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## Special issue: Research report

# Individual differences in aging and cognitive control modulate the neural indexes of context updating and maintenance during task switching

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### ABSTRACT

This study aimed to explore the combined influence of age and cognitive control on the behavioural and electrophysiological indicators of local, restart and mixing costs. Two groups of middle-aged (49–60 y.o.,  $N = 40$ ) and older (61–80 y.o.,  $N = 40$ ) adults were split according to their overall z-score in a composite of six neuropsychological measures of executive function. All participants performed a task-cueing version of the Wisconsin Card Sorting Test (WCST) adapted for measuring event-related potentials, whereby tonal cues instructed to switch or repeat the task rule. A single-task condition with identical sensory and motor response demands was used to aid interpretation of behavioural and brain responses to cues and target events. Working memory updating of stimulus–response mappings, as putatively indexed by local switch costs and cue-locked P3 activity (350–460 msec post-cue onset), was preserved in both older and low control adults. In turn, low control adults showed larger restart costs and enhanced cue-locked P2 amplitudes (190–250 msec) in the task-switching condition only, suggesting lesser preparatory control in the presence of interference. Low control adults showed comparatively larger mixing costs and smaller cue-locked fronto-central slow negativities (500–700 msec), suggesting an inefficient online maintenance of task-set information over time. In contrast, target-locked brain responses were mostly sensitive to age-related effects, with older adults showing two well-known effects: (1) an “anterior shift” in target P3 activity (350–460 msec), and (2) an attenuation of fronto-central slow negativities in single-task and task-switching conditions, respectively. The additive association found between age and cognitive control for different behavioural indexes of task-switch costs suggests a differential influence of these factors upon two successive information processing stages: individual differences in cognitive control mainly influenced the neural indexes of preparatory task-set activation and maintenance, whereas age-related effects influenced the neural indexes of target response selection and task execution.

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## 1. Introduction

Successful aging has been related to a flexible mind and efficient executive function (Kramer et al., 1999), and age-related cognitive deficits have been linked to dysfunction of the prefrontal cortex (West, 1996). A simple computational model of executive control argues that a variety of cognitive deficits observed in the elderly could be explained by a fundamental deficit in the ability to represent, maintain, and update contextual information in working memory (Braver et al., 2001; Braver and Barch, 2002; Braver and West, 2008). This general prediction about age-related cognitive deficits could be assessed by comparing the behaviour and brain responses of younger and older adults under task-switching and single-task conditions, since the former task context taxes working memory more than the latter one. Task switching involves the online maintenance and updating of higher-order sensorimotor associations between sets of sensory and motor representations that need to be intermittently updated – upheld, reversed, or replaced altogether – in a context-sensitive way. Usually subjects respond slower and less accurately when switching than when repeating a task, a phenomenon known as the behavioural switch cost (Meiran, 1996; Monsell, 2003).

Under the hypothesis that age-related cognitive decline owes to specific deficits in higher-order cognitive control, older adults are often expected to show larger local switch costs than younger adults. However, such a prediction has not received strong empirical support to date. Larger local costs in older compared to younger adults have been reported mostly with unpredictable task switches (Van Asselen and Ridderinkhof, 2000; Friedman et al., 2007), or when there is considerable stimulus–response overlap between task sets (Kray and Eppinger, 2006). In turn, many studies failed to find the purported age-related effects on local switch costs after controlling for task preparation, practice, and general motor slowing (Salthouse et al., 1998; Kray and Lindenberger, 2000; Cepeda et al., 2001; Mayr, 2001; Meiran et al., 2001, see Braver and West, 2008, for a review).

One cause for these inconsistencies could be a plausible confound between specific and nonspecific sources of task-switch costs, such as those associated with the infrequent task cues in intermittently-instructed task-cueing paradigms. This type of behavioural cost has been referred to as ‘restart costs’ (Allport and Wylie, 2000), and can be observed in the first target response following both task-switch and task-repeat cues (Monsell, 2003). Restart costs have been related to task-set (goal) activation, cue-task retrieval (Altmann, 2002), and the suppression of responses for a previous task (Allport and Wylie, 2000; Cepeda et al., 2001). These accounts are compatible with a general-purpose mechanism for the resolution of task uncertainty, whenever the infrequent cues prompt for a decision about whether to switch or to repeat the previous task rule (Barceló et al., 2008). Hence, the behavioural cost measured after an infrequent task-switch cue could well reflect a combination of general and specific task-switching mechanisms (Salthouse et al., 1998).

Another type of switch-nonspecific costs, known as “global set-selection costs”, is obtained when comparing behaviour

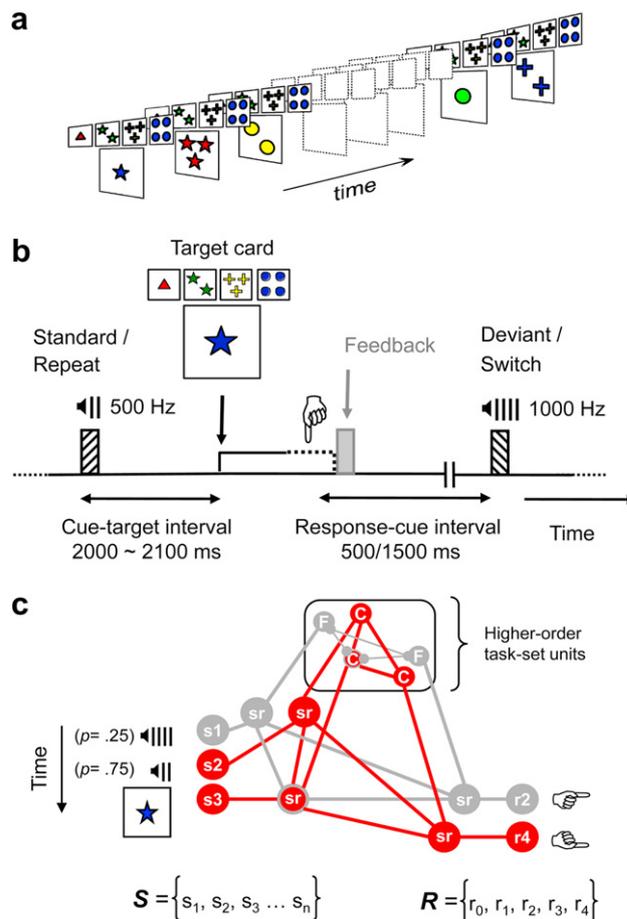
between task-switching and single-task blocks (Meiran et al., 2000; Mayr, 2001). A related index of mixing costs provides a purer measure of processes linked to the maintenance of two or more task rules in memory by comparing only task repetition trials uncontaminated from local switch or restart costs (Monsell, 2003). In contrast with the controversial effects for local switch costs, the task-switching literature shows consistent age-related increases in mixing costs (Kray and Lindenberger, 2000; Reimers and Maylor, 2005), indicating that the ability to manage two alternating task sets in working memory is negatively affected by advancing age. This age-related increase in mixing costs has been attributed to a deficit in the maintenance of task-set information over time (Braver and West, 2008), and has been accompanied by enhanced slow negative brain potentials during both task-switch and task-repeat trials (DiGirolamo et al., 2001; Goffaux et al., 2008; West and Travers, 2008).

The functional segregation of overall task-switch costs into local, restart, and mixing costs through experimental design has been supported by electrophysiological evidence showing that these three types of costs correlate with distinct cue-locked and target-locked brain event-related potentials (ERP) in a task-cueing paradigm, reflecting distinct information processing stages during task preparation and execution, respectively (Barceló et al., 2008; Periañez and Barceló, 2009). The largest source of individual variability, *mixing costs*, correlated with the amplitude of a slow negative potential widely distributed across fronto-posterior scalp regions, which also seemed to extend into the target period (Nicholson et al., 2005; Barceló et al., 2008). Task-switch cues also modulated two cue-locked ERP positivities (P2 and P3), whose mean amplitudes correlated with *restart* and *local switch costs*, respectively (Barceló et al., 2008; Periañez and Barceló, 2009). These two cue-locked ERPs form part of the endogenous P300 complex (Squires et al., 1976; Barceló et al., 2002), which has long been related to *uncertainty resolution* in response to surprising task events that demand context-updating operations in memory (Sutton et al., 1965; Donchin, 1981). The first switch-unspecific mechanism modulates an early cue-locked P2 (180–250 msec) that has been likened to general task-set re-activation (Rushworth et al., 2002), or cue-based task retrieval (Altmann, 2002), and presumably also involves momentary inhibitory control resulting in restart costs (Barceló et al., 2008). The second switch-specific mechanism modulates a later cue-locked P3 (300–450 msec) that has shown an inverse correlation with local switch costs, and has been likened to anticipatory updating of S–R associations in working memory. Overall, these recent studies establish a link between two sources of task-switch costs and two distinct cue-locked ERP positivities involved in the anticipatory updating of task information (Barceló et al., 2002, 2006, 2008; Periañez and Barceló, 2009). The functional significance of these cue-locked positivities contrasts with that of target-locked P3 activity (300–450 msec), which seems more related to target response selection and execution. Critically, whereas larger stimulus or task uncertainty results in larger cue-locked P3 amplitudes, those same task conditions reduce target-locked P3 activity (Kieffaber and Hetrick, 2005; Barceló et al., 2006, 2008). This dissociation between task preparation and execution processes does not transpire from the canonical P300 brain potential to unexpected *oddball* targets (Donchin, 1981; Polich, 1996), because this

measure confounds the preparatory resolution of task uncertainty (*oddballness*, *novelty P3*) with task execution processes (*targetness*, *target P3*) such as the selection of a target response (Barceló et al., 2006, 2008; Barceló and Knight, 2007). Task-cueing paradigms may help us to isolate these two distinct types of P300 activations related to two distinct and temporally ordered stages of task performance (Rubinstein et al., 2001; Barceló, 2003; Periañez and Barceló, 2009).

