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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