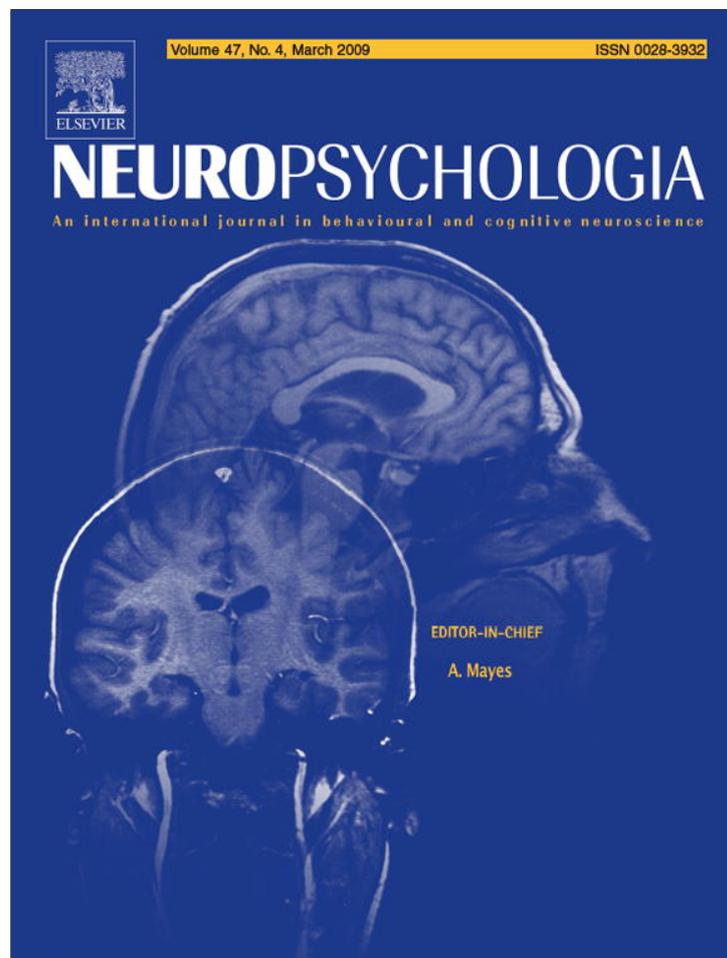


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Updating sensory *versus* task representations during task-switching: Insights from cognitive brain potentials in humans

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ABSTRACT

Task-cueing studies suggest that the updating of sensory and task representations both contribute to behavioral task-switch costs [Forstmann, B. U., Brass, M., & Koch, I. (2007). Methodological and empirical issues when dissociating cue-related from task-related processes in the explicit task-cueing procedure. *Psychological Research*, 71(4), 393–400]. Here we used transition cues to orthogonally manipulate Cue- and Task updating (switches vs. repetitions), in order to identify distinct behavioral indicators and event-related potentials (ERPs) associated with the exogenous and endogenous control of task preparation and execution. Both Cue- and Task updating, as well as their interaction, yielded significant behavioral costs, and evoked distinct cue- and target-locked ERPs. Task-switches enhanced cue-locked early P3 amplitudes (180–220 ms) over mid-central scalp regions, whereas cue switches reduced a fronto-central negativity (N2; 255–295 ms). In contrast, both cue- and task-switches enhanced cue-locked late P3 amplitudes (300–340 ms; *novelty P3*) over centro-parietal regions, supporting the hypothesis of a common neural substrate for processing stimulus and task novelty [Barceló, F., Escera, C., Corral, M. J., & Periañez, J. A. (2006). Task switching and novelty processing activate a common neural network for cognitive control. *Journal of Cognitive Neuroscience*, 18(10), 1734–1748]. In the target period, both cue- and task-switches reduced target P3 activity (310–730 ms) with short cue-target intervals only, suggesting that behavioral switch costs reflect the accrual of various time-dependent control operations during task preparation and execution. We conclude that the cognitive control of task-switching seems to emerge from a dynamic interplay between exogenous and endogenous sources of information.

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1. Introduction

In recent years task-cueing procedures have been adopted for studying the complex interplay between goal-driven (also *top-down*) and stimulus-driven (*bottom-up*) control of cognition. In task-cueing paradigms participants are asked to sequentially switch among two or more tasks on the basis of a pre-learned set of action rules. The most general finding has been that motor responses become slower and less accurate when switching than when repeating a task, a phenomenon known as “behavioral switch costs” (Allport & Wylie, 2000; Logan & Bundesen, 2003; Mayr & Kliegl, 2003; Meiran, 1996; Meiran, Chorev, & Sapir, 2000; Monsell, 2003; Rogers & Monsell, 1995; Rubinstein, Meyer, & Evans, 2001).