The present study aimed to explore the effects of age and cognitive control on the behavioural costs and brain responses to contextual cues and target cards in a task-cueing analogue of the Wisconsin Card Sorting Test (WCST) that has been adapted for measuring brain potentials (Barceló, 2003; see Fig. 1a, b). Two sub-groups of middle-aged (49–60 y.o.) and older (61–80 y.o.) adults were split by their overall median z-score in a composite of neuropsychological measures of executive function, in order to compare working memory function in response to the same task cues and target cards under either task-switching or single-task conditions. In order to aid interpretation of the behavioural and brain responses in the task-switching condition, we administered a control condition with identical sensory and response demands as our WCST analogue (Fig. 1), only without the requirement for task alternation. In this single-task condition, task cues were defined as mere distracters that had to be ignored for efficient task performance. This task design was inspired by the hypothesis that efficient cognitive control depends upon the representation, maintenance, and updating of contextual task representations in working memory (Braver and Barch, 2002; Braver and West, 2008). The resolution of uncertainty associated to cues and targets in each task condition was expected to elicit distinct cue-locked and target-locked P300 activations in a fronto-posterior network for cognitive control (Barceló et al., 2002, 2006, 2008). In order to calibrate the information processing demands of contextual cues and targets, we adopted Miller's (2000) model of prefrontal function combined with the information theoretical approach to cognitive control (Koechlin and Summerfield, 2007; Barceló and Knight, 2007; Barceló et al., 2008). From these theoretical premises, the information processing demands associated with a task-switch cue increase with the number of higher-order task-set units being held in working memory (Nyhus and Barceló, 2009). Accordingly, we predicted larger behavioural costs and larger cue-locked P300 activations for the same task-switch cues delivered under task switching relative to single-task conditions (Barceló et al., 2008; Nyhus and Barceló, 2009; see Fig. 1b, c). Moreover, an efficient representation and updating of the task context in the task-switching condition was expected to reduce all three kinds of general and switch-specific costs, even though different component processes may be responsible for each type of cost (Braver et al., 2001; Barceló et al., 2008). In the single task, an efficient representation of the task context was expected to result in lesser behavioural distraction by the irrelevant cues, since both irrelevant distracters and task-switch cues can elicit context-updating activations in the same fronto-posterior network for cognitive control (Chao and Knight, 1997; Barceló et al., 2006; Barceló and Knight, 2007).

Following the task-switching literature on aging, we set to explore four main hypotheses about age-related task-switch costs and brain responses during the task preparation and



**Fig. 1 – Card sorting protocol adapted for recording ERP.** (a) Schematic of one series of the MCST (Barceló, 2003), with choice cards that can be unambiguously matched with each key card based on only one perceptual dimension. In this study trial series begun with a switch cue followed by a variable number of between 1 and 4 task-repeat trials. (b) Schematic of one MCST trial where tonal ‘switch’ and ‘repeat’ cues signal changes or repetitions in the previous sorting rule, respectively. The same tones were instructed as to-be-ignored distracters in a single-task condition where cards were sorted by the colour rule only. (c) Integrative model of prefrontal function (adapted from Miller, 2000) used to formalize the intuitive idea that the information processing demands associated with a contextual task-switch cue increase with the number of higher-order task-set units held in working memory (cf., Nyhus and Barceló, 2009). Red indicates active task-set units or pathways. Small solid circles represent conflict between two antagonistic higher-order task-set units. For simplicity, only three stimuli and two motor responses are represented here from the pool of all available stimuli and responses in the two active task sets, namely, the colour (C) and form (F) rules (see the main text for an explanation).

execution stages of a WCST analogue. First, we hypothesized that if cognitive control hinges on a preserved ability to represent, maintain and update the task context – regardless

of age, – then adults with low cognitive control should show larger local costs and smaller cue-locked P3 activations than high control adults, indicative of inefficient context-updating operations during preparatory S–R remapping in working memory. Conversely, in the single-task condition low cognitive control adults should exhibit comparatively larger behavioural distraction and abnormally enhanced cue-locked P3 amplitudes to the now irrelevant task cues, reflecting inefficient updating of irrelevant task representations – and independent of age. Second, similar predictions were made for restart and mixing costs in adults scoring low on a composite score of neuropsychological tests of executive function. Thus, larger restart costs in low control adults were expected to correlate with enhanced cue-locked P2 amplitudes during task switching. In turn, larger global/mixing costs in low control adults were expected to correlate with abnormally reduced slow negative potentials in the task-switching condition (Kray et al., 2005; West and Moore, 2005; Goffaux et al., 2006; West and Travers, 2008). Third, we predicted a multiplicative interaction between age and cognitive control, implying that both factors selectively influence the same processing stage(s) (Ruthruff et al., 2001; Sternberg, 1969), or draw on a common pool of cognitive resources (Kahneman, 1973). In turn, an additive association between age and cognitive control would be expected under the alternative hypothesis that these two factors selectively influence distinct processing stages in the temporal organization of cognitive control during task switching (Meiran et al., 2001; Ruthruff et al., 2001).

Finally, we tested the hypothesis of a posterior–anterior shift in aging that predicts larger engagement of frontally-mediated control systems (Davis et al., 2008), normally observed as an “anterior shift” in the scalp distribution of target P3 amplitudes in simple *oddball* tasks (Friedman et al., 1993, 1997, 2007; Fabiani et al., 1998). As said before, target P3 potentials to surprising *oddball* targets likely reflect a mixture of preparatory resolution of task uncertainty (*oddballness*, *novelty* P3) together with target response selection and execution (*targetness*, *target* P3; Barceló et al., 2002; Barceló and Knight, 2007). The present task-cueing design allowed us to isolate these two types of P300 activations, and hence, to examine whether the age-related anterior shift in P300 activity relates to the preparatory resolution of uncertainty (cue-locked P3), or to target response selection and execution processes (target P3).

## 2. Methods

### 2.1. Participants

An initial sample of 104 adults took part in the study (mean age = 62.2 years, standard deviation – SD = 8.2 years, range 48–90 years, 70 females). They were recruited with advertisements at the university campus and the city council of Palma de Mallorca. They all had normal or corrected to normal visual acuity. History of neurological disease, psychiatric illness, head injury, stroke, substance abuse (excluding nicotine), learning disabilities, or any difficulty that could interfere with behavioural testing were criteria for

exclusion from this sample. All participants completed a battery of neuropsychological tests during two 60-min sessions scheduled two weeks apart. Neuropsychological assessment was performed in accordance with the Declaration of Helsinki, and informed consent was obtained from all participants. Twenty-four participants with scores lower than 28 on the Mini Mental State Examination (MMSE; Folstein et al., 1975), higher than 14 points on the Geriatric Depression Scale (GDS; Yesavage et al., 1982), or higher than .5 in the Clinical Dementia Rating scale (CDR; Hughes et al., 1982) were discarded from the analyses. This left a final sample of 80 healthy participants. Two age groups were extracted from the group median for age: middle-aged ( $N = 40$ ; mean  $\pm$  SD =  $55.7 \pm 2.8$ ; range = 49–60 y.o.), and older adults ( $N = 40$ ; mean  $\pm$  SD =  $67.3 \pm 5.1$ ; range = 61–80 y.o.). Age groups did not differ in years of formal education (middle-aged = 11.9; older = 10.8), CDR scores (middle-aged = .03; older = .03), GDS scores (middle-aged = 6.1; older adults = 6.2), and gender distribution (middle-aged women = 62.5%; older women = 69%; see Table 1).

### 2.2. Neuropsychological estimation of cognitive control

A battery of neuropsychological tests was administered to encompass several cognitive skills including visuo-motor speed of processing (digit symbol of the Wechsler Adult Intelligence Scale III – WAIS-III; Wechsler, 1999), visual-spatial memory (Rey complex figure; Rey, 1954), associative learning (CANTAB-Paired Associates Learning; Robbins et al., 1997), semantic fluency (animals), verbal fluency (Controlled Oral Word Association Test – COWAT; Benton and Hamsher, 1976), long-term memory access (Boston Naming Test; Kaplan et al., 2001), working memory span (forward and backward Digit Span, WAIS-III), control of interference (Stroop test; Jensen and Rohwer, 1966), and several indexes of cognitive flexibility such as the Brixton test (Burgess and Shallice, 1997), and the Trail Making Test (TMT) (Reitan, 1954). A composite index of cognitive control was then computed as the average z-score collapsed across six measures often used as indexes of executive function, namely, Stroop colour-word, TMT B:A, Digits forward and backward, number of errors in the Brixton test, and the COWAT. The median of this composite z-score was used to split the final sample of 80 participants into two groups. The high and low cognitive control groups so obtained did not differ in terms of age, gender distribution, MMSE and mood scores, but they did in years of formal education. Table 1 summarizes the neuropsychological results for the four sub-groups after the double median group split for age and the composite index of cognitive control. There was a slight bias in the number of participants across the four sub-groups, although these differences did not reach significance [ $\chi^2(1) = 1.8, p = .18$ ], and no further adjustments were made. Mean z-scores differed between the high and low cognitive control groups ( $F_{1,76} = 72.4, p < .0001$ ), but did not between middle-aged and older adults ( $F_{1,76} = 2.3, p = .14$ ). Main effects and interactions between the age and cognitive control factors for the full list of neuropsychological measures can be found in Table 1.

