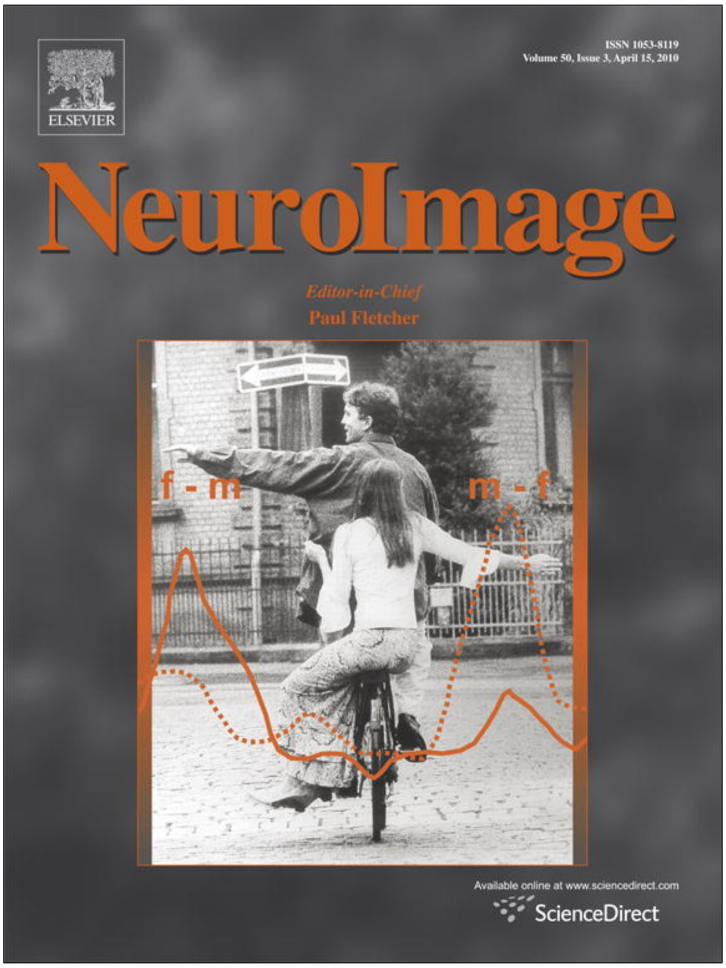
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Excessive sub-threshold motor preparation for non-target stimuli in normal aging

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ABSTRACT

Problems in suppressing neural activity related to distracting information increase with age. We investigated whether age-related changes in processing non-target material are present even when behavioral performance is matched between age groups. Younger (19–36 years) and older (61–80 years) participants performed a go/nogo task with different degrees of cognitive interference for two types of nogo stimuli. On each block, either the left or the right hand was used for the go responses. EEG was recorded to compute the Lateralized Readiness Potential (LRP), a measure of unilateral motor response preparation. Although performance was similar in the two groups, older adults showed a pronounced LRP partial response preparation not only for high-conflict nogo stimuli, but even for low-conflict ones, when both age groups performed at ceiling. These results indicate that, even without age-related performance differences, older individuals show enhanced response preparation to non-target stimuli that can be detected with more sensitive measures such as the LRP. Negative correlations between nogo-LRPs and go-RTs in the older group only suggest the possibility that partial response preparation for nogo stimuli is the cost to pay to maintain optimal speed to go stimuli in normal aging.

The hypothesis that older people have problems in suppressing the processing of distracting information (Hasher and Zacks, 1988) has received support in different domains such as visual and auditory selective attention (Madden and Langley, 2003; Wild-Wall and Falkenstein, 2010), reading (Connelly et al., 1991) and semantic priming (Duchek et al., 1995). An age-related decline in the suppression function especially occurs with non-target material that produces conflict because of its similarity to target stimuli (Juncos-Rabadan et al., 2008; Sweeney et al., 2001; Tun et al., 2002). However, no age-related behavioral impairment is usually reported when irrelevant stimuli are easily distinguishable from targets on the basis of salient perceptual (Scialfa et al., 1998), spatial (Carlson et al., 1995; Zeef et al., 1996), or semantic features (Connelly et al., 1991; Li et al., 1998).

