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Object individuation and compensation in healthy aging

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ABSTRACT

Theories on neural compensation suggest that aged participants overactivate the brain areas involved in a task to compensate for the age-related decline. In this electrophysiological study, we investigated the temporal locus of neural overactivation in aging during multiple target processing. We measured performance and three event-related brain potential responses (N1, N2pc, and contralateral delay activity) in young and old adults, while they enumerated a variable number (1–4) of targets presented in an easy (distractor absent) or difficult (distractor present) condition. The main results indicated that although N2pc (~200 ms) increased in amplitude in the distractor-present condition in the young group, no modulation occurred for the old group. Old participants were associated with larger N2pc amplitudes than young participants in the distractor-absent condition, where both groups had comparable levels of accuracy. These effects were not present for N1 and contralateral delay activity. Overall, the data suggest that in enumeration, aging is associated with compensatory effects that rely on the selection mechanism responsible for target individuation.

1. Introduction

Aging is characterized by moderate to severe decline in a broad range of cognitive domains (Park et al., 2002). The decline is usually measured as a decrease in accuracy or speed of behavioral performance and as an underactivation of the neural areas associated with a specific cognitive function (Grady et al., 1998; Jonides et al., 2000). However, there are also other neural changes measured in aging. For instance, PET (Grady et al., 1994; Reuter-Lorenz et al., 2000) and fMRI (Cabeza, 2002; Cappell et al., 2010; Heuninckx et al., 2008) studies have shown that old adults tend to overactivate the neural sites that are involved in the execution of a task with respect to young adults. This overactivation sometimes correlates with little or no difference in the behavioral performance between old and young individuals (Heuninckx et al., 2008; van der Veen et al., 2006) and is thus interpreted as evidence of compensatory mechanisms. However, when task difficulty increases, the performance of old adults decreases steadily, and it is associated with little or no changes in the neural activity (Cappell et al., 2010). Numerous fMRI studies have shown that age-related compensation is associated with neural overactivation in prefrontal cortices (Cappell et al., 2010; Davis et al., 2008; van de Vijver et al., 2014). A growing number of fMRI studies indicate that age-related compensation also correlates with increases in activation of the parietal cortices in Stroop-like (Vallesi et al., 2010) and Go-no Go tasks (Geerligs et al., 2014). This finding suggests that together with prefrontal cortex, posterior areas may have a role in age-related compensatory activity.

These results have led to the formulation of the CRUNCH model (Compensation-Related Utilization of Neural Circuit Hypothesis, Reuter-Lorenz and Cappell, 2008). The model hypothesizes that to achieve a good level of performance, old adults recruit more resources than the younger counterparts already at low levels of task requirements (Reuter-Lorenz and Cappell, 2008). In contrast, when task requirements increase, there is a large decrement in the elderly performance, due to the fact that neural resources are limited and because old adults have fewer resources available than young adults (Cappell et al., 2010). Other theories about cognitive aging, such as PASA (Posterior to Anterior Shift in Aging, Davis et al., 2008) and HAROLD (Hemispheric Asymmetry Reduction in Old Adults, Cabeza, 2002), have hypothesized the presence of significant compensatory activity in the aged brain, reflected either by recruitment of frontal sites (PASA) or by additional recruitment of areas symmetric to the ones observed in young adults (HAROLD).

The theories described previously rely mostly on fMRI data and therefore provide an excellent framework to understand age-related changes in recruitment of neural resources in specific regions of the brain. However, the time course of these changes is yet poorly understood. For this reason, in the present study, we

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adopted an electrophysiological (EEG) approach, which enables to pinpoint the stage/s of processing where compensatory activity may take place. Specifically, we relied on the event-related brain potential (ERP) technique to evaluate the existence of specific ERP components signaling neural overactivation in old individuals. The few existing ERP findings (Gajewski and Falkenstein, 2014; Missonnier et al., 2004; Wiegand et al., 2014) indicate that neural overactivation is mainly visible in the central positivity and in the P300 components (late responses occurring at approximately 300 ms poststimulus), thus suggesting a relatively late locus of compensation. However, most studies conducted thus far involved tasks where participants had to maintain in memory a specific item for a variable amount of time (n-back tasks, see Jaeggi et al., 2010; Daffner et al., 2011). Therefore, it is currently unclear whether the time course of the overactivation found at approximately 300 ms, and the related compensatory effect, is a generalized feature or if they are selectively related to the task used in previous studies. In addition, the memory task used previously requires the processing of single target stimuli (presented sequentially), whereas there are several contexts requiring processing of multiple objects presented simultaneously. To our knowledge, the study of Wiegand et al. (2014) on working memory and aging is the only study involving multiple objects that found compensatory effects.

To extend the examination of neural compensatory activity in tasks that imply simultaneous multiple object processing, in the present study, we used an enumeration task. The task implies the simultaneous presentation of a variable number of target elements for a brief amount of time. Enumeration tasks have recently been used by different researchers to investigate the neural correlates of multiple object processing in young adults (Ester et al., 2012; Pagano and Mazza, 2012; for a review, see; Mazza and Caramazza, 2015), as well as to assess the behavioral decline related to aging (Watson et al., 2002, 2005).

So far, little is known about the neural patterns of activity elicited by aged participants during enumeration. Previous fMRI studies on young adults (Ansari et al., 2007; Dehaene et al., 2003; Vetter et al., 2011) have indicated that visual enumeration activates mainly the parietal areas. Therefore, one could predict that activity in posterior areas also has a role in enumeration and compensation during aging. Recent EEG studies have examined the neural activity associated with visual enumeration in healthy young adults (Ester et al., 2012; Hyde and Spelke, 2009; Mazza and Caramazza, 2011; Mazza et al., 2013; Nan et al., 2006; Pagano et al., 2014) and to single and multiple object processing in old adults (Lorenzo-López et al., 2008; Sander et al., 2011; Störmer et al., 2013a, 2013b). These studies focus on three posterior ERP visual components—N1, N2pc, and contralateral delay activity (CDA).