Task-cueing paradigms offer many advantages for dissociating the mechanisms underlying behavioral costs during the stages of task preparation and execution (Meiran, 1996; Rubinstein et al., 2001). Top-down control during anticipatory task-set switching can

be inferred by manipulating the cue-target interval (CTI) (Meiran et al., 2000; Monsell, 2003). Often task-switching can also be driven exogenously, or bottom-up, by changes in the environment (i.e., as when the phone rings while cooking; cf., Monsell, 2005, p. 164). What still remains controversial is the relative contribution from exogenous and endogenous sources, and their complex interplay, to behavioral switch costs. This controversy seems partly motivated by methodological difficulties to extricate the relative contribution from sensory and task representations to the switch cost. Thus, Logan and Bundesen (2003) argued that most evidence about the top-down control of task-switching could derive from a confound between cue- and task-switches in explicit task-cueing procedures where each cue denotes one task. Using such 1:1 cue:task mappings, any switch in task is always prompted by a switch in cue (i.e., **AB** or **BA**, where cues ‘A’ and ‘B’ denote the two tasks), whereas task-repetitions always imply cue-repetitions (i.e., **AA** or **BB**). It turns out that, for such explicit cueing, task-switch costs could simply reflect a “cue-repetition benefit” caused by low-level processes such as sensory priming of cue encoding, or learning of a cue-task compound, which would question any “endogenous act of control” to account for behavioral switch costs (Logan and Bundesen, 2003).

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More recently, sensory processes have been controlled for using *transition cues* that allow for an orthogonal manipulation of cues and tasks employing 2:2 cue:task mappings (Barceló, 2003; Forstmann, Brass, & Koch, 2007; Schneider & Logan, 2007). Transition cues inform about whether to switch or repeat a task, but do not inform about task identity. Using transition cues, Forstmann et al. (2007) found switch costs associated to both task and cue transitions. The interaction between these factors revealed cue-switch costs only during task-repetition trials. Moreover, cue-switch benefits were observed in trials where the task also switched. Forstmann et al. (2007) proposed that, in addition to the effects of sensory priming and task-set reconfiguration, participants seemed to develop associative *bindings* between cues and tasks over successive trials that interfered with performance in incongruent cue-task transitions, but did not in congruent trials (i.e., when both cue and task switch, or both repeat). Arguably, these bindings would involve associative learning of cue-task contingencies from trial to trial (Forstmann et al., 2007). In any case, these paradoxical “switch benefits” posit an interpretative challenge to current models of task-switching, and point to a complex interplay among hierarchically ordered sensory and task representations, whenever these representations are to be integrated over time for goal-directed behavior (Nobre, Correa, & Coull, 2007).

An alternative – though partly compatible – account derives from the probabilistic approach to cognition, as formalized with Bayesian models (Friston, 2005), and Information theory concepts (Koechlin & Summerfield, 2007). The basic assumption is that the preparatory control of action hinges upon a continuous updating of contextual (*task-set*) expectancies based on the incoming stimulation. From this perspective, behavioral switch costs would result whenever “prediction errors” signal a mismatch between bottom-up inputs (sensory cues) and top-down inputs (task-sets) along a putative hierarchy of representations in our brains (cf., Friston, 2005, p. 826). The concept of prediction errors concurs with the notion of advance preparation implicit in some models of task-switching (Meiran, 1996), and has also been proposed to underlie the transient expression of endogenous P300 brain potentials (Friston, 2005). To continue with Forstmann et al. (2007) rationale, incongruent cue-task transitions could be seen as more prone to prediction errors than congruent cue-task transitions, based on the recent history of cue-task contingencies (i.e., when a sensory cue repeats, the task is also expected to repeat, and so on). Such sequential changes in event expectancy may be formally expressed as changes in the amount of *novelty* or *surprise* (Baldi, 2005), or as the *mutual information* between sensory and task representations estimated over the course of an experiment (Koechlin & Summerfield, 2007), a notion recently adopted to quantify the information processing resources associated with task-switching operations and concurrent brain activations (Barceló & Knight, 2007; Barceló, Periañez, & Nyhus, 2008). Hence, we controlled for the global probabilities of task events, and the local probabilities of cue-task transitions in two-trial sequences, as these determine the amount of *novelty* conveyed by sensory stimuli (Baldi, 2005), and are known to influence behavioral and brain responses (Donchin, 1981; Mars et al., 2008; Squires, Wickens, Squires, & Donchin, 1976).

The excellent temporal resolution of brain event-related potentials (ERPs) offers an advantage for studying the fast pace of cognitive operations underlying task-switch costs (Barceló et al., 2008; Barceló, Periañez, & Knight, 2002; Brass, Ullsperger, Knoesche, von Cramon, & Phillips, 2005; Hsieh & Cheng, 2006; Jost, Mayr, & Rosler, 2008; Kieffaber & Hetrick, 2005; Kopp, Tabeling, Moschner, & Wessel, 2006; Miniussi, Marzi, & Nobre, 2005; Nicholson, Karayanidis, Poboka, Heathcote, & Michie, 2005; Rushworth, Passingham, & Nobre, 2002; Swinson, Jackson, & Jackson, 2006). In a study by Barceló et al. (2002) auditory tran-