One possible interpretation of these results is that normal aging does not affect the processing of irrelevant information that is easy to distinguish from relevant material. However, the absence of age-related behavioral changes does not necessarily suggest similar underlying processing. This issue was investigated in a recent study (Vallesi et al., 2009c) using go/nogo tasks while recording event-related potentials (ERPs). The tasks included conflicting go and nogo stimuli, obtained with complementary combinations of letters and colours, and a low-conflict nogo condition, namely coloured numbers that were easy to distinguish from the task-relevant letters. Subjects had to respond with the (dominant) right hand to go stimuli only. Both older and young individuals performed at ceiling on low-conflict nogo stimuli, but the older group showed a bigger posterior P2 to this kind of stimuli than to high-conflict nogo stimuli. Moreover, the central P3 associated to low-conflict nogo stimuli was more pronounced in the older adults than in younger adults. Thus, even though the overt performance data would suggest that aging does not affect processing of easily distinguishable irrelevant information, the electrophysiological results reveal the "hidden" story—there is a difference between young and old individuals at the neural level, even with this considerably simple condition.

Whether the nogo P3 component reflects an active inhibitory process is still a matter of debate, with some studies confirming this account (Roberts et al., 1994; Smith et al., 2008) and others disconfirming it (e.g., Falkenstein et al., 1999; Verleger et al., 2006). In line with the inhibition account, the amplitude of the nogo P3 increases with stimuli invalidly cueing a go response, that is with increased previous preparation (Smith et al., 2007). On this account, older adults might have needed to suppress partial responses to low-conflict nogo stimuli to a greater extent than young controls.

In this context, the findings in Vallesi et al's (2009c) study suggest that the older individuals' attention was more attracted by low-conflict nogo stimuli at the perceptual level (posterior P2) and they needed to use more neural resources at the response suppression (central P3) stage. It is conceivable that the missing link between

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abnormal perceptual processing and the need for a greater suppression is an inappropriate increase in partial response preparation for these nogo stimuli with age. The central nogo N2–P3 complex was slightly left-lateralized but, since only the right hand was used for go responses, it was not possible to unequivocally attribute this left lateralization to motor-related processes rather than to other left-lateralized processes (e.g., language).

To investigate more directly whether motor processes are involved, the current study used a modified version of the simple task in Vallesi et al. (2009c), in which participants had to respond to go stimuli with the right and left hand in different blocks. By using unimanual responses with both hands, it was possible to compute the Lateralized Readiness Potential (LRP), a continuous electrophysiological index of covert response preparation (De Jong et al., 1988; Eimer, 1998; Gratton et al., 1988; Vallesi et al., 2005). The LRP, which is computed from the event-related potentials recorded over motor cortical areas that control right and left hand movements, represents the net increase of EEG negativity over the motor cortex contralateral to a prepared movement, and it is sensitive to partial unilateral response preparation (Eimer and Schlaghecken, 1998; Leuthold et al., 1996), even during nogo conditions (Shin et al., 2004).

While earlier studies have already shown that LRP is a valid measure to detect age-related decline in suppressing inappropriate responses elicited by conflicting information (e.g., Wild-Wall et al., 2008; Zeef et al., 1996), to the best of our knowledge, this is the first study of aging that records LRP in the context of a go/nogo task, in which the necessity to keep the response system in check is maximally emphasized by the task demands. Given the documented age-related selective attention problems in filtering out non-target information (e.g., Hasher et al., 1999; Fabiani et al., 2006), and the ERP results in our previous go/nogo study (Vallesi et al., 2009c), we expected a disproportional early response preparation in the older group as measured with LRP, with respect to the young controls, not only with high-conflict nogo stimuli but also with low-conflict ones.

Method

Participants

Fourteen healthy older adults (6 females; mean age: 71 years, range: 61–80) and 14 younger controls (7 females; mean age: 25 years, range: 19–36) gave their informed consent to volunteer for the study. The participants had normal or corrected-to-normal sight and reported no history of neurological, psychiatric or neuropsychological problems (e.g. memory). All were right-handed on the Oldfield (1971) questionnaire and had at least 13 years of education. They received 20 $ for their time. No older participant had dementia as assessed with the Mini Mental State Examination (range: 27–30). The study was previously approved by the Baycrest Research Ethics Board.

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. Visual stimuli were presented through a computer display at a distance of 60 cm.