The first response (N1) is a bilateral neural activity peaking at around 150 ms poststimulus onset that has been found in a variety of visuospatial attention tasks (Mangun et al., 1993; Vogel and Luck, 2000). Recent studies on young adults have shown that the N1 amplitude is sensitive to object quantity (Hyde and Spelke, 2009; Libertus et al., 2007; Park et al., 2016), but does not discriminate between the numerosity of the target versus distracter objects (Mazza et al., 2013). This suggests that N1 reflects the functioning of an early segmentation mechanism that is sensitive to the overall numerosity of the objects presented in the visual field, regardless of whether these are relevant for the task at hand (Gebuis et al., 2014; Libertus et al., 2007). Studies on multiple object processing in old adults (Störmer et al., 2013a) have measured N1, while participants were engaged in tracking multiple moving objects. A decrease in N1 amplitude was found in old adults, suggesting an age-related decline in the functioning of early perceptual mechanisms.

The N2pc (N200 posterior contralateral) component is a negative deflection arising at around 200 ms poststimulus onset and represents a difference between the activity of the posterior ipsilateral versus contralateral electrodes when lateralized targets are presented among distractors (Eimer, 1996; Luck and Hillyard, 1994). The N2pc is sensitive to the numerosity of targets during enumeration (Ester et al., 2012; Mazza and Caramazza, 2011; Pagano and Mazza, 2012; Pagano et al., 2014) and multiple object tracking (Drew and Vogel, 2008) tasks. In addition, the numerosity-related modulation of N2pc reaches an asymptote at approximately 3–4 target elements, which correlates with the behavioral subitizing effect (namely, the fast and accurate apprehension of up to 3–4 elements in a scene, Kaufman et al., 1949; Trick and Pylyshyn, 1994). These results suggest that this component indexes the functioning of an object individuation mechanism that is able to represent a limited number of target items as distinct individuals and that is therefore the core component for exact enumeration (Mazza and Caramazza, 2011). ERP studies on aging have proved that N2pc is also a valuable tool to study attentional processing of single (Lorenzo-López et al., 2008) and multiple objects (Pagano et al., 2015; Störmer et al., 2013b) in aged individuals. In all these studies, the N2pc amplitude was significantly reduced in old adults, suggesting the presence of an impairment in the ability to selectively individuate single and multiple objects during aging.

Finally, the CDA (also known as sustained posterior contralateral negativity) is a posterior lateralized component arising approximately 400 ms poststimulus in delayed-match-to-sample and multiple object tracking tasks (Drew and Vogel, 2008; Robitaille et al., 2010; Vogel and Machizawa, 2004). Similar to the N2pc, the CDA is also sensitive to the number of objects maintained in visual working memory (Ikkai et al., 2010) and reaches a plateau at approximately 3–4 elements. Recently, the CDA and its numerosity-related modulation have been recorded in visual enumeration tasks (Pagano and Mazza, 2012; Pagano et al., 2014). The CDA modulation related to the number of target elements indicates that once the relevant objects are individuated, they are further maintained in a memory buffer for mapping onto a symbolic numerical value. CDA has been recently studied in aged participants in memory (Sander et al., 2011; Störmer et al., 2013b; Wiegand et al., 2014) and enumeration (Pagano et al., 2015) tasks. These studies show that the numerosity-related modulation of CDA is reduced in old participants, thus highlighting the involvement of a working-memory component in the age-related decline in multiple object processing. In the case of enumeration, the CDA reduction is present only for relatively large numerosities (>3 targets), suggesting that working-memory efficiency for small target numerosities (up to approximately 3–4 elements) in enumeration tasks is relatively preserved in aging.

Overall, the studies described previously indicate that the mechanisms reflected by posterior N1, N2pc, and CDA undergo age-related decline. However, whether (at least one of) these mechanisms may also reflect compensatory mechanisms in aging is currently unknown. The CRUNCH model predicts that older adults may show neural overactivation with low task loads and that this correlates with a performance level comparable to the one of young adults. In contrast, no further increase in the neural activity of old participants should be visible for high task loads, and this should correlate with a large decline in performance. To assess the stage of processing (early segmentation, target individuation, or active maintenance) at which compensatory activity (if present) arises in old participants during multiple object processing, in the present study, we recorded N1, N2pc, and CDA, while old and young participants performed a visual enumeration task. The targets were presented in relative isolation (i.e., there were no distractors in the target side, low load) or they were intermingled with some distracters (distractor condition, high load). If compensatory activity existed, old participants should perform approximately as well as young participants in the low perceptual load condition (i.e., no distractors in the target hemifield), with a decline in accuracy for the high load condition. At the neural level, in the low load condition, the old group should be associated with higher amplitudes than the young group in the neural component(s) responsible for compensation. Additionally, little or no increase of the critical neural component(s) should be expected for the old group in the high load condition.

2. Methods

2.1. Participants

A sample of 36 (18 young, mean age 24.6 and 18 old, mean age 68.8) participants volunteered for the study. All participants reported no history of neurological or psychiatric disorders and had normal or corrected-to-normal vision. Part of the data from the young participants (12 of 18 subjects) were published in a previous study (Mazza et al., 2013) and were reanalyzed here for the purposes of the present study. All participants gave their written informed consent. The procedures were approved by the University of Trento Ethics Committee.

2.2. Neuropsychological testing

The group of old participants underwent a neuropsychological session of tests to assess their cognitive integrity, with a particular focus on visuospatial abilities. The testing was done to exclude the presence of major visuospatial or working-memory disorders that could interfere with the task at hand. The test session was performed some days (ranging from 7 to 15) before the EEG session. The results of the tests together with demographic data are presented in Table 1.