**Table 1 – Means (and standard errors of the mean) of several neuropsychological test scores for middle-aged and older adults split by their level of cognitive control.**

	Middle-aged		Older		Age	Control	Age × control
	High control (n = 23)	Low control (n = 17)	High control (n = 17)	Low control (n = 23)			
Cognitive control (z)	.40 (.05)	-.31 (.06)	.38 (.06)	-.44 (.05)	ns	***	ns
Age	54.2 (.9)	55.6 (1)	68.5 (1)	68.3 (.9)	***	ns	ns
Education (years)	12.2 (.7)	11.6 (.8)	11.7 (.8)	9.8 (.7)	ns	*	ns
MMSE	29.7 (.13)	29.6 (.15)	29.5 (.15)	29.1 (.13)	ns	ns	ns
CDR	0 (.02)	.06 (.03)	0 (.03)	.06 (.02)	ns	*	ns
GDS	5.9 (.73)	6.3 (.85)	5.8 (.85)	6.6 (.73)	ns	ns	ns
Stroop W	101.8 (3.4)	101.3 (3.9)	95.6 (3.9)	91.6 (3.4)	*	ns	ns
Stroop C	67.8 (2.2)	66.3 (2.5)	66.5 (2.5)	59.8 (2.2)	ns	*	ns
Stroop CW <sup>a</sup>	41.2 (1.6)	36.4 (1.9)	41.2 (1.9)	31.5 (1.6)	ns	***	ns
TMT-A	34.1 (2.8)	32.4 (3.3)	40.1 (3.3)	44.4 (2.8)	**	ns	ns
TMT-B	63.4 (8.2)	76.3 (9.6)	79.5 (9.6)	123.5 (8.2)	***	**	ns
TMT-B (errors)	.34 (.20)	.53 (.23)	.35 (.23)	.78 (.20)	ns	ns	ns
TMT B:A <sup>a</sup>	1.88 (.18)	2.54 (.21)	2.04 (.21)	2.88 (.18)	ns	***	ns
Digits forward <sup>a</sup>	9.61 (.43)	7.2 (.50)	9.43 (.52)	7.3 (.43)	ns	***	ns
Digits backward <sup>a</sup>	7.43 (.35)	5.82 (.41)	7.31 (.42)	4.6 (.35)	ns	***	ns
Rey copy	35.6 (.60)	33.7 (.7)	34.7 (.7)	33.6 (.60)	ns	*	ns
Rey memory	22.4 (1.2)	18.4 (1.4)	20.2 (1.4)	14.1 (1.2)	*	**	ns
COWAT-FAS <sup>a</sup>	39.7 (2.2)	34.7 (2.5)	43.1 (2.5)	28.6 (2.2)	ns	***	*
Semantic Fluency	23.2 (1)	22.7 (1.2)	23.2 (1.2)	18.2 (1)	ns	*	*
Boston Test	57.7 (.94)	53.5 (1.1)	56.4 (1.1)	50.9 (.94)	ns	***	ns
PAL (first correct)	18.2 (1)	15.8 (1.2)	17.6 (1.2)	13.9 (1.1)	ns	**	ns
PAL (errors)	3.65 (1)	6.5 (1.2)	4.6 (1.3)	7.8 (1.1)	ns	**	ns
Brixton (errors) <sup>a</sup>	12.7 (.93)	19.1 (1.1)	13.8 (1.1)	21.8 (.93)	ns	***	ns
Digit Symbol	61.8 (2.7)	60.5 (3.2)	65.9 (3.2)	42.9 (2.7)	**	***	**

Note. Stroop C = Stroop colour; Stroop W = Stroop word; Stroop CW = Stroop colour-word; PAL = Paired Associate Learning (no. of items correctly placed at first attempt and total errors); cognitive control (z) = standardized composite score of cognitive control. The significance levels of main effects and interaction of age and cognitive control for each test score are listed on the three right-most columns.

\* $p < .05$ ; \*\* $p < .01$ ; \*\*\* $p < .001$ ; ns, non-significant.

a Test scores used to compute the composite z-score of cognitive control.

### 2.3. Experimental task and procedures

We used two versions of a computerized task-cueing paradigm inspired in the WCST (Barceló, 2003; Rubinstein et al., 2001), each corresponding to the single-task and task-switching procedures. These two task conditions shared the same visual and auditory stimulation, but involved different sets of instructions under both single-task and task-switching response requirements, respectively (Fig. 1). Our WCST analogue used the 24 choice cards that can be unambiguously matched with the key cards based on one stimulus dimension only (i.e., either the colour or shape of items in the card). Unambiguous card sorts are required for a sensitive scoring of different types of errors (Barceló, 2003). The colored geometrical shapes were outlined in black against a white background to improve visual contrast, and were matched in luminance. In both task conditions, each trial consisted of a contextual tonal cue [either 500 Hz or 1000 Hz binaural tones, 200 msec duration, 10 msec rise/fall times, 75 dB sound pressure level (SPL)] followed by a visual target display with four key cards on top of one choice card, all centred on a computer screen 2 m away from the participant. The target stimulus subtended a visual angle of 4° horizontally and 3.5° vertically, and remained on display until a response was given, or up to a maximum of 3 sec (Fig. 1b). Both task conditions consisted of a single block

of 216 target trials that were cued either by one relatively infrequent tone ( $p = .25$ ), or by the other tone ( $p = .75$ ), according to a semi-random sequential arrangement described below. The cue-target interval (CTI) was jittered between 2000 and 2100 msec with a uniform distribution to prevent systematic noise in the target-locked waveforms. The response-cue interval randomly adopted the values of either 500 or 1500 msec within subjects, but this variable will not be considered in the analyses. Immediately after responding, the Spanish word for “right” or “wrong” was displayed for 200 msec. Also the Spanish words for “too fast” or “too slow” appeared whenever the button was pressed either before 300 msec, or after 3 sec from target onset, respectively. All testing was performed in a PC with a 17-inch monitor controlled by the Presentation® software (<http://www.neurobs.com>). The same stimulus materials, inter-stimulus and inter-trial intervals, and number and sequence of target trials were used in the two task conditions. However, by way of instructions, the task significance of tonal cues differed between both task conditions.

In the task-switching procedure participants were requested to start sorting cards by the colour rule, and then to alternate between the colour and shape rules. The tonal cues informed whether to switch or repeat the previous rule with mean probabilities  $p = .25$  and  $p = .75$ , respectively. Thus, in

the task-switching condition tones denoted either a change or repetition in the previous S–R mapping, and switch trials occurred pseudorandomly after a variable number of between 1 and 4 task-repeat trials (Fig. 1a, b). In the single-task condition, participants were instructed to sort cards always by the colour rule, and the tones were mere auditory distracters that had to be ignored for efficient task performance. These tones had the same overall probability in the single-task and task-switching conditions, with  $p = .25$  for 'deviant'/'switch' tones, and  $p = .75$  for 'standard'/'repeat' tones. For half the participants the 500 Hz and 1000 Hz tones served as deviant/switch and standard/repeat cues, respectively, but this mapping was reversed for the rest of participants. The order of administration of both tasks was counterbalanced across subjects.

In both task conditions, motor responses were given to visual targets only. The task sets defined with the task instructions consisted of 4-stimulus to 4-response mappings. Thus, participants used a 4-button panel to match the choice card with one of the four key cards on top. The far left button designated the key card on the far left of the display; the far right button designated the key card on the far right, and so on. Participants used their left and right thumbs to press two left and two right buttons in a response pad. For instance, when sorting by the colour rule, a blue choice card was to be matched with the blue key card by pressing the right-most response button. Before the testing session, participants were fully instructed and practiced each task for about 10–15 min, until they reached a criterion of 100% correct trials during 5 min. This task-cueing procedure was intended to segregate distinct contributions from cue- and target-locked brain activations to task performance (cf., Barceló, 2003; Periañez and Barceló, 2009).

#### 2.4. Behavioural data acquisition and analyses

Several indicators of behavioural switch costs and distraction were obtained from correct (mean reaction times – RTs) and failed trials (error rates). In the single-task condition, failed trials were defined as those where subjects did not sort the choice card with the colour rule. In the task-switching condition, failed trials were defined as those where subjects (a) did not follow the instruction cue to switch or repeat the previous rule, or (b) failed to select the correct response within the currently relevant task rule (Barceló, 2003). In both task conditions, any responses performed earlier than 300 msec post-card onset ("too soon"), or later than 3 sec ("too late") were also computed as errors. The analyses of RTs considered data from correct series only, containing no errors (cf., Barceló et al., 2002; Barceló, 2003).

Switch-specific 'local' costs were computed according to previous studies (Meiran et al., 2001; Goffaux et al., 2008; West and Travers, 2008). A measure of local switch costs was obtained as the difference in mean RT between switch trials and all repeat trials. Local costs were computed in single-task (following a deviant tone) and in task-switching conditions (following a switch cue). These will be referred to as *local distraction costs* and *local switch costs*, respectively. Moreover, three types of switch-unspecific costs (restart, global, and mixing) were also obtained. Restart costs were computed as the difference in mean RT between the first and third repeat

trials in the task-switching condition (cf., Rushworth et al., 2002; Barceló et al., 2008), and between the first and third standard trials in the single-task condition. Global costs were computed as the difference in overall mean RT between task-switching and single-task conditions, whereas mixing costs were computed as the difference in mean RT in the third repeat/standard trials between the task-switching and single-task conditions (Monsell, 2003). Only the colour rule was used as a single-task baseline for task-switching and only task-repeat trials sorted by the colour rule entered in the estimations of global and mixing costs (hence, these estimations were noncommittal regarding any likely task asymmetries). All measures of task-switch costs were subjected to an analysis of variance (ANOVA) with age (middle-aged, older) and cognitive control (high, low) as the between subject factors. Statistical analyses were conducted using SPSS v.15 software. All post-hoc tests of simple effects were performed using the Bonferroni correction with a significance level of  $p < .05$ .

#### 2.5. Electroencephalographic (EEG) recordings and analyses

EEG recordings were obtained from a nylon cap fitted with tin electrodes (Electrocap, Eaton, Ohio). The electroencephalogram (EEG) was recorded from 29 tin electrodes positioned according to the extended 10–20 system, and referenced to the left mastoid. The EEG was amplified with a band pass from DC to 30 Hz (24 dB/octave), and digitised at 500 Hz over a 900 msec epoch including a 100 msec pre-stimulus baseline. Impedances were kept below 5 k $\Omega$ . The electrooculogram (EOG) was recorded bipolarly from electrodes placed at the outer canthi of both eyes (horizontal EOG) and above and below the left eye (vertical EOG). EOG artefacts were corrected off-line using a regression algorithm (Gratton et al., 1983). After EOG correction, trials exceeding EEG amplitudes of  $\pm 75 \mu\text{V}$  at any of the active electrodes, or with residual muscle or movement artefacts, were discarded. Trials from the first Madrid Card Sorting Test (MCST) series or with response latencies below 300 msec or over 3 sec were also discarded. As in previous studies, only data from MCST series with no errors entered the ERP averages (Barceló et al., 2002), and these were recomputed off-line to a linked-mastoid reference.