The task was a modified version of that used in our previous works (Vallesi et al., 2009a, 2009c; see Fox et al., 2000, for a similar design). Go responses were given by pressing "B" in the computer keyboard with the right or left hand in different blocks. Go/nogo stimuli were letters and numbers coloured in red or blue. For half of the subjects, go stimuli were "blue O" and "red X", and nogo stimuli were "red O" and "blue X" (high-conflict nogo) or the coloured numbers 2 and 3 (low-conflict nogo). The association between colour and go/nogo letters was counterbalanced for the other half of the subjects (i.e., go stimuli: "red O" and "blue X").

On each trial, a go/nogo stimulus was initially presented for 300 ms at the centre of the computer screen. A blank screen followed the stimulus offset for an interval that varied randomly between 2.4 and 4.4 sec. Four blocks of trials were administered. On each block, 80 go (50%), 40 high-conflict nogo (25%) and 40 low-conflict nogo (25%) stimuli were presented randomly. Participants were instructed to press "B" on a computer keyboard when a go stimulus occurred, and not to respond to nogo stimuli. The right hand was used for the go responses in two consecutive blocks of trials, while the left hand was used in the two other blocks (order counterbalanced across subjects). Speed and accuracy were equally emphasized. Each block was preceded by 6 practice trials (not analysed).

The experimental design consisted of a 2 hand (right, left) by 3 go/nogo condition (go, high-conflict nogo, low-conflict nogo) by 2 age group (younger, older) design.

Behavioral data analysis

Practice trials, the first trial of each block and trials with go responses outside 100–1500 ms after the stimulus onset were discarded from further analyses. RTs to go stimuli were submitted to a 2×2 mixed ANOVA with age as the between subjects factor and responding hand as the within-subject factor. The percentage of errors in the two age-groups was compared using non-parametric Kolmogorov–Smirnov tests separately for each hand and each go/nogo category.

Electrophysiological recording and analysis

Scalp voltages were recorded using NeuroScan 4.0 and two SynAmps amplifiers. ElectroCaps (Electro-Cap International, Inc.) with 64 pure tin electrodes (10/20 system) including two pairs of ocular sites on the outer canthi and infra-orbital ridges were used for the recording. The online reference electrode was Cz and the ground was AFz. Electrode impedance was kept under 5 kΩ. Continuous EEG was digitized (sampling frequency: 250 Hz) through a 0.01–100 Hz band-pass filter.

For each subject, continuous data were first re-referenced to an average reference and digitally filtered (0.1–30 Hz). With these filter settings most of the electromyographic (EMG) activity was filtered out. Eye artifacts (i.e., eye-blinks, lateral and vertical movements) were compensated from the ERP waveforms using source components derived from the recordings obtained before and after the performance of the task (Picton et al., 2000). Three noisy electrodes (in three different subjects) were interpolated using the BESA (MEGIS Software GmbH, Munich, Germany) algorithm. ERP segments with EEG voltage over ±150 µV were automatically rejected in BESA.

Stimulus-locked ERP data from correct trials were first averaged as a function of the 6 conditions obtained by crossing 3 go/nogo types (go, high-conflict nogo, low-conflict nogo) by 2 responding hands. Each ERP was averaged over a 1000-ms period beginning 200 ms before the stimulus and corrected to the pre-stimulus baseline.

LRP was calculated over the scalp motor channels C3 and C4 using a similar formula as in Vallesi et al. (2005) for all go/nogo types: ([C3 − C4 (left hand blocks)] + [C4 − C3 (right hand blocks)]) / 2. In this formula, positivity indicates activation of the contralateral hand. Two-sample *t*-tests (two-tailed) were performed to compare LRP for each condition in the younger and older group on each time-point between 0 and 800 ms. To partially correct for multiple comparisons, data were considered reliable only when at least 5 consecutive time-points (20 ms) were significant ($p<0.05$).

In our previous study (Vallesi et al., 2009c), a posterior P2 component (at CB1 electrode) was more pronounced for low-conflict nogo stimuli than for the conflicting go/nogo stimuli in the older group, and a central P3 component (at electrodes Cz and C1) was more pronounced for low-conflict nogo stimuli in the older group than in the younger controls. Therefore, additional tests were run to