2.3. Stimuli and procedure

Stimuli were identical to those used in Mazza et al. (2013) and consisted of equiluminant (17 cd/m^2) green and red diamond shapes (0.6° × 0.8°) presented on a black background (1 cd/m^2). Each diamond had a trimmed corner (0.4°) either on the left or on the right side. The diamonds appeared within an invisible grid of 10 rows × 8 columns and could never appear in the extreme columns or rows of the invisible matrix. On each trial, a variable number of targets (1–4) occurred with equal probability and in a random order either to the right or left side of the screen. Targets were defined by color (either green or red, counterbalanced between participants). Stimuli were presented for 150 ms. The maximum time for response was 1500 ms. The intertrial interval was set at 1500 ms. Participants' task was to report the number of targets by pressing one of four buttons arranged vertically on a keyboard with their index or middle finger of both hands. In the distractor-present condition, we presented a fixed number of 16 diamonds (8 elements per side), varying the number of targets (1–4) in one hemifield (see Fig. 1). In the distractor-absent condition, targets and distractors were presented in two different hemifields and the number of distractors was equated to the number of targets in each condition (total display size: 2 for 1 target, 4 for 2 targets, 6 for 3 targets, and 8 for 4 targets). In this way, we aimed to balance the sensory input from both sides, avoiding possible EEG effects due to sensory imbalance (see also Mazza et al., 2013). However, because the number of targets was the same as the number of distracters, participants could have counted either targets or distractors to produce the correct response. To avoid this strategy, we included 5% of catch trials in which the number of distractors and targets differed in the two hemifields (see also Mazza et al., 2013). Given their small number, catch trials were not considered for the EEG analyses.

Table 1
Scores of the old group in the neuropsychological session

	Mean (SD)	Median	Cutoff[a]
Demographic data			
Age old	68.8 (3.4)	67	/
Education old[b]	11.1 (3.2)	10.5	/
Age young	24.6 (2.3)	22	/
Education young	15.8 (1.8)	15.5	/
Neuropsychological tests	*Correct scores*		
MMSE[c]	26.06 (1.10)	26	≤24
RCPM 47	34.9 (4.1)	36.5	<17.5
Attentive matrices (visual search)	53.7 (3.5)	53.5	<30
TMT A	16.2 (8.8)	14.5	>94
TMT B	54.6 (32.1)	52.5	>283
Stroop reaction times	13.9 (5.2)	12.3	>36.9
Stroop errors	−0.05 (3.19)	−0.6	>4.2
Phonemic fluency	40.7 (8.6)	39	<16
Digit span forward	5.8 (0.8)	6	<4
Digit span backward	4.8 (1.2)	5	/
ROCF copy	34.9 (1.8)	35.75	<28.8
ROCF recall	22.6 (4.5)	23.25	<9.4
RAVLT immediate recall	51.6 (6.9)	51	<28.5
RAVLT delayed recall	12.8 (2.4)	13.1	<4.6
Geriatric Depression Scale	3.8 (2.7)	3	>14

The tests assessed the following cognitive functions: cognitive efficiency (Mini Mental State Examination—MMSE, Magni et al., 1996); nonverbal logic (Raven's Colored Progressive Matrices—RCPM 47, Basso et al., 1987); selective attention (attentive matrices, Spinnler and Tognoni, 1987); visual attention and task switching (trail making tests A and B- TMT A and B, Giovagnoli et al., 1996); lexical access and executive functions (verbal fluency Novelli et al., 1986); short-term memory and working memory (digit span forward and backward, Monaco et al., 2013); executive planning and visuospatial memory (copy and recall of the Rey-Osterreith complex figure—ROCF; (Caffarra et al., 2002); long-term memory (Rey's Auditory Verbal Learning Test—RAVLT 15 items; Carlesimo et al., 1995); and geriatric depression (Geriatric Depression Scale; Yesavage et al., 1982)
Key: SD, standard deviation.

[a] The symbol <indicates that values below the cutoff are problematic; the symbol >indicates that values above the cutoff are problematic.

[b] When tested for differences other than age, the two groups differed significantly in education (t=−5.4, $p < .05$).

[c] Abbreviations: Mini Mental State Examination—MMSE (Magni et al., 1996), Raven's Coloured Progressive Matrices—RAVLT (15 items), and Geriatric Depression Scale—RCPM 47 (Basso et al., 1987); attentive matrices, trail making tests A and B-TMT A and B (Giovagnoli et al., 1996), Stroop test, verbal fluency with phonemic cue, digit span forward and backward, copy and recall of Rey-Osterrieth complex figure—ROCF, Rey's Auditory Verbal Learning Test.

Participants completed one training block of 40 trials followed by 10 blocks of 144 trials each, for a total of 1088 trials (128 trials for each numerosity and distractor condition; 64 catch trials).

2.4. EEG recording and analysis

EEG was recorded from 25 electrodes (including PO7/8) arranged according to the standard International System and referenced to the right mastoid activity (A/D rate 1000 Hz, 0.01–250 Hz band-pass filter). The signal was rereferenced offline to the average of both mastoids and filtered at 40 Hz (12 dB/octave) with a low-pass filter. Impedance was kept below 10 kΩ for all channels. Ocular artifacts (blinks and saccades) were corrected using a standard Infomax Independent Component Analysis algorithm. The removal of other artifacts, such as muscular activity or head movements (any channel exceeding ±80 μV criterion), was computed on the EEG segments (see below) and after the Infomax Independent Component Analysis procedure.

The signal was segmented in 800-ms-long epochs starting 200 ms before stimulus onset. Averages for correct responses were calculated separately for numerosity (1, 2, 3, and 4 targets) and