Mean ERP amplitudes were measured relative to a 100 msec pre-stimulus baseline at three mid-line electrode locations (Fz, Cz and Pz) routinely used in many previous studies. For cue-locked ERPs, the mean amplitudes were obtained for cue-locked P2 (190–250 msec post-cue onset), cue-locked P3 (350–460 msec) and cue-locked slow negative potentials (500–700 msec). For target-locked ERPs, the mean amplitudes were obtained for target-locked P2 (110–170 msec), target P3 (350–460 msec), and slow negative potentials (500–700 msec). These latency windows were determined after inspection of the individual and group grand averages. Each of these measures were submitted to a mixed ANOVA with age (middle-aged, older adults) and cognitive control (high, low) as between subject factors, and task (single task, task switching), trial (switch, repeat1, repeat2), and Frontality (Fz, Cz, Pz) as within-subject factors. In the single-task condition, the levels within the trial factor were labelled as "deviant", "standard1", and "standard2". The predicted functional differences

between cue-locked P3 and target-locked P3 were explored in a mixed ANOVA with age (middle-aged, older adults) and cognitive control (high, low) as between subject factors, and P300 type (cue-locked, target-locked), task (single task, task switching), trial (switch, repeat2), and Frontality (Fz, Cz, Pz) as within-subject factors. Appropriate adjustments in this main statistical design were made whenever necessary in order to preserve the statistical power of some specific contrasts (i.e., tests of effects for cue-locked P3 activity focused on switch/deviant trials). The degrees of freedom were adjusted where appropriate using the Greenhouse-Geisser (G-G) correction. As with behavioural analyses, a Bonferroni-corrected significance level of  $p < .05$  was adopted for all tests of simple effects involving multiple comparisons. Finally, a series of correlation analyses examined the association between behavioural and brain responses to events in switch and repeat trials. Mean RTs and RT costs were submitted to a series of Pearson product-moment correlation analyses with the mean amplitudes of cue-locked and target-locked P2, P3 and slow wave potentials measured at the three mid-line positions.

### 3. Behavioural results

#### 3.1. Accuracy

Across all participants, accuracy was always better than 70% in the task-switching condition (mean = 86.6%, SD = 14.6% correct trials), and better than 90% in the single task (mean = 99.1%, SD = 1.6% correct trials). This ceiling effect motivated that all statistical tests of effects for error rates considered task-switching data only. Thus error rates were subjected to an ANOVA with age (middle-aged, older adults) and cognitive control (high, low adults) as the between subject factors, and with trial (switch, repeat1, repeat2), as the repeated measures factor. A main age effect revealed larger error rates in older compared to middle-aged adults during task switching ( $F_{1,76} = 16.6, p < .0001, \eta^2 = .17$ ; Table 2). Likewise, a main effect of cognitive control indicated that low control adults were more error prone than those scoring high

in the composite measure ( $F_{1,76} = 7.9, p < .01, \eta^2 = .09$ ). A main trial effect ( $F_{2,304} = 27.2, p < .0001, \eta^2 = .26, GG = .82$ ) revealed larger error rates in either switch or first repeat trials compared to the second and third repeat trials ( $p < .0001$ ), with no differences between switch and first repeat trials, nor among the first and second repeat trials. No other effects or interactions reached statistical significance for error rates in the task-switching condition (see Table 2).

#### 3.2. Single task: behavioural distraction

Mean RTs were subjected to an ANOVA with age (middle-aged, older adults) and cognitive control (high, low adults) as the between subject factors, and with trial (deviant, standard1, standard2), as the repeated measures factor. A main age effect suggested that older adults sorted cards slower than middle-aged adults in the single-task condition ( $F_{1,76} = 18.7, p < .001, \eta^2 = .2$ ; older = 1018 msec, middle-aged = 867 msec). High and low cognitive control adults differed only marginally in their mean RTs ( $F_{1,76} = 3.4, p < .07$ ; high = 910 msec, low = 975 msec). A main trial effect indicated that target responses were comparatively slower following a deviant than a standard tone ( $F_{3,228} = 29.6, p < .001, \eta^2 = .28$ ). Target responses following the first standard tone were also slower than subsequent standard trials ( $p < .01$ ), thus suggesting a special status of the first standard following a deviant tone. These trial-by-trial distraction effects interacted neither with age nor cognitive control in the single task (see Table 2).

#### 3.3. Task switching: mean RTs and specific 'local' switch cost

Mean RTs were subjected to an ANOVA with age (middle-aged, older adults) and cognitive control (high, low adults) as the between subject factors, and with trial (switch, repeat1, repeat2), as the repeated measures factors. With regard to mean RTs, a main effect for age indicated that older adults were slower than middle-aged adults ( $F_{1,76} = 18.04, p < .0001, \eta^2 = .19$ ). A main effect for cognitive control indicated that the group scoring low in the composite z-score showed the

**Table 2 – Mean RT (and standard error of the means, in msec) and percent errors in the single-task and task-switching conditions for each of the four groups of middle-aged and older adults split by their level of cognitive control.**

	Middle-aged adults (49–60 y.o.)				Older adults (61–80 y.o.)			
	High control		Low control		High control		Low control	
	RT	% Errors	RT	% Errors	RT	% Errors	RT	% Errors
<b>Single task</b>								
Deviant	852 (34)	.05% (.06)	920 (40)	.17% (.08)	1007 (40)	.12% (.08)	1090 (34)	.19% (.06)
Standard 1	835 (32)	.04% (.06)	908 (37)	.14% (.08)	996 (37)	.02% (.08)	1049 (32)	.25% (.06)
Standard 2	829 (32)	.05% (.06)	897 (38)	.12% (.07)	977 (38)	.02% (.07)	1029 (32)	.23% (.06)
Standard 3	818 (32)	.07% (.07)	876 (37)	.12% (.08)	967 (37)	.10% (.08)	1031 (32)	.23% (.07)
<b>Task switching</b>								
Switch	1164 (51)	1.75% (.56)	1303 (59)	2.57% (.66)	1364 (59)	3.11% (.66)	1591 (51)	5.03% (.56)
Repeat 1	1177 (48)	1.23% (.58)	1334 (56)	2.84% (.67)	1349 (56)	3.22% (.67)	1561 (48)	5.41% (.58)
Repeat 2	1135 (47)	.85% (.40)	1250 (54)	1.23% (.46)	1318 (54)	1.99% (.46)	1458 (47)	3.57% (.39)
Repeat 3	1062 (45)	.56% (.50)	1160 (52)	.82% (.58)	1245 (52)	1.50% (.58)	1377 (44)	3.74% (.50)

slowest mean RTs during task switching ( $F_{1,76} = 9.52, p < .003, \eta^2 = .11$ ). A main trial effect revealed slower target responses in switch and first repeat trials compared to subsequent repeat trials ( $F_{3,228} = 27.2, p < .0001$ ), with no differences between switch and first repeat trials (Table 2), thus confirming also the special status of the first repeat tone following a switch tone. An interaction between cognitive control and trial revealed that the largest group differences in mean RTs were apparent during switch and first repeat trials ( $F_{1,76} = 4.5, p < .01, \eta^2 = .06$ ; Table 2). The interaction between age and cognitive control did not reach significance, and neither did other higher-order interactions involving age and cognitive control.

Local costs were subjected to an ANOVA with age (middle-aged, older) and cognitive control (high, low) as the between subject factors. Marginally larger local switch costs were found for older compared to middle-aged adults ( $F_{1,76} = 3.5, p < .07, \eta^2 = .04$ ; mean local RT cost = 92.8 vs 47.4 msec, respectively), and this was also marginally larger in low control relative to high control adults ( $F_{1,76} = 2.9, p < .09, \eta^2 = .04$ ; mean RT cost = 90.7 vs 49.6 msec, respectively). Age did not interact with cognitive control for the local switch cost ( $p = .3$ , see Fig. 2).

### 3.4. Task switching: unspecific restart, global and mixing costs

Restart costs were subjected to an ANOVA with age (middle-aged, older) and cognitive control (high, low) as the between subject factors. A main effect of cognitive control ( $F_{1,76} = 7.5, p < .01, \eta^2 = .09$ ), indicated larger restart costs in low compared to high cognitive control adults (mean restart RT cost = 179 vs 109 msec, respectively), but neither the main effect of age, nor its interaction with cognitive control approached significance ( $F_s < 1$ ; Fig. 2).

Two other switch-unspecific indexes of behavioural costs, global and mixing costs, involved a comparison between the task-switching and single-task conditions. Global and mixing costs were also subjected to a main ANOVA with age (middle-aged, older) and cognitive control (high, low) as the between subject factors. A main age effect indicated that older adults showed marginally larger global RT costs ( $F_{1,76} = 3.3, p < .08, \eta^2 = .04$ ), and larger mixing RT costs ( $F_{1,76} = 4.8, p < .03, \eta^2 = .06$ ) compared to middle-aged adults (Fig. 2). A main effect for cognitive control indicated that adults with low composite z-scores showed larger global costs ( $F_{1,76} = 7.3, p < .01, \eta^2 = .09$ ), and marginally larger mixing costs ( $F_{1,76} = 3.5, p < .07$ ,