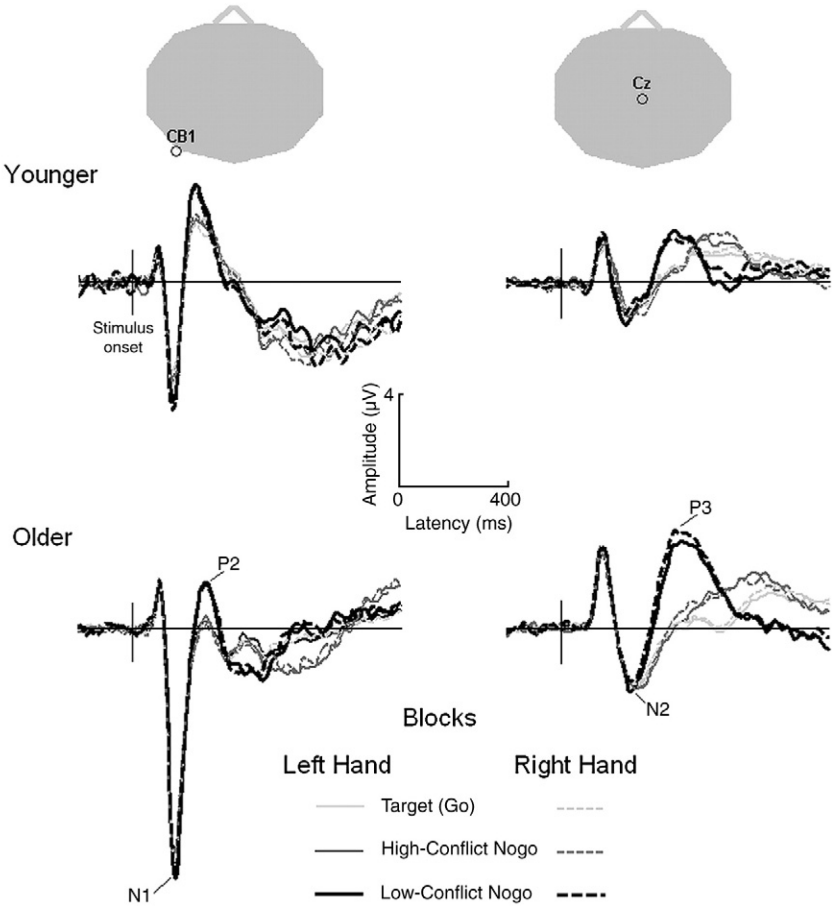

Fig. 1. ERPs at CB1 and Cz according to the group (younger vs. older), responding hand (left vs. right) and go/nogo condition (go, high-conflict nogo, low-conflict nogo). The main ERP components are labelled.

investigate whether these components correlated with the LRP for low-conflict nogo conditions in each group. The ERPs at electrodes CB1 and Cz can be appreciated in Fig. 1. The P2 component at CB1 peaked at around 240 ms and 276 ms in the younger and older participants, respectively. Therefore, P2 peak amplitude was searched within the 220- to 296-ms time-window for each subject (hand factor collapsed). The P3 at Cz for low-conflict nogo stimuli peaked at around 424 ms and 440 ms in the younger and older groups, respectively (see Fig. 1). Therefore, the P3 peak amplitude was searched around the 404- to 460-ms time-window (hand factor collapsed). First, to check whether previous findings (Vallesi et al., 2009c) were replicated here, two analyses were carried out: (i) the peak amplitude for the P2 component was submitted to a 2×2 mixed ANOVA with group (younger vs. older) as the between subjects factor and nogo condition (high- vs. low-conflict nogo) as the within subject factor; (ii) P3 peak amplitude in the two groups was contrasted in a two-sample *t*-test. Finally, to test whether P2 and P3 correlated with response preparation, their peak amplitude was correlated with LRP mean amplitude (for low-conflict nogo stimuli) through Pearson correlation analyses separately for each group.

Pearson correlation analyses were also performed between LRP mean amplitudes and average RTs to go stimuli for each group separately, in order to investigate the relation between partial response preparation and speed. The first LRP peak in the older group occurred at around 312 and 216 ms for high- and low-conflict nogo conditions, respectively. Therefore, for each subject, the values of the LRP mean amplitude that were used in the correlation analyses were computed on 40 ms time-windows around these peaks, namely in the 292–332 and 196–236 ms time-windows for high- and low-conflict nogo conditions, respectively. Similar correlation analyses were performed between LRP mean amplitude and accuracy data for go, high-conflict and low-conflict nogo stimuli.

Results

Behavioral data

Performance data are reported in Table 1. Responses were faster with the right hand than with the left one [$F(1,26) = 8.5$, $p < 0.01$]. No other effect was significant in the ANOVA on RTs. No age difference emerged for any condition in the accuracy analyses.