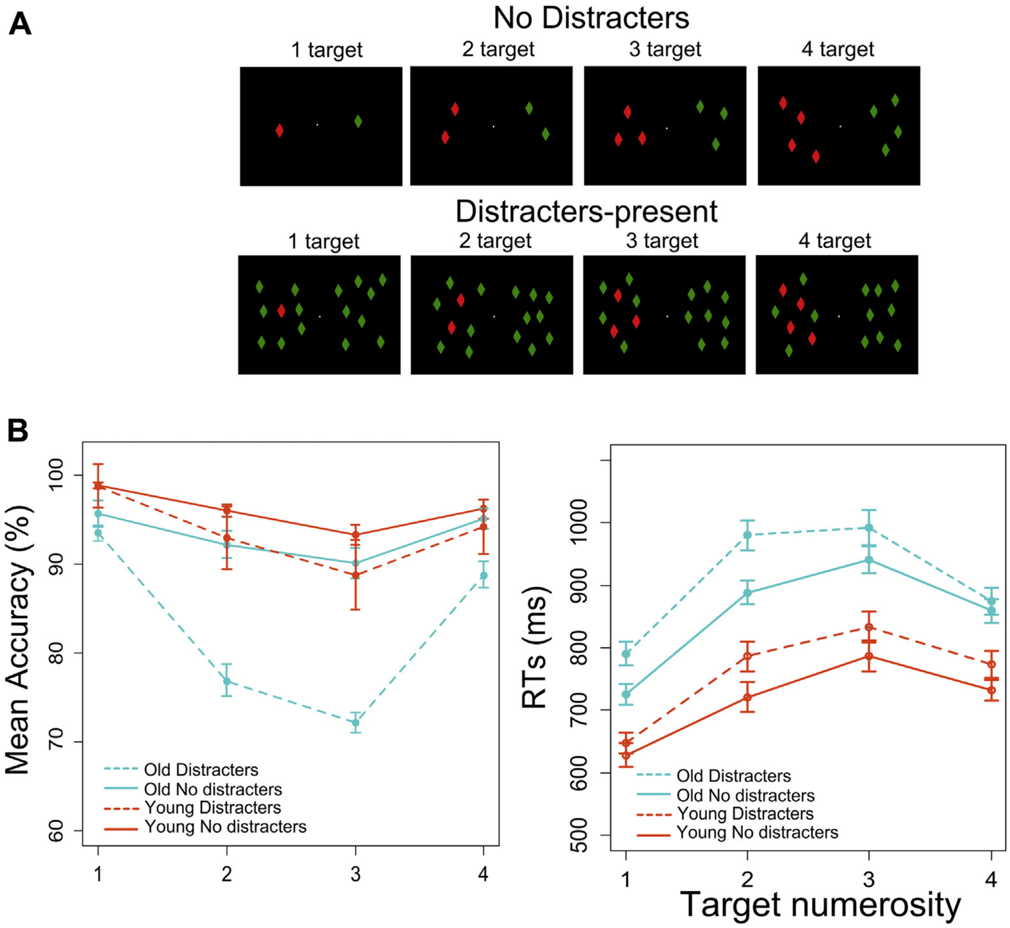

Fig. 1. (A) Example of a four-target trial in the distracter-present (bottom) and distracter-absent (top) conditions. (B) Reaction times and accuracy as a function of target numerosity for the old and young group in each condition.

distractor presence (present vs. absent), for a total of eight conditions. Statistical analyses on N2pc and CDA were conducted on difference values calculated by subtracting the contralateral minus the ipsilateral activity of a cluster of parieto-occipital electrodes (PO7/8, P7/8, and O1/2) in the 180–300 ms (N2pc) and 400–600 ms (CDA) interval, respectively. Ipsilateral and contralateral activities were obtained by collapsing electrodes across target sides (e.g., PO7 was labeled as contralateral for right targets and ipsilateral for left side targets; vice versa for PO8). We also measured the bilateral N1 by averaging the activity measured at P7/8, PO7/8, and O1/2 in the interval between 120 and 180 ms. For each of the three measures (N1, N2pc, and CDA), we computed an analysis of the variances (ANOVA) with age (2 levels: old vs. young), distractor presence (2 levels: present vs. absent), and numerosity (4 levels: 1, 2, 3, and 4) as factors. The Greenhouse–Geisser correction was used to correct for violation of sphericity in the ANOVAs. We report only corrected p values. Post hoc tests were conducted by means of t-tests, corrected using the false discovery rate procedure (Benjamini and Hochberg, 1995) for multiple comparisons.

3. Results

3.1. Behavior

3.1.1. Reaction times

The ANOVA on reaction times with distractor presence (3 levels: catch, present, absent), age (2 levels: young and old), and numerosity (4 levels: 1, 2, 3, and 4) showed a significant effect of age ($F(1,34) = 28.1$, $p < 0.001$), indicating that old adults were significantly slower than young adults. There was also a significant effect of numerosity ($F(3,102) = 126.4$, $p < 0.001$): Participants in both groups were increasingly slower for numerosities up to three targets. An “end effect” (Mandler and Shebo, 1982; Trick, 2008) emerged for the largest numerosity in the set, with numerosity 4 being associated with faster reaction times than numerosity 3. The ANOVA also showed a significant effect of distractors ($F(2,68) = 79.4$, $p < 0.001$), with slower reaction times for the distractor-present condition than for catch and distractor-absent trials (see Fig. 1). The age × numerosity, $F(3,102) = 4.5$, $p < 0.01$, and distractor × numerosity, $F(6,204) = 10.0$, $p < 0.001$ interactions were significant, as well as the three-way interaction ($F(6,204) = 4.8$, $p < 0.001$). Post hoc comparisons contrasted the two groups for each numerosity and distractor condition separately. The old group was significantly slower than the young group for all numerosities in the distractor-present condition (all $ps < 0.001$), in the distractor-absent condition (all $ps < 0.001$), and on catch trials (all $ps < 0.001$).

3.1.2. Accuracy

The ANOVA on accuracy showed a significant effect of age ($F(1,34) = 19$, $p < 0.01$), with the old group being less accurate than the young group. All participants were in general less accurate in the distractor-present condition, as indicated by the significant effect of distractor presence ($F(2,68) = 68.9$, $p < 0.001$). In line with the reaction times results, all participants were also increasingly less accurate as a function of numerosity up to three targets, as indicated by a significant main effect of target numerosity ($F(3,102) = 31.3$, $p < 0.001$); an "end effect" was also visible for the largest numerosity in the set. The two-way interactions between age and distractor presence ($F(2,68) = 24.9$, $p < 0.001$), and numerosity and distractor presence ($F(6,204) = 14.9$, $p < 0.001$) were significant, as was the age × distractor presence × numerosity interaction ($F(6,204) = 6.3$, $p < 0.001$). Post hoc comparisons between the two groups for each distractor condition showed a significant difference between groups in the distractor-present condition for all target numerosities (all $ps < 0.05$). No significant difference emerged for the distractor-absent condition and on catch trials (all $ps > 0.1$), but for trials with 2 targets ($p = 0.05$). To further test for the difference in accuracy between old and young people in the easy versus difficult conditions, we computed the difference in correct responses between old and young people and directly compared the distractor-absent and distractor-present conditions. The t-test indicated a larger difference in the distracter-present condition ($t(17) = 5$, $p < 0.01$). Overall, these results indicate that performance was nearly equivalent for both groups in the easy conditions (i.e., with no distracters in the target side), whereas it greatly differed in the difficult condition (i.e., where distracters and targets were presented in the same hemifield, see Fig. 1).