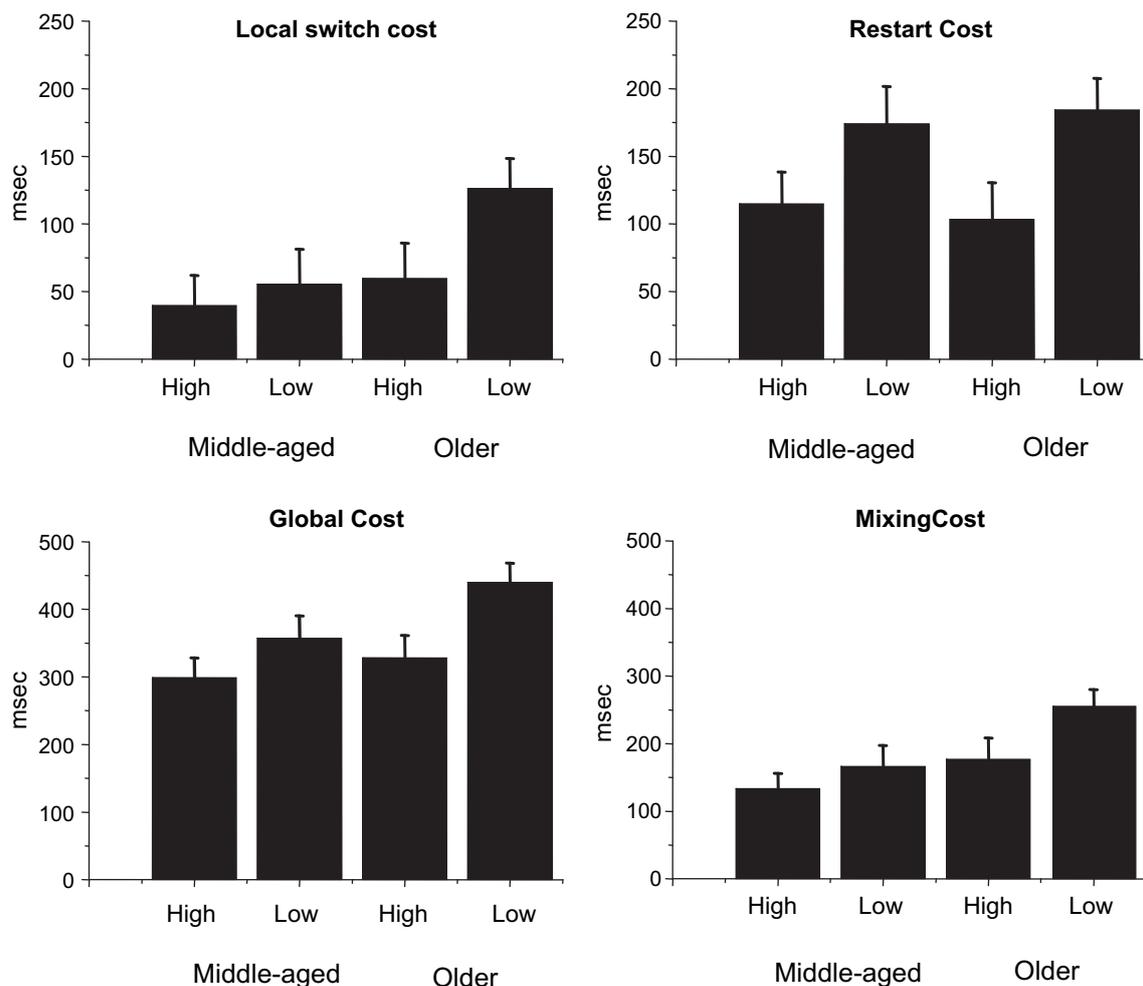


Fig. 2 – Mean local, restart, global and mixing costs (in msec) in middle-aged and older adults with high and low cognitive control. Vertical bars are standard errors of the mean.

$\eta^2 = .04$ ), compared to adults scoring high in cognitive control (Fig. 2). Higher-order interactions involving age and cognitive control did not reach significance for global and mixing costs.

#### 4. Electrophysiological results

The figures in this section illustrate the brain responses to cues and targets for each of the four median split sub-groups for age and cognitive control. Figs. 3 and 4 illustrate the grand cue-locked ERPs to deviant/switch and standard/repeat sounds in the single-task and task-switching conditions, respectively. Figs. 5 and 6 compare the grand target-locked ERPs to deviant versus switch and standard versus repeat target trials, respectively. Finally, Fig. 7 illustrates the mean amplitudes of cue-locked P3 and target-locked P3 activations across single-task and task-switching conditions in each of the four sub-groups for age and cognitive control. The analyses focused on three sub-components of the endogenous P300 complex (P3, P3 and slow negativity), in response to both cues and targets, as these were relevant for examining the context-updating hypothesis of the P300 potential in connection with the updating and maintenance of task representations during task switching (Barceló et al., 2002, 2006, 2008; Periáñez and Barceló, 2009; Squires et al., 1976).

##### 4.1. Cue-locked brain responses in single-task versus task-switching conditions

Cue-locked ERPs were submitted to a mixed ANOVA with age (middle-aged, older adults) and cognitive control (high, low) as

between subject factors, and task (single task, task switching), trial (switch, repeat1, repeat2), and Frontality (Fz, Cz, Pz) as within-subject factors. The cue-locked P2 showed a mid-central scalp maximum ( $F_{2,152} = 42.8$ ,  $p < .0001$ ,  $\eta^2 = .39$ ,  $GG = .81$ ). Larger cue-locked P2 amplitudes were elicited by standard than by deviant tones in the single task, whereas no analogous difference between switch and repeat cues was found in task switching, as revealed by a task  $\times$  trial  $\times$  electrode interaction ( $F_{2,152} = 8.7$ ,  $p < .0001$ ,  $\eta^2 = .1$ ). This third-order interaction was further modulated by cognitive control ( $F_{2,152} = 3.8$ ,  $p < .05$ ,  $\eta^2 = .04$ ), revealing that enhanced P2 amplitudes to standard tones were apparent in low – but not high – control adults. Likewise, in the task-switching condition an age  $\times$  cognitive control  $\times$  electrode interaction revealed larger cue-locked P2 mean amplitudes in low compared to high control older adults at the mid-frontal electrode ( $F_{1,76} = 4.2$ ,  $p < .03$ ,  $\eta^2 = .05$ ; see Figs. 3 and 4).

Neither repeat cues nor standard tones elicited visible cue-locked P3 activity in either task condition, and hence, analyses focused on P3 activity elicited by switch cues and deviant tones only. In both cases, larger P3 amplitudes were observed at Pz relative to Cz and Fz sites ( $F_{2,152} = 20.7$ ,  $p < .0001$ ,  $\eta^2 = .21$ ,  $GG = .86$ ), but this effect was not modulated by age or cognitive control. A task  $\times$  electrode interaction ( $F_{2,152} = 7.1$ ,  $p < .003$ ,  $\eta^2 = .08$ ,  $GG = .76$ ) revealed larger mean P3 amplitudes in the task switching compared to the single-task condition at the Pz site only. Likewise, a fourth-order age  $\times$  cognitive control  $\times$  task  $\times$  electrode interaction ( $F_{2,152} = 3.6$ ,  $p < .05$ ,  $\eta^2 = .04$ ), suggested that these task differences in parietal cue-locked P3 activity were apparent only in middle-aged low control adults ( $p < .02$ ) and older high control adults ( $p < .02$ ). This was due

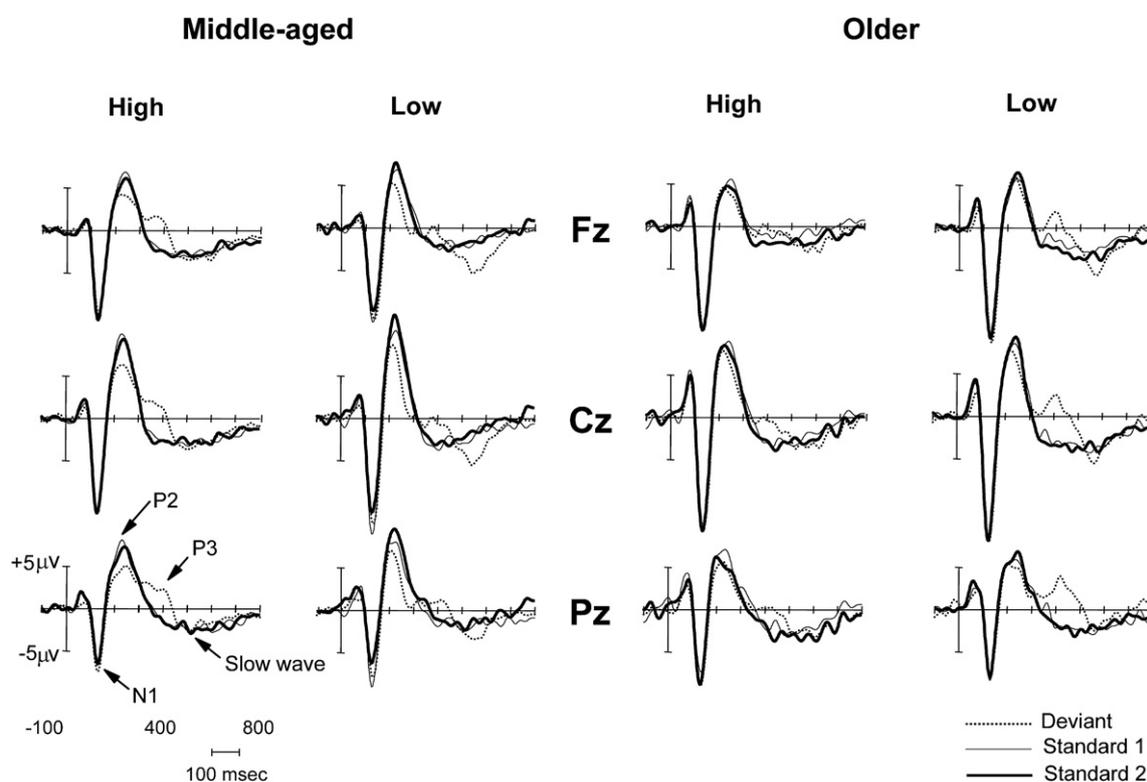
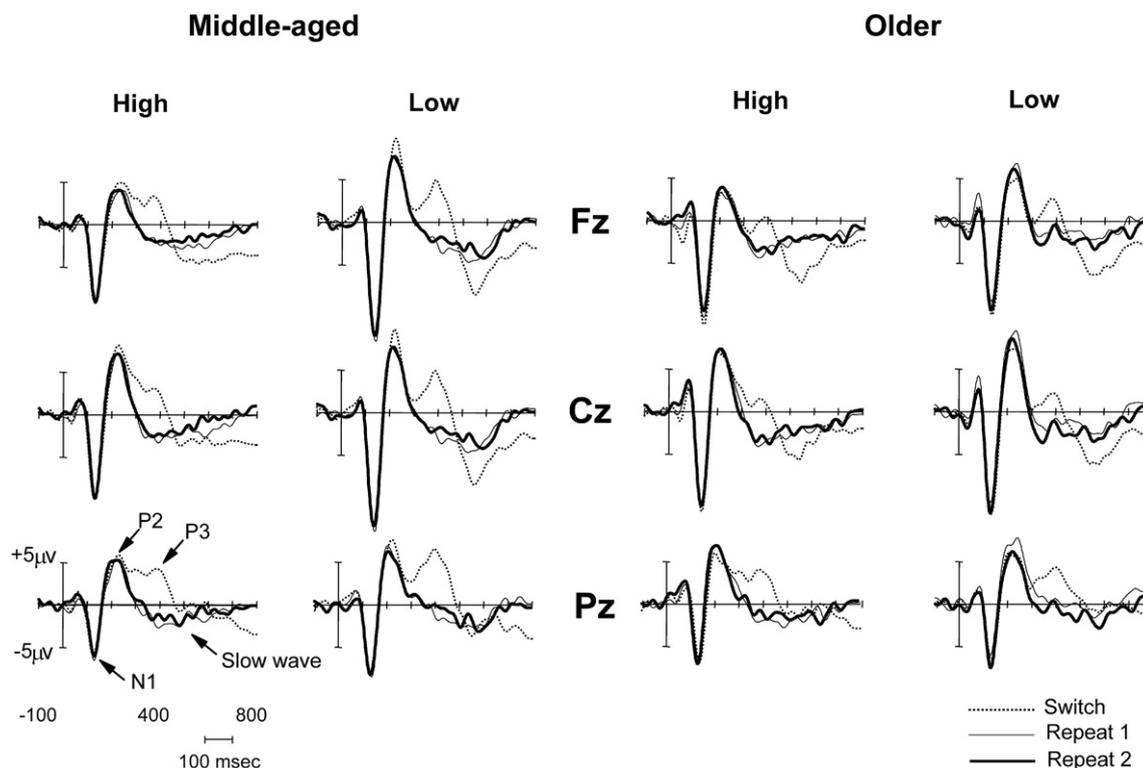


Fig. 3 – Cue-locked ERPs to deviant and standard sound distractors delivered in the single-task condition for middle-aged and older adults with high and low cognitive control.