LRP

The topographic distribution of the event-related lateralization at LRP peak latencies in the two groups and all the conditions can be

Table 1
Above: average error percentage (and standard error of the mean) for each task condition and age group. Below: average go-RT in ms (and standard error of the mean) for each responding hand and age group.

Error rate (%)	Go		High-Conflict nogo		Low-conflict nogo	
	L	R	L	R	L	R
Younger	2.9 (1)	2.4 (1)	4.4 (0.8)	3.5 (0.9)	0.4 (0.2)	0.3 (0.2)
Older	1.4 (0.7)	1.7 (0.7)	4.5 (1.1)	4.8 (1)	0.1 (0.1)	0.2 (0.1)
RT (ms)	L	R				
Younger	670 (25)	659 (23)				
Older	711 (18)	690 (16)				

appreciated in Fig. 2 (see Praamstra et al., 1996, for a similar plotting procedure). As it appears from this figure, locations C3/C4 are, among all the recording electrodes, those where the LRP can be mostly detected.

LRP waveforms can be better appreciated in Fig. 3. The LRP waveforms were more pronounced in the older group than in the younger group for the high-conflict nogo condition in the following time-windows between 236 and 404 ms: 236–256, 304–320, 352–372, 388–404 ms; and for the low-conflict nogo condition in an early time-window (208–308 ms), and in a later one (656–684 ms). There were no significant differences in the LRP for go stimuli.

The amplitude of the P2 component in CB1 was more pronounced for the low-conflict nogo stimuli than for the high-conflict ones [$F(1,26)=49$, $p<0.001$]. This component was more pronounced in the younger than in the older subjects [$F(1,26)=11.7$, $p<0.01$], probably due to the fact that the previous N1 component in the older group was almost twice the size of the N1 component in the younger group (see Fig. 1). However, in contrast with our previous results (Vallesi et al., 2009c), there was no interaction between group and nogo condition ($p=0.37$). The P3 component for low-conflict nogo stimuli was instead more pronounced in the older group than in the younger controls [$t(26)=-2.69$, $p=0.012$], thus replicating previous findings (Vallesi et al., 2009c).

The correlation between LRP and P3 amplitude for low-conflict nogo condition was positive and significant in the older group ($r=0.62$, $p=0.018$) but not in the younger group ($r=-0.01$, $p=0.99$). This pattern suggests that these two ERP components are functionally linked in the older group. On the other hand, the correlation between the posterior P2 and LRP was not significant for either group (both $ps>0.09$).

In the older group, the correlation between LRP and go-RTs was significantly negative for both high-conflict ($r=-0.54$, $p=0.046$) and low-conflict ($r=-66$, $p=0.01$) nogo conditions (see Fig. 4). This pattern indicates that the faster elderly subjects were those who prepared more sub-threshold response for nogo stimuli. These correlations were not significant in the young group (both $ps>0.51$). Similar correlations between LRP and accuracy were never significant in either group (all $ps>0.63$).

Discussion

The present study tested how the motor processing of non-target material changes in normal aging during a go/nogo task. Although older subjects were slower than their younger controls in the RTs to go stimuli by 36 ms on average (see Table 1), this difference was not significant. An age-related response slowing may have been expected based on previous literature, but this pattern is more likely to occur with more complex task conditions (e.g., Yordanova et al., 2004; Vallesi, McIntosh and Stuss, under review). Performance was also matched in terms of accuracy. This result provides a good experimental context to investigate the neural mechanisms by means of which the aging brain maintains a good level of performance.

