity peaking between 900 and 600 ms before the response may be interpreted as a marker of inhibitory control; it is likely that such control serves to avoid response anticipations. After the peak, this activity rapidly decreased and developed into the sharp positivity that peaked 170 ms after the response; this rapid change might be related to the release of inhibitory control to facilitate the response execution. This entire pattern of prefrontal activity was more marked in older and middle-aged adults than in young participants.

Regarding the analysis of the stimulus-locked ERP components, a partial consistency with evidence in the literature emerged (Kolev et al., 2006; Vallesi et al., 2009). From the present results, we may conclude that only a small portion of the general slowing of RTs with aging should be attributed to slowing at the perceptual and attentional levels: differences with respect to younger adults were small and often non-significant in the early phases of stimulus analysis (P1, N1, P2), and differences were more marked and significant for the later cognitive P3. Overall, we speculate that the ubiquitous involvement of the PFC and the slow stimulus categorization (i.e., delayed P3 component) are responsible for longer RTs in older individuals. Further investigations are needed to provide additional validation to this hypothesis and to improve our understanding of the role played by the larger involvement of the PFC in response planning that accompanies aging.

Correlation analyses support this view, confirming that the age-related slowing at the behavioral and cognitive levels in the SRT was associated with anticipation of motor preparation (indexed by earlier BP peak latencies) over prefrontal and central electrodes, which was, in turn, associated with longer times needed to classify the stimuli (marked by the P3 latency; Yordanova et al., 2004). It seems likely that in very simple reaction tasks, both RT and P3 latency increase with age, while the BP peak latency decreases, suggesting that the increasing effort of older adults in the preparation phase does not compensate for the slowing of RTs in either task.

Thus, PFC over-recruitment favors accuracy, but not speed. Prefrontal hyperactivity likely causes the behavioral slowing by activating a highly controlled top-down performance rather than a faster stimulus-triggered behavior (Park and Reuter-Lorenz, 2009). Stimuli are classified more slowly by older subjects, and actions require longer anticipation and stronger prefrontal control.

The joint consideration of brain electrical and behavioral results offers even more compelling insights into the transition from young

to older adults. Previous studies either did not include a middle-aged group, or merged the data from middle-aged and older adults. The present findings showed that middle-aged adults lacked a significant RT slowing, being more similar to younger than to older adults. This might seem surprising when considering that both P2 and P3 latencies showed a linear age-related increase, with latencies in middle-aged adults being significantly longer than those of younger adults. On the other side, the BP showed middle aged adults being more 'older adult-like': the prefrontal involvement was present in the SRT, although it was not as marked as it was in the older, and in the DRT, the prefrontal cortex started its activity very early, similar to older adults. Therefore, the prefrontal overactivation seems to be a common characteristic of middle-aged and older adults. It can be interpreted as a compensatory activity whose effectiveness differs in middle-aged and older adults. In middle-aged adults, it allows compensating the slowing of information processing reflected in the P2 and P3 latencies and maintaining 'younger adult-like' reaction speed. In older adults, the prefrontal overactivation seems no longer to offset the behavioral consequences of the age-related slowing of information processing, but rather it seems to ensure the maintenance of response accuracy. Given that the overactivation in older adults does not seem to be paralleled by the maintenance of task relevant speeded performance, it is plausible that the compensation mechanisms, which are effective for middle-aged adults, are less efficient in older adults possibly due to the larger dedifferentiation (Park and Reuter-Lorenz, 2009). With reference to the task complexity effect, we may note that the BP onset over Cz depended on task complexity (the more difficult the task, the earlier the BP onset will be). This dependency held for all age groups, indicating that flexible, task-dependent allocation of resources was also present in older adults. In contrast, BP onset and peak latency recorded at prefrontal leads (AFz) were modulated by task difficulty only in the younger and middle-aged groups. In older adults, the onset and peak latency of the BP were similar in the SRT and the DRT, indicating the sustained involvement of the PFC in anticipation of a response signal regardless of task complexity. This finding is in line with the findings of Sterr and Dean (2008) showing age-related recruitment of frontal areas in anticipation of a response signal. In accord with previous LRP findings that showed that aging affects not only motor execution (Roggeveen et al., 2007) but also motor preparation (Sterr and Dean, 2008) and motor response generation (Yordanova et al., 2004), the present findings show that the age-related slowing of RT cannot be reliably explained by slowing at the level of stimulus processing but that it mostly originates during the motor preparation processing. In summary, the preparation of responses in older people had a very high cost, even in the easier task. The so-called "complexity effect" (Yordanova et al., 2004) was reversed by the present data: the differences between younger and older adults were more evident in the easier rather than the more complex task. Indeed, the preparation for the forthcoming motor response was substantially different along the lifespan. Older people recruited prefrontal brain regions in anticipation during pre-motor planning in both the DRT and the SRT, whereas the younger participants did so only in the DRT. Thus, the complexity effect was present in young and middle-aged adults but not in older participants.

Conclusions

We suggest that the long-lasting hyperactivity of the PFC before action in the elderly reflects highly controlled processing: the motor responses are prepared in advance and controlled in order to execute them with the appropriate timing. This procedure is dominant in older adults even for very simple tasks, whereas younger adults only adopt it when the task is more challenging and the stimulus-triggered procedure becomes inconvenient. Future research employing the manipulation of the involvement of different executive function subsets

may improve our understanding and account for this divergence, as well as address this topic in special aging populations affected by secondary aging syndromes. The present findings based on fine-grain temporal analysis may contribute to fill the gap between behavioral and neuroimaging data in the literature on the elderly and to improve our knowledge about the timing and sources of cortical motor preparation that underpin responses to external stimuli in healthy individuals of different ages.

Acknowledgments

This work was supported by the University of "Foro Italico" funds [grant number RIC1062010].

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2012.06.031>.

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