3.2. Event-related brain potentials

3.2.1. N1

The N1 component was larger in young than in old participants, as indicated by a significant effect of age ($F(1,34) = 8.9$, $p < 0.01$). The mean amplitude of N1 was also larger in the distractor-present condition, as shown by a significant effect of distractor presence ($F(1,34) = 33.1$, $p < 0.001$), and it increased as a function of target numerosity ($F(3,102) = 45.5$, $p < 0.001$). However, the effect of numerosity was not equal in the two distractor conditions, as indicated by a significant distractor presence × numerosity interaction ($F(3,102) = 40.15$, $p < 0.001$). Post hoc analyses (ANOVA) indicated a significant effect of numerosity only for the distractor-absent condition ($F(3,102) = 58.8$, $p < 0.001$), with the N1 increasing as a function of target numerosity, as confirmed by t-test comparisons (all $ps < 0.01$). In line with previous results (Mazza et al., 2013), these findings indicate that N1 amplitude was modulated by target numerosity only when distractors were not present in the hemifield of the targets (see Fig. 2).

3.2.2. N2pc

The ANOVA on N2pc showed significant effects of numerosity ($F(3,102) = 32.1$, $p < 0.001$) and distractor presence ($F(1,34) = 33.04$, $p < 0.001$). The N2pc mean amplitude was modulated by target numerosity and was overall larger in distracter-present trials. The numerosity × distractor presence interaction ($F(3,102) = 8.4$, $p < 0.001$) was also significant, although follow-up ANOVAs revealed a significant effect of numerosity both with ($F(3,105) = 9.1$, $p < 0.001$) and without ($F(3,105) = 37.09$, $p < 0.001$) distracters. Pairwise comparisons (t-tests) showed that the N2pc increased up to a maximum of three elements both when distractors were present in the same hemifield of the targets (all $ps < 0.05$) and when they were not (all $ps < 0.001$; see Fig. 3). Crucially, the age × distractor presence interaction ($F(1,34) = 15$, $p < 0.01$) was also significant. Follow-up comparisons (t-tests) indicated a difference in the N2pc amplitude between the two distractor conditions in the young group: The distractor-present condition elicited larger N2pc than the distractor-absent condition ($t(17) = -6.9$, $p < 0.001$). In contrast, no significant difference was found for the old group ($t(17) = -1.3$, $p = 0.20$). In line with the CRUNCH, the N2pc in the distracter-absent condition was larger in the old participants with respect to the young ones ($t = 2.1$, $p < 0.05$). The N2pc in the distracter condition had a similar amplitude for both groups.

We further characterized the N2pc modulation in old and young participants by computing topographical maps of the scalp activity in the interval between 180 and 300 ms (see Fig. 3). The maps show that relative to young participants, the activity in the distracter-absent condition for the old group was spread across multiple sites and sustained over time. Together with the amplitude effect, this pattern suggests that old participants might recruit more areas (and more intensively) to support task performance in the distracter-absent condition.

3.2.3. Contralateral delay activity

The CDA amplitude was modulated by target numerosity (effect of numerosity: $F(3,102) = 51.7$, $p < 0.001$), as found in previous studies (e.g., Pagano et al., 2014). No other significant effect emerged (see Fig. 3).

3.2.4. Individual efficiency and N2pc

To further explore how the age-related difference in the N2pc for the distracter-absent condition was linked to performance efficiency, we conducted a post hoc analysis for this condition based on a median-split division of accuracy values. Participants in each age group were classified as high and low performers, on the basis of their ranked value on accuracy. This procedure led to four groups of participants (young high performers, young low performers, old high performers, and old low performers). The factor numerosity was not considered here, given that no significant interaction with age emerged from the main analysis.

The ANOVA on accuracy values with two between-subject factors (age: old vs. young; efficiency: high vs. low performers) indicated that the two main effects were significant (both $Fs > 22.6$, both $ps < 0.001$). Old participants were overall less accurate than young participants, and high performers were better than low performers (Fig. 4). Thus, this result confirms that the median-split criterion allowed us to capture variation in the individuals' accuracy level.

The ANOVA on the N2pc with the same factors as for accuracy indicated a significant effect of age ($F(1,32) = 4.8$, $p = 0.035$) and a marginally significant effect of the age × efficiency interaction ($F(1,32) = 3.3$, $p = 0.078$). The interaction captured the fact that in the high-performing group, the N2pc for old adults was larger than the N2pc for young adults ($t(16) = 2.5$, $p = 0.024$), but no difference was found between old and young participants in the low-performing group. A tendency toward opposite directions was visible when we compared high and low performers separately for the old and young groups, but these differences failed to reach statistical significance (Fig. 4).

The results indicate that the most successful individuals in executing the task (i.e., some of the young participants) were associated with the smallest N2pc amplitude and suggest that the old individuals who overactivated the individuation mechanism performed the task better.

3.3. Discussion

According to CRUNCH, elderly individuals are able to compensate for the age-related decline in some cognitive domains by activating more areas and/or by overactivating the areas that are involved in the execution of a particular task (Park and Reuter-Lorenz, 2009; Reuter-Lorenz et al., 2000). The neural overactivation is associated with a good level of performance in relatively easy tasks. In contrast, there is no overactivation, and a