**Fig. 4 – Cue-locked ERPs to task-switch and task-repeat tonal cues delivered in the task-switching condition for middle-aged and older adults with high and low cognitive control.**

to the significant cue-locked P3 responses to infrequent sound distracters in the two extreme groups (see Figs. 3 and 4).

Finally, cue-locked slow negative potentials in response to switch cues were larger than to deviant tones or repeat cues at mid-frontal and mid-central sites, as revealed by a third-order task  $\times$  trial  $\times$  electrode interaction ( $F_{2,152} = 15.5$ ,  $p < .0001$ ,  $\eta^2 = .17$ ,  $GG = .91$ ; Figs. 3 and 4). In the task-switching condition, cognitive control – but not age – interacted with trial type, with low control adults showing larger cue-locked slow negativities in switch than repeat trials ( $F_{2,304} = 3.1$ ,  $p < .04$ ,  $\eta^2 = .4$ ,  $GG = .74$ ). No such a difference was found in subjects scoring high in cognitive control (Fig. 4).

#### 4.2. Target-locked brain responses in single-task versus task-switching conditions

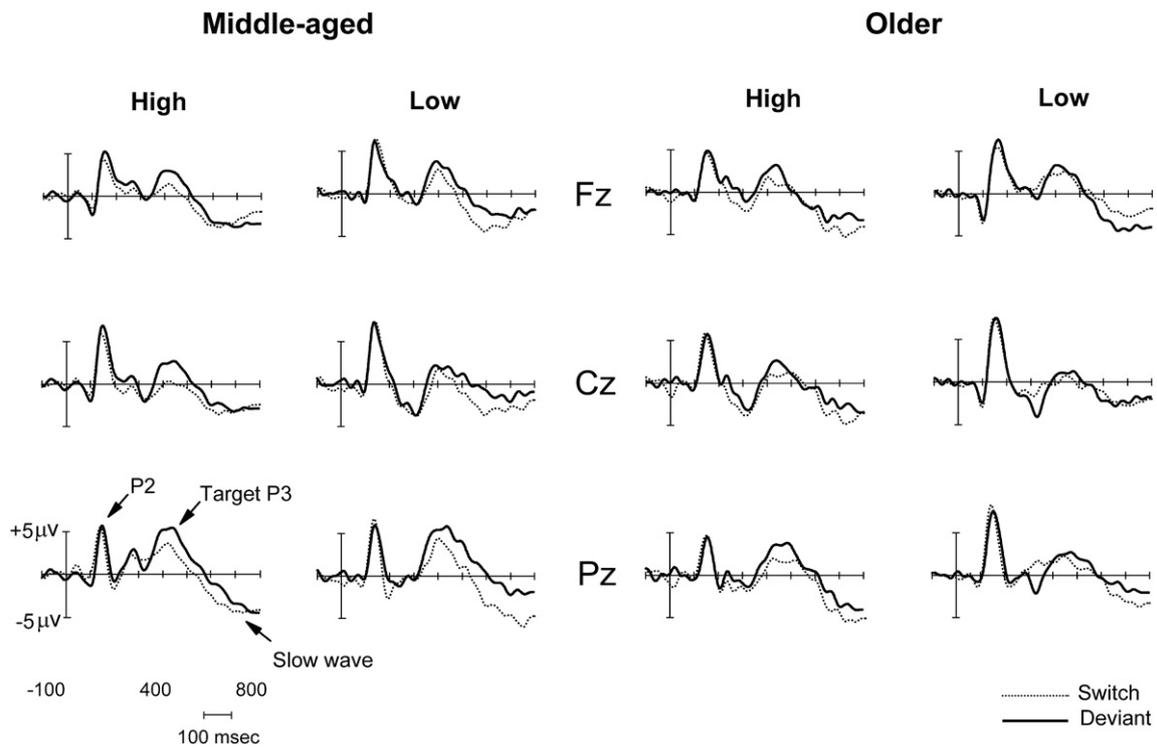
Target-locked ERPs were also submitted to a mixed ANOVA with age (middle-aged, older adults) and cognitive control (high, low) as between subject factors, and task (single task, task switching), trial (switch, repeat1, repeat2), and Frontality (Fz, Cz, Pz) as within-subject factors. Mean target-locked P2 amplitudes were not modulated by the present task conditions. Mean target-locked P3 amplitudes recorded at Pz were larger in the single task than in the task-switching condition (main task effect:  $F_{1,76} = 8.3$ ,  $p = .005$ ,  $\eta^2 = .1$ ), but this was true only for middle-aged adults in response to the first target following a switch/deviant tone, as revealed by a triple interaction between age, task and trial ( $F_{1,76} = 4.3$ ,  $p = .04$ ,  $\eta^2 = .05$ ; Fig. 5). Similar target P3 amplitudes were elicited across all

groups in subsequent repeat/standard trials in both task conditions (see Fig. 6). Hence, further analyses focused on the first target trial following a switch/deviant tone, which elicited the largest group differences in target P3 activity (see Fig. 5). An age by electrode interaction ( $F_{2,152} = 5.7$ ,  $p = .007$ ,  $\eta^2 = .07$ ,  $GG = .87$ ), revealed larger target P3 amplitudes over parietal than central ( $p < .04$ ) or frontal sites ( $p < .001$ ) for middle-aged adults, whereas no such differences in scalp distribution were found for older adults. This outcome suggests that target P3 amplitudes were more evenly distributed over fronto-parietal scalp regions in older than middle-aged adults. Finally, a fourth-order interaction between age, cognitive control, task and electrode ( $F_{2,152} = 4.2$ ,  $p = .03$ ,  $\eta^2 = .05$ ,  $GG = .76$ ), revealed reduced parietal target P3 amplitudes to switch cues compared to deviant tones in all groups except for older low control adults (see Fig. 5).

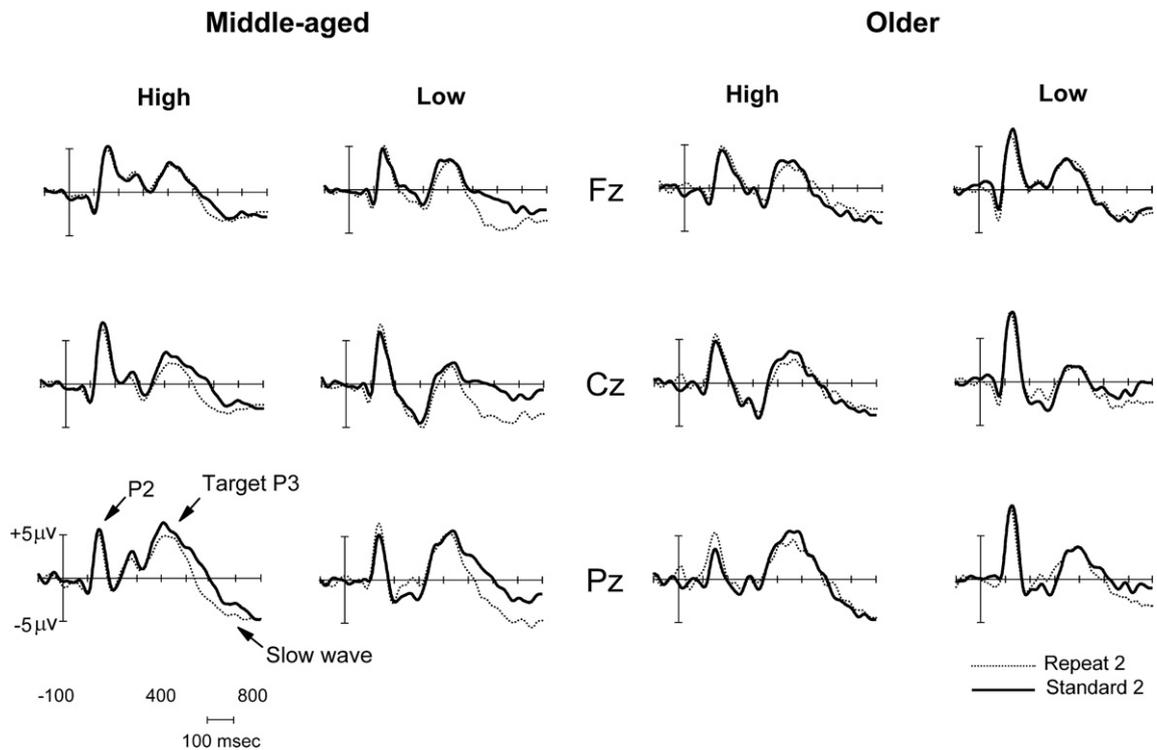
Target-locked slow negative potentials were larger in the task switching than in the single-task condition for middle-aged adults only, as suggested by a task by age interaction ( $F_{1,76} = 5.6$ ,  $p < .02$ ,  $\eta^2 = .07$ ). No further effects involving age or cognitive control were found for target-locked slow negative potentials.