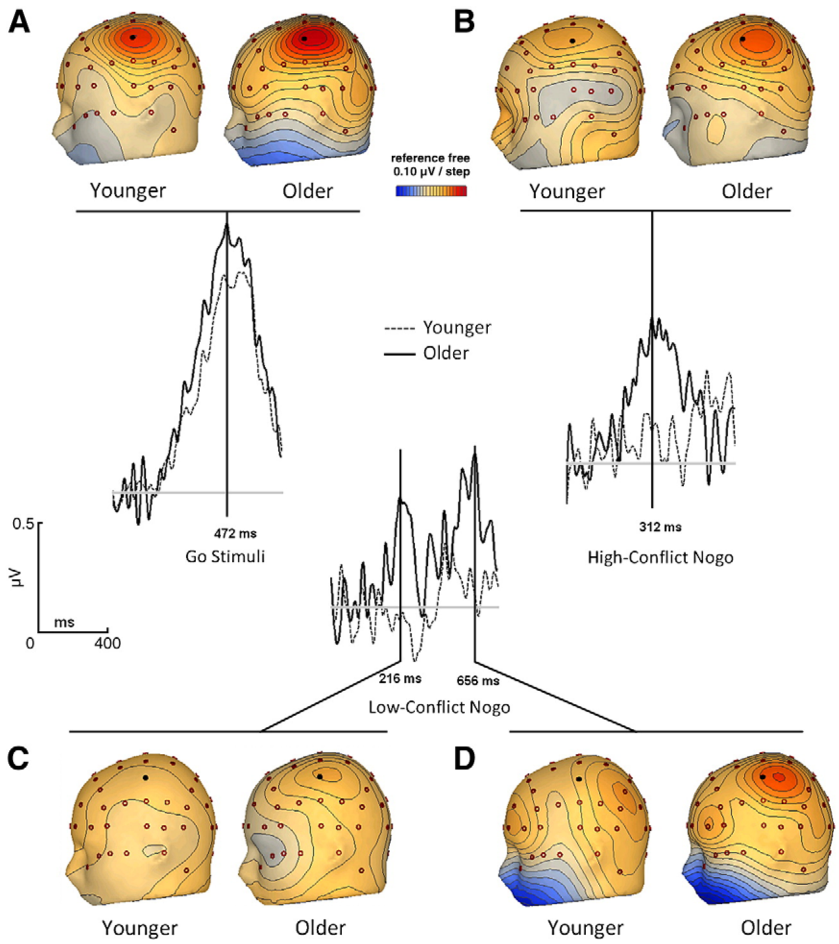

Fig. 2. The topographic distribution of the event-related lateralisations (ERLs) according to age group, go/nogo condition and LRP peak latency in the older group is shown by means of normalized isovoltage maps. The circles on the head models indicate how the geometry of the map is related to the electrode sites. Since the LRP measures voltage differences between homologous electrodes over the right and left hemispheres, the left hemispheric projection of the maps is arbitrary. The black circles show electrode C3 (and C4), representing the locations from which the LRP was computed. The vertical lines in these waveforms indicate the latencies where the LRP peaked in the older group. The isovoltage maps refer to those LRP peak latencies (A: go stimuli; B: high-conflict nogo stimuli; C and D: early and late LRP peaks for low-conflict nogo stimuli, respectively).

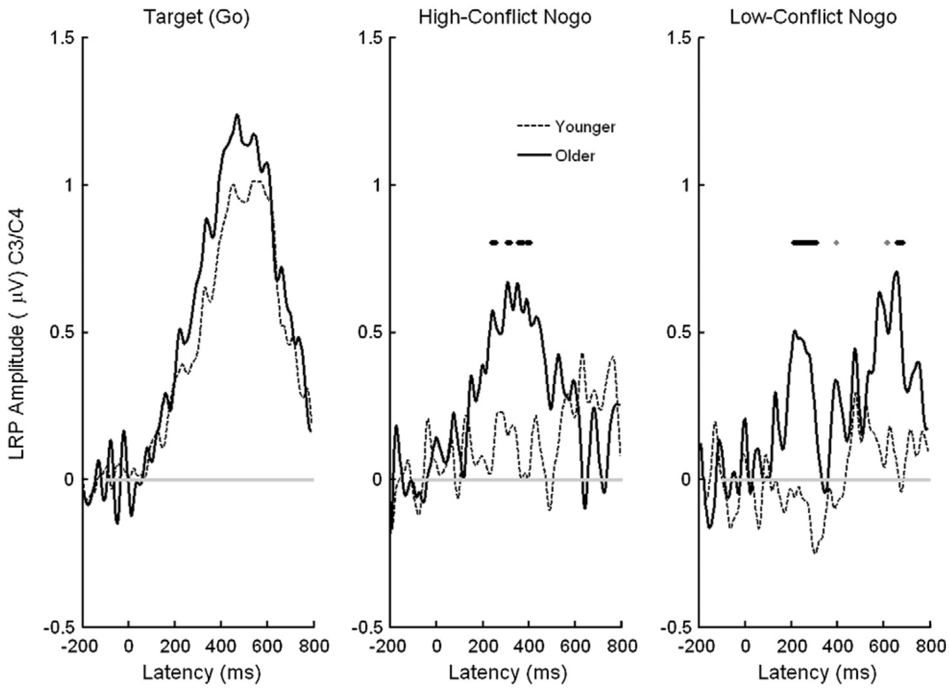

Fig. 3. Lateralized Readiness Potential calculated over the electrodes C3 and C4 for each condition and group. Black circles on the top of each panel denote at least 5 consecutive time-points when two-sample *t*-tests showed a significant difference between age-groups [$t(26)>2.05$, $p<0.05$]. Gray circles indicate when the t-test was significant in less than 5 consecutive time-points.