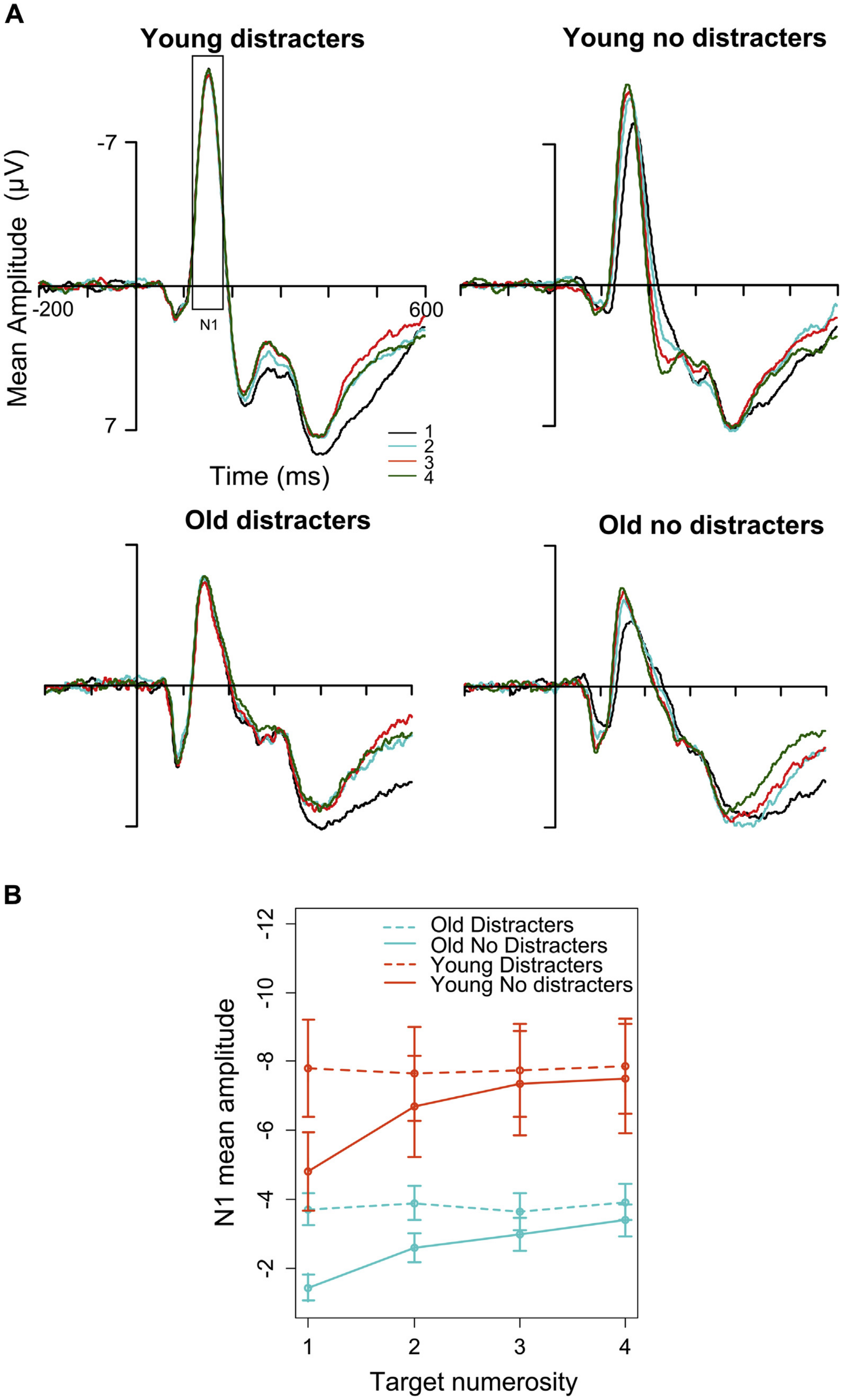

Fig. 2. (A) The bilateral grand-average ERP waveforms represent the N1 component, as a function of target numerosity in the young group (distracter-present condition: top left; distracter-absent condition: top right) and in the old group (distracter-present condition: bottom left; distracter-absent condition: bottom right). The time window considered for the analyses is shown by the outline rectangle. (B) Mean amplitude values of N1 (120–180 ms) in the different conditions. Abbreviation: ERP, event-related brain potential.