#### 4.3. Cue- versus target-locked brain responses

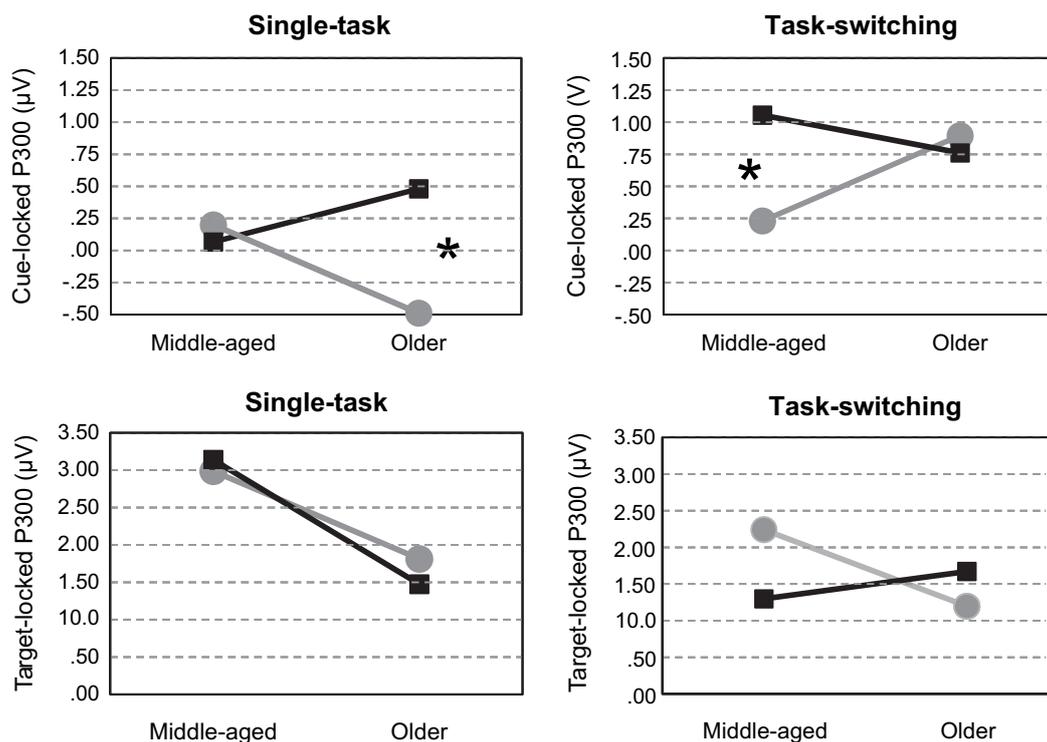
In this section, cue- and target-locked P3 activations are compared in a mixed ANOVA with age (middle-aged, older adults) and cognitive control (high, low) as between subject factors, and P300 type (cue-locked, target-locked), task (single



**Fig. 5 – Target-locked ERPs to task-switch cues and deviant distractors delivered in both task conditions for middle-aged and older adults with high and low cognitive control.**



**Fig. 6 – Target-locked ERPs to task-repeat cues and standard distractors delivered in both task conditions for middle-aged and older adults with high and low cognitive control.**



**Fig. 7 – Mean cue-locked P3 amplitudes (upper panels) and target-locked P3 amplitudes (lower panels) in the single-task (left column) and task-switching conditions (right column) for middle-aged and older adults scoring high (circles) and low (squares) in the composite index of cognitive control.**

task, task switching), trial (switch, repeat2), and Frontality (Fz, Cz, Pz) as within-subject factors. The predicted functional differences between cue- and target-locked P3 activations were confirmed by a significant third-order interaction between P300 type  $\times$  trial  $\times$  electrode ( $F_{1,76} = 8.6$ ,  $p < .005$ ,  $\eta^2 = .1$ ), suggesting that the two P300 types differed across the three mid-line electrodes mostly during the second repeat/standard trial (i.e., whereby absent cue-locked P3 activity contrasted with maximal target-locked P3 amplitudes). No such differences between cue-locked P3 and target P3 amplitudes were apparent in switch/deviant trials. This effect was confirmed at the mid-parietal electrode by a highly significant P300 type  $\times$  trial interaction ( $F_{1,76} = 61.3$ ,  $p < .0001$ ,  $\eta^2 = .45$ ). Moreover, a P300 type  $\times$  task interaction ( $F_{1,76} = 13.5$ ,  $p < .0001$ ,  $\eta^2 = .15$ ), indicated larger cue-locked P3 amplitudes in task switching compared to single-task conditions, whereas the reverse was true for target-locked P3 amplitudes (see Figs. 3–6). A third-order P300 type  $\times$  task  $\times$  trial interaction ( $F_{1,76} = 5.5$ ,  $p < .03$ ,  $\eta^2 = .07$ ), again confirmed that functional differences between the two types of parietal P300 were most apparent during repeat/standard trials (Figs. 3–6). More importantly, a significant age  $\times$  cognitive control  $\times$  P300 type  $\times$  task interaction ( $F_{1,76} = 6.6$ ,  $p < .02$ ,  $\eta^2 = .08$ ; Fig. 7), indicated that older adults with high and low cognitive control were better discriminated by cue-locked P3 amplitudes in the single-task condition, whereas middle-aged adults with high and low control were better discriminated by cue-locked P3 amplitudes in the task-switching condition. In turn, target-locked P3 amplitudes were sensitive to age-related

differences, but were less sensitive to differences in cognitive efficiency for either middle-aged or older adults (see Fig. 7).

Mean RTs and RT costs were submitted to a series of Pearson product-moment correlation analyses with the mean amplitudes of cue-locked and target-locked P2, P3 and slow wave potentials measured at the three mid-line positions. Significant Pearson product-moment correlations between mean RTs for switch and repeat trials and the mean amplitude of target-locked slow negativities were found for the whole sample of 80 participants ( $r_s > .24$ ,  $p_s < .04$ ), indicating that larger fronto-central slow negativities were associated with faster responses in both switch and repeat trials. Larger target-locked mid-frontal negativities were also associated with smaller mixing costs ( $r = .26$ ,  $p < .02$ ) and reduced global costs ( $r = .24$ ,  $p < .04$ ). Finally, the mean amplitude of the fronto-central cue-locked P2 to the first repeat trial was correlated with restart costs in the task-switching condition ( $r = .26$ ,  $p < .02$ ). No significant linear correlations were found between behavioural costs and mean cue-locked P3 or target-locked P3 amplitudes.

## 5. Discussion

This study aimed to explore the combined influence of age and cognitive control on the behavioural and electrophysiological indexes of local, restart and mixing costs. In doing so, we employed a task-cueing paradigm inspired in the WCST and adapted for measuring brain potentials (Barceló, 2003; see

Fig. 1a, b), whereby the same stimulus material was administered under both single-task and task-switching conditions. This procedure served to tax working memory during the online maintenance and updating of sensory, motor, and sensorimotor representations (Fig. 1c), in order to explore the effects of age and cognitive control on three different sources of behavioural task-switch costs and the accompanying ERP modulations. As predicted, and consistent with the extant literature, three different sources of task-switch costs were associated with different cue-locked and target-locked ERPs during the preparation and execution stages of task performance (Barceló et al., 2008; Periañez and Barceló, 2009). Next we discuss the implications of the present results for the hypothesis of an age-related deficit in the ability to represent, maintain, and update contextual information in working memory (Braver et al., 2001), with a special interest in addressing the context-updating hypothesis of the endogenous P300 brain potential (Sutton et al., 1965; Donchin, 1981).

### 5.1. Effects of age and cognitive control on local switch costs

In line with previous findings, individual differences in age and cognitive control influenced local switch costs only marginally (Salthouse et al., 1998; Kramer et al., 1999; Kray and Lindenberger, 2000; Reimers and Maylor, 2005), and these two factors did not interact for most behavioural measures (cf., Ruthruff et al., 2001). Neither age nor cognitive control modulated an otherwise reliable cue-locked P3 potential elicited by the task-switch cues. Taken together, these results suggest that the anticipatory updating of S–R mappings in working memory, as putatively indexed by local switch costs and cue-locked P3 activations, seems not critically affected by old age or low cognitive ability (cf., Kramer et al., 1999; Kray and Lindenberger, 2000). This finding was contrary to our first hypothesis. One possible explanation for the reduced age-related local switch cost could be that most older adults were enrolled in university courses, and hence, they showed an unusually high level of cognitive performance (see Tables 1 and 2). However, this was also true for our middle-aged adults, and besides, age-related effects were present for other behavioural measures. Another plausible cause for these moderate age-related effects on local switch costs was the relatively high frequency of task-switch trials, which might have encouraged older adults to adopt “conservative response strategies effectively helping them to stay in a switch-ready state” (Goffaux et al., 2008, p. 64). This account seems plausible given the relatively high probability of switch trials in the present study ( $p = .25$ ), compared to other studies that reported age-related local costs (c.f., Friedman et al., 2007). The marginal influence of age and cognitive control on local switch costs could also be attributed to the rather long CTI used ( $\sim 2000$  msec), which probably allowed enough preparation time before the next target card (c.f., West and Travers, 2008; Periañez and Barceló, 2009). This feature of our task design could have minimized the magnitude of local switch costs (and behavioural distraction), and hence, it could also explain the absence of a significant correlation between local costs and cue-locked P3 amplitudes.

#### 5.1.1. Local switch costs and task preparation

The long CTIs used cannot explain the absence of modulatory effects of either age or cognitive control upon an otherwise reliable cue-locked P3 response to the task-switch cues. This cue-locked P3 response has been proposed to index activity in a fronto-posterior network for the preparatory updating of S–R mappings in working memory (Barceló et al., 2002; Periañez and Barceló, 2009), and can be elicited both reactively to irrelevant novel sensory events, and also proactively in preparation for novel task demands (Barceló et al., 2006; Braver and West, 2008; Periañez and Barceló, 2009). Task-switch cues elicited similarly enhanced cue-locked P3 amplitudes across all groups of middle-aged and older adults. In turn, a fourth-order interaction between age, cognitive control, task and electrode suggested that this fronto-posterior network became active during reactive updating to the irrelevant sound distracters only in the two extreme groups of middle-aged high control adults and older low control adults. These group differences in cue-locked P3 activity to the sound distracters did not translate into any behavioural differences probably due to the long CTIs used. This effect suggests a non-linear relationship between age, cognitive control and reactive cue-locked P3 activations. Thus, the largest cue-locked P3 activations to sound distracters were elicited by the two subgroups with the highest and lowest working memory capacity, respectively. It remains to be seen whether this non-linear association also translates into behavioural distraction with shorter distracter-target intervals. In the absence of behavioural evidence, these different cue-locked P3 responses to the sound distracters in the two extreme groups cannot be interpreted unequivocally. However, since the underlying fronto-posterior neural network may be activated by both reactive (bottom-up) and proactive (top-down) information processes (Periañez and Barceló, 2009; Braver and West, 2008), one could speculate about larger bottom-up reactivity in older low control adults and larger top-down modulations in middle-aged high control adults.