LRP waveforms to go stimuli were similar in both age groups, in line with some previous LRP studies (e.g., Yordanova et al., 2004), and in contrast to others (e.g., Sterr and Dean, 2008; Wild-Wall et al., 2008). A possible reason for this discrepancy in the LRP literature on aging can be the substantial differences in the paradigms employed across studies. In Sterr and Dean (2008) study, for instance, the use of a short ISI (1300 ms) between a response priming stimulus (S1: left, right, neutral response) and a second stimulus (S2) cueing for a left vs. right hand response might have favored a strategy of sustained response inhibition in the older adults in order to avoid premature responding to S1 (i.e., enhanced frontal nogo P3-like component), which might explain the absence of LRP-like preparatory activity after S1.

More relevant for the present purposes, reliable age-related differences emerged for nogo stimuli. A differential partial response preparation elicited by nogo stimuli indeed significantly occurred in the older group with respect to the younger controls. The present findings, when considered together with those of our previous ERP study (Vallesi et al., 2009c), show that several cognitive processes concerning non-target material are enhanced with age even when performance is matched. However, although an age-related abnormal perceptual processing for non-target material was indirectly supported by an enhanced posterior P2 component in our earlier ERP study (Vallesi et al., 2009c), this result was not replicated here since the P2 was more pronounced for low-conflict nogo stimuli than for high-conflict ones in both age groups.

In the present study, the use of a covert measure of response preparation, such as the LRP, allowed us to detect enhanced partial response preparation for non-target stimuli in a sample of highly functioning older subjects, not only for high-conflict nogo stimuli, but also for an undemanding nogo condition, even in the absence of any age-related difference in the behavioral performance. In this respect, the current study complements previous LRP studies of aging that have already shown, using paradigms different from the go/nogo task,

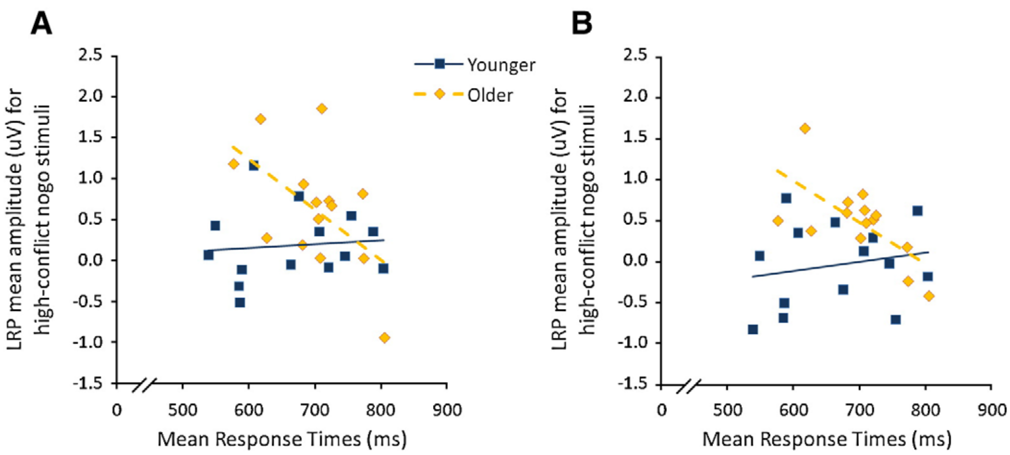

Fig. 4. Correlation between LRP mean amplitude and mean RTs (collapsing the responding hand factor) according to age group (continuous lines: younger group; dashed lines: older group) and nogo condition (Panel A: high-conflict nogo stimuli; Panel B: low-conflict nogo stimuli). See text for details.

abnormal activation of the wrong response side following conflicting information in older individuals (e.g., Zeef et al., 1996). In addition, the present study shows that the inappropriate partial response preparation may occur in the older group regardless of the degree of conflict, although it can last longer for the high-conflict nogo condition than for the low-conflict one.