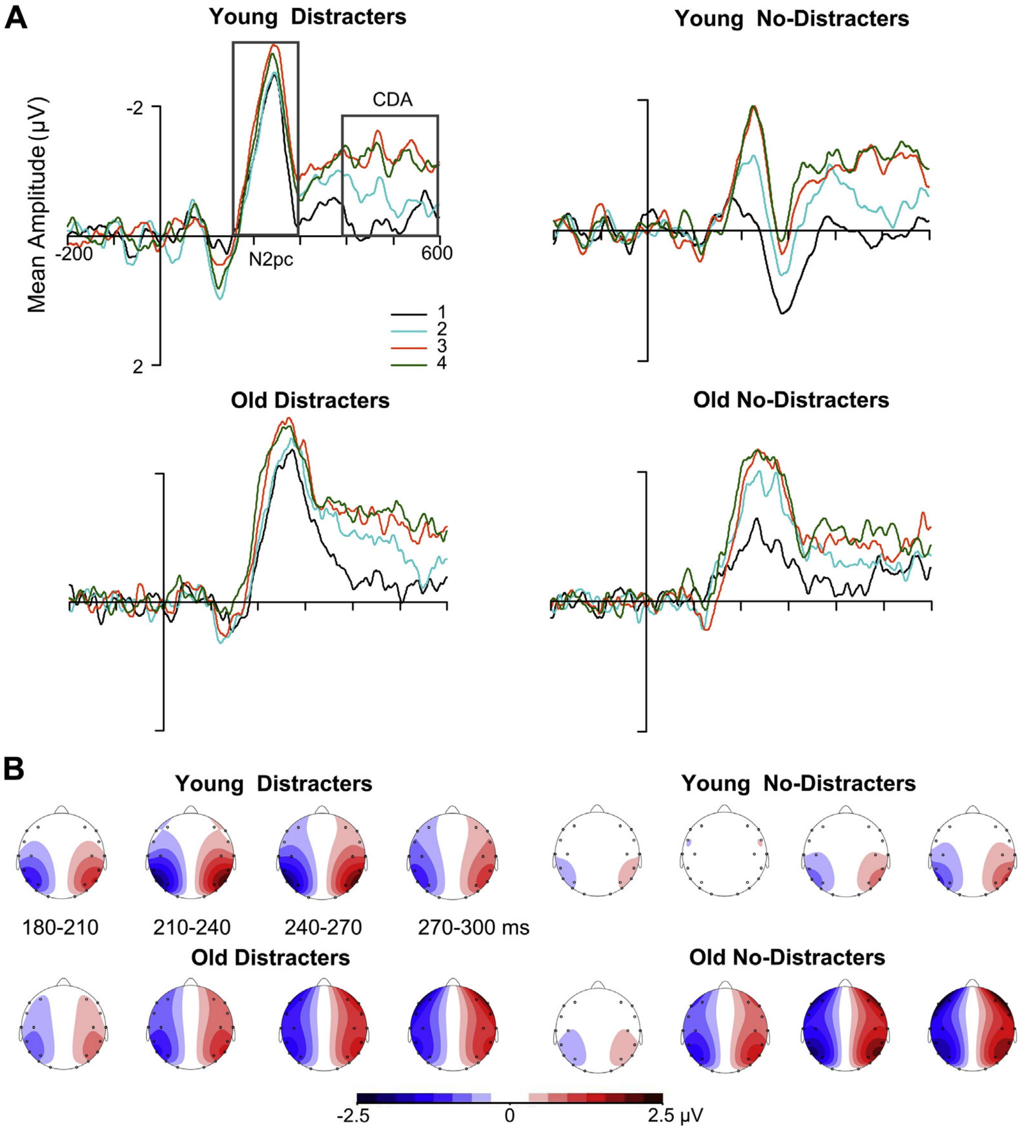

Fig. 3. Lateralized ERP waveforms. (A) ERP difference waveforms for N2pc (180–300 ms) and CDA (400–600 ms) as a function of age group, numerosity, and distracter presence. Panels represent, respectively, the evoked activity as a function of numerosity for the young group (distracter-present condition: top left; distracter-absent condition: top right) and for the old group (distracter-present condition: bottom left; distracter-absent condition: bottom right). (B) Topographical maps of the N2pc activity (180–300 ms) in the two age groups as a function of distractors presence. The maps were constructed considering four time windows of 30 ms each for each group and distracter condition and are computed on difference values (contralateral minus ipsilateral activity) mirrored across the midline. Abbreviations: CDA, contralateral delay activity; ERP, event-related brain potential.

large decline in performance is visible for difficult tasks, presumably because no more neural resources are available in the latter case. In the present EEG study, we aimed at understanding the temporal locus of the compensatory neural activity in aging during a visual enumeration task. Task load was manipulated by varying the presence of distracters in the target hemifield.

The results on response times did not indicate any compensatory activity, as old participants were slower in enumerating targets with respect to younger adults in all conditions (see Salthouse, 1996). In contrast, the accuracy was overall good for aged participants in the easy condition (i.e., when no distractors were presented in the target hemifield). In line with CRUNCH (Reuter-Lorenz and Cappell, 2008), this result suggests the presence of compensatory phenomena for old adults. As predicted by CRUNCH, old adults performed worse than young controls in the distractor-present condition. The (relatively) high error rate for old participants in the condition with distracters in the target hemifield could be explained either in terms of lack of resources to select the target information with respect to distracters or as evidence for the inability to suppress the representations of distracters when these surround the target elements (Cashdollar et al., 2013; Clapp and Gazzaley, 2012)

The ERP results were instrumental to clarify the time course of age-related neural overactivation and to uncover the mechanism/s responsible for compensation.

In both groups, the N1 amplitude was modulated by target numerosity only in the absence of distractors, further supporting the idea that N1 indexes a relatively early mechanism that operates over the stimulus configuration as a whole, and allows for coarse representations of the overall number of elements, independently of their relevance for the task at hand (see Mazza et al., 2013). The present results additionally indicated a general suppression of the