In the task-switching condition, the fronto-posterior scalp distribution of cue-locked P3 to the task-switch cues was similar for older adults with high and low cognitive control. Therefore, these cue-locked P3 amplitudes did not reflect the presence of compensatory strategies in the older adults. Previous studies have reported larger age-related frontal compensatory activations in participants with preserved executive capacity (Davis et al., 2008; DiGirolamo et al., 2001). Instead, fronto-central slow negativities could be a more sensitive index of such compensatory mechanisms, since task-switch cues elicited larger slow negativities than task-repeat cues in participants with low – but not high – cognitive control. This compensatory effect could have ultimately contributed to the group differences in local switch costs, as has been suggested in previous studies (cf., Kray et al., 2005; West and Moore, 2005; West and Travers, 2008).

#### 5.1.2. Local switch costs and task execution

Unlike the effects of cognitive control on cue-locked brain responses, the strongest age-related effects were apparent in the brain responses to target onset. First, in line with most previous literature, target P3 amplitudes were larger at

parietal than frontal sites (Donchin, 1981), although older adults showed reduced parietal target P3 amplitudes relative to middle-aged adults in the single-task condition only. This result also suggests that target P3 activity was more evenly distributed over fronto-parietal scalp regions in the older adults (Polich, 1996; Fabiani et al., 1998). Second, larger target P3 amplitudes were elicited in single-task than in task-switching conditions, also consistent with previous studies (Barceló et al., 2002; Kieffaber and Hetrick, 2005; Goffaux et al., 2006). Interestingly, this effect was significant only for middle-aged adults, whereas older adults elicited similar target P3 amplitudes in both task conditions (cf., West and Travers, 2008). The reduced mid-parietal target P3 amplitudes in older adults actually results in a more even distribution of target P3 activity across frontal-parietal scalp regions, which concurs with the age-related “anterior shift” in target P300 amplitude observed in a number of paradigms (e.g., Friedman, et al., 1993, 1997; Kray et al., 2005). Therefore, the present results suggest that the anterior shift in P300 activity relates to task execution (target-locked P3) rather than task preparation (cue-locked P3) processes, and could thus be interpreted as inefficient or compensatory resource allocation specifically linked to the stage of target evaluation and/or target response selection (Polich, 1996; Friedman et al., 2007).

In the task-switching condition, an increase in target-locked P3 amplitude was apparent from switch to late repeat trials, and this was paralleled with an improvement in response speed and accuracy. These trial-by-trial effects have been attributed to the gradual rehearsal and consolidation of task sets in memory (Barceló et al., 2002, 2006; Barceló, 2003). The presence of an interaction between age, cognitive control, task and electrode revealed reduced parietal target P3 amplitudes in switch compared to deviant trials across all groups except for older low control adults (Fig. 5). This outcome supports the hypothesis of a multiplicative interaction between age and cognitive control for the neural substrates of local switch costs. However, this effect could also reflect the temporal convergence of different underlying neural component processes at target onset. Thus, it is plausible that this multiplicative interaction reflects the joint contribution from switch-specific (local) and nonspecific (restart and mixing) sources of task-switch costs, since all these component processes are probably present at the onset of the first target following a task-switch cue.

### 5.2. Effects of age and cognitive control on restart costs

The finding of an association between larger restart costs and enhanced cue-locked P2 amplitudes confirms recent evidence (Barceló et al., 2008), and supports the presence of a general-purpose mechanism that seems a prerequisite for higher task-switching operations. A main effect for cognitive control indicated larger restart costs in low relative to high control adults in the task-switching condition. Together with the enhanced mid-frontal cue-locked P2 for low control older adults, and the reliable correlation between restart costs and cue-locked P2 amplitudes in the task-switching condition, this outcome points to a significant role of cognitive control on task-set activation (Barceló et al., 2008; Periañez and Barceló, 2009), and/or cue-task retrieval processes (Altmann, 2002;

West and Travers, 2008), which is also compatible with the inhibitory control of responses for a previously performed task (Allport and Wylie, 2000; Cepeda et al., 2001). Enhanced cue-locked P2 amplitudes to the standard tones were also observed in low control adults in the single task, although their association with restart costs and the multiplicative interaction between age and cognitive control became apparent only in the most demanding task-switching condition. These results lend support to the hypothesis that cognitive control influences behavioural restart costs regardless of age, even though a multiplicative interaction with age for cue-locked P2 amplitudes in the most demanding task-switching condition pointed to a likely convergence of age and cognitive control upon the neural underpinnings of restart costs.

There have been previous reports of age-related increases in the amplitude of the auditory P2 component in simple attention tasks in the presence of sensory interference (Crowley and Colrain, 2004), that have been related to impaired attentiveness (Näätänen and Picton, 1987), or to deficits in the inhibitory control of task-irrelevant stimulation (Friedman et al., 1993; Chao and Knight, 1997; Amenedo and Diaz, 1998). These interpretations concur with a previous study whereby enhanced cue-locked P2 potentials were elicited in task conditions requiring filtering of competing irrelevant task representations (Periañez and Barceló, 2009). This association between anticipatory cue-locked P2 amplitudes and cognitive control contrasts with the relative absence of similar effects for target-locked P2 amplitudes. The present evidence suggests a determinant role of cognitive control, as estimated with classic neuropsychological paper-and-pencil tests of executive function, on the behavioural and ERP indexes related to the preparatory control of behaviour. Further research will be necessary to attest the relationship of these fronto-central P2 activations with more specific cognitive control operations, such as anticipatory task-set retrieval or activation (Barceló et al., 2008), but also with the interruption, inhibition, and deactivation of a previously active task set (c.f., Allport and Wylie, 2000; Cepeda et al., 2001; Barceló et al., 2006; Periañez and Barceló, 2009).

### 5.3. Effects of age and cognitive control on global and mixing costs

In agreement with the extant literature, the main effects for age and cognitive control revealed that older and low cognitive control adults showed larger global and mixing costs than middle-aged and high control adults, respectively (c.f., Mayr, 2001; Meiran et al., 2001; Goffaux et al., 2008; West and Travers, 2008). Increased age-related global and mixing costs have been attributed to larger processing demands during maintenance and retrieval of two task sets concurrently held in working memory (DiGirolamo et al., 2001; Goffaux et al., 2006). Since adults with high control capacity performed better than low control adults in tests of working memory span (e.g., digits subtests; see Table 1), it is likely that the reduced mixing costs in high control adults arises from a baseline offset in working memory capacity (Goffaux et al., 2008). Moreover, the main age effects for mixing costs were sensitive to a mean age difference of only 12 years between

middle-aged and older adults. This is an original and valuable finding that argues about the validity and sensitivity of our task procedures and behavioural measures, since the majority of task-switching studies on aging typically compared groups with a mean age difference of over forty years (Kramer et al., 1999; Mayr, 2001; Meiran et al., 2001), thus making it more likely to find age-related effects even with coarser behavioural indicators of task-switch costs.

The putative ERP signatures of mixing costs, namely the slow negativities, showed larger amplitude over mid-frontal and mid-central scalp regions in response to switch cues compared to repeat cues or deviant sounds. In the task-switching condition, low control adults showed enhanced cue-locked slow negativities in switch trials, which agrees with reports about enhanced slow negative potentials associated to inefficient maintenance of task-set information over time (DiGirolamo et al., 2001; Goffaux et al., 2008; West and Travers, 2008). Together with the larger mixing costs found in lower control adults, these results lend support to the second of our hypotheses. These results also concur with reports about an age-related reduction in the original differences between task-switching and single-task conditions, which has been attributed to difficulties in the ability to maintain the task context over time (Braver et al., 2001).

Target-locked mid-frontal slow negative potentials were reduced in older adults relative to middle-aged adults in the task-switching condition only. This age-related reduction of target-locked slow negativities has been associated with rule mapping and response selection processes during task switching, and concurs with previous results (West and Moore, 2005). For instance, West and Travers (2008) found a broadly distributed slow negativity during maintenance of two task sets in working memory that was enhanced in older adults and was absent in the younger. This was interpreted as an age-related difficulty to fully engage, or implement, the relevant task-set prior to stimulus onset by older adults (De Jong, 2001). This is consistent with the absence of similar effects in the single-task condition, which did not demand any S–R remapping operations. The present finding of an age-related diminution of slow negative potentials during task switching, together with their significant correlation with global and mixing costs, seems compatible with the hypothesis of age-related difficulties in the online maintenance of task-set information in working memory (Braver and West, 2008). These results support the purported association of global and mixing costs with frontal slow negative potentials (Goffaux et al., 2006; Barceló et al., 2008; West and Travers, 2008), despite that our estimates of global and mixing costs were limited to the easiest single-task colour condition. A more appropriate control using two single-task conditions would be necessary to examine the influence of age and cognitive control on any task asymmetries in these behavioural and brain indexes.

## 6. Conclusions

The behavioural and brain responses measured to the same task stimuli under single-task and task-switching conditions revealed both independent and interdependent effects of age

and cognitive control during the selection and inhibition of high- versus low-order task-set representations (Fig. 1c; Miller, 2000; Nyhus and Barceló, 2009). Three main findings are worth summarizing here. First, age and cognitive control yielded main effects on most indexes of task-switch costs, confirming the validity of our group split and the sensitivity of the behavioural indexes of task-switch costs. The additive – rather than multiplicative – effects found for most behavioural measures suggested that these two factors influenced two distinct processing stages in the temporal organization of behaviour (Meiran et al., 2001; Ruthruff et al., 2001). Second, we confirmed that the age-related “anterior shift” in P300 activity relates to task execution (target-locked P3) rather than to task preparation (cue-locked P3) processes, consistent with a deficit in resource allocation specifically linked to target evaluation and/or response selection (Polich, 1996; Friedman et al., 2007). Third, mixing costs correlated with slow negative potentials at fronto-central scalp regions, probably reflecting the extra processing demands of contextual cues during task switching as compared with single-task conditions (Goffaux et al., 2006; West and Travers, 2008). Accordingly, larger age-related mixing costs and slow negativities could index deficits in the maintenance of task-set information over time (DiGirolamo et al., 2001; Goffaux et al., 2008).

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