While there was no correlation between the LRP and the P2 component, the positive correlation between the LRP and the P3 amplitude for low-conflict nogo condition in the older group suggests that these two ERP components are functionally linked. Since the P3 component (peak at 440 ms in the older group) followed an inappropriate partial response preparation (LRP peak at 216 ms) for low-conflict nogo conditions, it might indicate a higher need for the compensatory inhibition of a partial response in the older group, also in line with previous studies that link the nogo P3 to response inhibition (Roberts et al., 1994; Smith et al., 2007, 2008; but see Falkenstein et al., 1999).

This pattern suggests that response suppression declines with advancing age and, even when it is not possible to detect age-related deficits with overt performance measures such as false alarms, this deficit can still be tracked using more sensitive covert measures of cortical response preparation, such as the LRP. More generally, these findings support the view that suppressing cognitive and neural processing of non-target information becomes less efficient with aging (Fabiani et al., 2006; Gazzaley et al., 2005; Hasher et al., 1988, 1999; Wild-Wall and Falkenstein, 2010).

It is worth noting that while the present study shows an increased reactivity of the preparatory system after the onset of interfering information in the older group, previous findings have shown that the anticipatory frontally-based preparation following a preparatory or warning signal decreases with aging (Sterr and Dean, 2008; Vallesi et al., 2009b; Wild-Wall and Falkenstein, 2010). This dissociation suggests a shift from a top-down to a stimulus-driven regulation of motor control (see Paxton et al., 2008, for similar fMRI evidence).

The correlation analyses between nogo-LRPs and go-RTs help understanding the functional meaning of the partial response preparation to nogo stimuli in the older group. These correlations were negative (i.e., the faster subjects were also those with higher preparatory activity to nogo stimuli), suggesting that the preparation of a response as soon as a stimulus (either go or nogo) appears might represent a strategy to maintain a reasonable response speed to go stimuli, thus explaining the lack of a statistical difference in the go-RTs of the two age groups. Although in this experiment the false alarm rate was not different in the two age groups, it would be interesting to investigate whether increasing go/nogo conflict or time pressure would also enhance inappropriate response preparation for nogo stimuli above the response threshold level.

The LRP for low-conflict nogo stimuli showed a biphasic pattern in the older group. However, the late LRP increase was not expected. We acknowledge this effect but may only speculate on its possible functional meaning since it has never been reported in the literature before. This late component may be related to the motor efferences and somatosensory afferences associated to slightly lifting the finger from the response key after older people realized that an easy nogo stimulus had been presented. Unfortunately, the present study did not video-record hand movements or use electromyography (EMG) to confirm this possibility. However, one experimenter recalled that this behavior was prominent in two older subjects. That this possible behavior is unlikely to have also generated the earlier low-conflict nogo LRP peak is suggested by the short latency (peak at 216 ms), that occurs much earlier than the average RTs (700 ms). Moreover, the topographic maps (see Fig. 2D) show that this age-related lateralized component had a different scalp distribution with respect to the other ones (slightly more posterior, with another smaller positivity in ventro-lateral frontal electrodes), which suggests a different functional meaning. Further studies should investigate the functional role of this late LRP component.

A possible limit of the present study is the fact that it did not use force-sensitive response devices or EMG recording. Future studies should investigate, by means of these measures, whether abnormal sub-threshold responses to nogo stimuli can also be detected peripherally in the effector muscles with aging, although a dissociation between LRP and these measures is possible (e.g., Praamstra et al., 1999).

In conclusion, the current LRP study suggests an age-related decline in the efficiency of response suppression for non-target material even when behavioral performance is matched between age groups and at ceiling. This decline is probably due to disruptive changes in frontal functionality (West, 1996) or, more generally, in fronto-striatal dopaminergic systems (Beste et al., 2010; see Cropley et al., 2006, for a review) with advancing aging. However, inefficient response preparation for non-target stimuli is probably a cost that older subjects had to pay in order to maintain a reasonable response speed, as suggested by the negative correlation between nogo-LRP and go-RTs. Future studies should further investigate the potential behavioral consequences of this excessive age-related motor preparation for distracting material, whether it comes from an endogenous compensatory strategy or from external demands (e.g., excessive time pressure), and the possible prognostic value of LRP as a covert index of response suppression failure in both normal aging and subclinical conditions such as incipient Parkinson's disease.

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