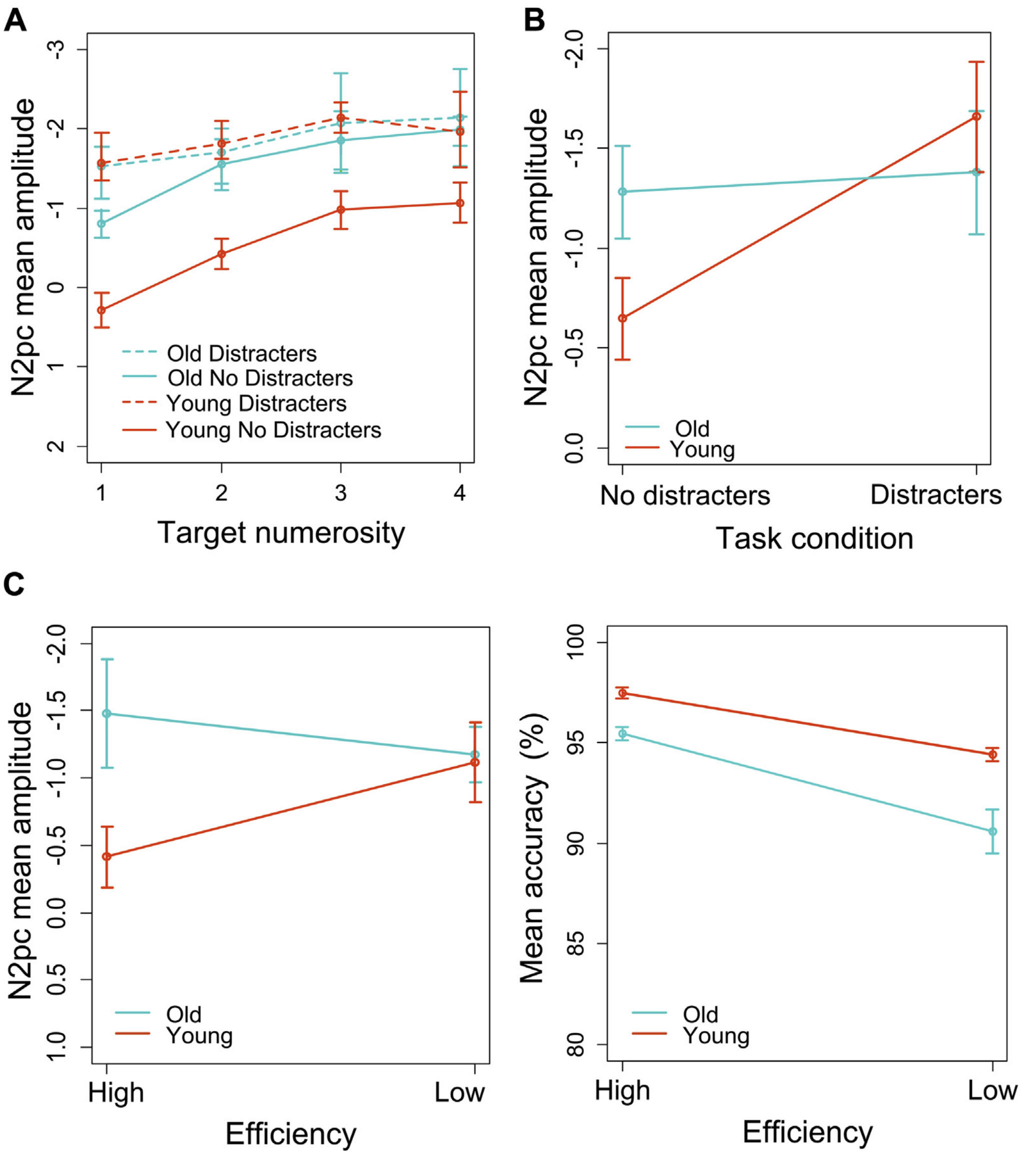

Fig. 4. (A) Mean amplitude values for the N2pc (180–300 ms) as a function of age group, numerosity, and distracters presence. (B) N2pc effect as a function of age group and distracter presence, collapsed across numerosity levels. (C) Results of the efficiency analysis: N2pc values and accuracy data as a function of age and efficiency.

N1 response in the old group, replicating the results of previous studies on aging (Ceponiene et al., 2008; Störmer et al., 2013a; Zanto et al., 2010), and suggesting that the perceptual representation of the overall stimulus configuration is degraded in aging.

The results indicated that N2pc was modulated by target numerosity in both age groups, replicating previous findings on young adults (Ester et al., 2012; Pagano and Mazza, 2012; Pagano et al., 2014), and suggesting that old individuals were able to -process relevant items as distinct elements during visual enumeration (see also Pagano et al., 2015). Crucially, although the N2pc amplitude increased in the distractor-present condition in the young group, no such modulation occurred for the old group. In addition, the N2pc was larger for old as compared to young participants in the easy condition (i.e., when no distracters were presented in the target hemifield). These results resemble the accuracy data found in this study, although with a reversed pattern (i.e., the difference in the N2pc between old and young individuals was maximal for the condition with equivalent accuracy). The effect of perceptual load on N2pc for old versus young adults did not interact with numerosity. This aspect deserves future investigation, but the relatively small range of target numerosities used in the present study—all within the subitizing range and easy to process in the no-distracter condition, see Fig. 1—may (at least partially) explain the lack of an interaction between the N2pc overactivation (as visible in the no-distracter condition) and numerosity in older participants.

The N2pc findings are in line with CRUNCH and resonate with previous fMRI research showing that old adults more likely overactivate the neural areas involved in the execution of a certain task to reach a level of performance similar to young adults (Cappell et al., 2010; Reuter-Lorenz and Cappell, 2008). In contrast, no further increase in the neural activity related to multiple object individuation is possible for old individuals in difficult task conditions (in our study, when targets and distracters are intermingled), as reflected by the lack of difference in the N2pc amplitude between the easy and difficult conditions.

The post hoc analysis on efficiency for the distracter-absent condition revealed that the N2pc for old adults was larger than the N2pc for young adults in the high-performing group, whereas no difference was visible between old and young participants in the low-performing group. More in general, young high-performing individuals were associated with the smallest N2pc. Taken together, these results confirm that variation in N2pc amplitudes track variation in age and efficiency and suggest the presence of compensatory phenomena in old adults.

Overall, the N2pc results seem to support the view that the locus of age-related compensatory effects during enumeration is represented by the functioning of an attention-based mechanism of object individuation. Together with the N1 findings, the N2pc pattern for the easy condition additionally suggests that the overfunctioning of the individuation mechanism may act specifically to compensate for the underfunctioning of the early perceptual process (indexed by the N1).

In our study, we rely on the specific definition of "compensation" delineated by CRUNCH (Reuter-Lorenz and Cappell, 2008). According to this hypothesis, compensation occurs when the neural overactivation is accompanied by: (1) a decrease in performance between easy and difficult contexts in old adults; and (2) a reduction (or absence) of difference in performance between old and young individuals for the easy task. However, it should be noted that there is no general consensus on the issue of compensatory brain activity in aging. Other researchers set additional criteria for the definition of compensation (such as the presence of a unique neural pattern supporting task execution specifically related to aging) and provided alternative explanations for the neural overactivation visible in old adults under certain circumstances. For instance, overrecruitment of brain areas may be the result of increased interindividual variability in the brain structures, or a sign of dedifferentiation, namely the loss of selective processing associated with aging (for a review, see Grady, 2012).

In contrast with the N1 and N2pc results, the analysis on the CDA did not reveal any age-related effect. This suggests that working memory-related procedures are not involved in compensatory phenomena in enumeration tasks. Additionally, the present results invite the inference that working memory is not the crucial locus for the age-related decline in enumeration of small object numerosity (i.e., up to 3–4 elements; for similar results see Pagano et al., 2015). In contrast with our pattern, previous studies on aging and multiple object processing (Sander et al., 2011; Störmer et al., 2013b) showed a CDA reduction in aging for all target quantities. We speculate that differences in the overall involvement of working memory related to task requirements could explain this discrepancy. Indeed, the extant studies indicating an age change in CDA (e.g., Sander et al., 2011) used a delayed-match-to-sample task, which likely relies on the working-memory system more heavily than the speeded enumeration task used in the present study.

In conclusion, this study shed light on how old adults compensate for diminished perceptual abilities to perform visual tasks with different levels of difficulty. In particular, the results showed an age-related decline in the early perceptual mechanisms that are sensitive to the overall configuration of targets and distracters (as reflected by a diminished N1). The underactivation was followed by an overactivation of the mechanism responsible for multiple target individuation (indexed by N2pc) in easy conditions, which led to good accuracy levels in older participants. This compensatory effect did not occur when the task became more difficult (i.e., in the presence of distractors), likely because of a limited pool of neural resources during individuation (see CRUNCH). Thus, in enumeration, aging is associated with phenomena of neural plasticity that rely on the overactivation of the individuation mechanism and that have compensatory effect for easy perceptual conditions.

Disclosure statement

The authors have no conflicts of interest to disclose.

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