sition cues that directed a switch in the participants' mental set to a new task, also elicited a fronto-parietally distributed *task novelty P3* complex that resembled classic *novelty P3* responses to novel distracters delivered in simple perceptual discrimination tasks (cf., Friedman, Cycowicz, & Gaeta, 2001). The novelty P3 complex reflects activity in a distributed neural network of multimodal cortical and subcortical structures, and consists of two distinct scalp recorded sub-components, namely, an early fronto-central P2 (or *early P3*), plus a longer-latency and mid-parietally distributed *late P3* component (or *novelty P3* proper). The novelty P3 complex had long been related to involuntary attention switching to surprising distracters in simple perceptual tasks (Escera, Alho, Winkler, & Naatanen, 1998; Friedman et al., 2001). In contrast, Barceló and collaborators (2006) showed that intentional task-switching and involuntary attentional capture by novel distracters both engage the same novelty P3 network, thus lending support to the “task novelty hypothesis” that novelty P3 potentials index resolution of *contextual novelty* regardless of whether this novelty is brought about by changes in sensory or task representations (for analogous early and late novelty P3 effects in response to auditory and visual task-switch cues, see Barceló, 2003; Barceló et al., 2002; Jost et al., 2008; Nicholson et al., 2005; Rushworth et al., 2002).¹

In line with recent proposals about a hierarchy of cognitive control processes for task-switching (Kleinsorge, Heuer, & Schmidtke, 2004; Lien & Ruthruff, 2004; Schneider & Logan, 2006), the early and late aspects of the novelty P3 complex have been proposed to index two hierarchically ordered operations involved in the updating of task representations. Using an intermittently cued task-switching paradigm similar to that of Rushworth et al. (2002), Barceló and collaborators (2008) found enhanced cue-locked early P3 responses to the intermittent onset of all (switch *and* repeat) cues, which mirrored the behavioral restart costs found to the first target responses following either cue (cf., Allport & Wylie, 2000). In addition, task-switch cues elicited enhanced late P3 amplitudes that predicted switch-specific behavioral costs. This double dissociation between the neural correlates of restart and switch costs led Barceló et al. (2008) to propose that the early and late aspects of novelty P3 indexed two sequential and hierarchically ordered mechanisms related to (1) the intermittent re-activation of task-set information in working memory, and (2) the updating of stimulus–response mappings within the currently active task-set, respectively. This proposal is consistent with two stage models of task-switching (Altmann, 2004; Meiran, 1996). On the other hand, target-locked P3 amplitudes were sharply reduced following the unpredictable onset of task-switch cues, and then gradually recovered to pre-switch amplitude levels along several task-repetition trials. This reduction in target P3 amplitude following a task cue has been related to proactive interference, or delayed control operations whenever these overlap the stage of task execution at target onset (Barceló, Muñoz-Céspedes, Pozo, & Rubia, 2000; Hsieh & Cheng, 2006; Nicholson et al., 2005; Rushworth et al., 2002). However, to date it is not clear whether this post-switch reduction in target P3 amplitude was caused by cue-switching rather than task-switching operations, given the previous confound between these conditions.

The present study aimed to dissociate the neural correlates underlying the updating of sensory representations (*cue-switching vs. cue-repetition*), and task-set representations (*task-switching vs. task-repetition*), and how these two factors and their putative

¹ The chronologically *early* and *late* aspects of the novelty P3 complex have also been referred to as its *anterior* and *posterior* aspects, respectively, owing to their scalp distribution (Escera et al., 1998; Friedman et al., 2001). In this paper we adopt the qualifiers *early* and *late* to emphasize the temporal dynamics of these components, as this was easier to define with ERPs than any anatomical boundaries.

interaction, each contribute to the switch costs in a task-cueing paradigm. We used the term “updating” in the sense of bringing up to date the contents of working memory, and to denote either intermittent changes or repetitions in sensory and/or task representations. This terminology provides a link with the influential context-updating hypothesis of the endogenous P300 brain potential (Donchin, 1981; Friedman et al., 2001), in an attempt to clarify the nature of the representations being updated during its elicitation. The context-updating model predicts lesser RT costs and reduced P300 amplitudes in response to more expected (i.e., repeated) events within a stimulus sequence (Duncan-Johnson & Donchin, 1977; Squires et al., 1976). The habituation of novelty P3 potentials with stimulus repetition has been likened to the “repetition suppression” of neural activity accompanying perceptual priming phenomena (Friston, 2005), consistent with the idea that recurrent representations are less surprising because “repetition improves prediction” (Grill-Spector, Henson, & Martin, 2006, p. 20). However, most past ERP studies used single task settings like *oddball* tasks, and could not decide whether the sequential effects of novelty P3 (P300) reflect the updating of only sensory, or also task representations (Barceló & Knight, 2007; Barceló et al., 2008; cf., Donchin, 1981).

The measurement of novelty P3 potentials together with the orthogonal manipulation of Cue- and Task updating may provide new insights about the nature of representations underlying behavioral switch costs. Most current models would predict lesser behavioral costs and reduced novelty P3 amplitudes with repeated and less novel cue-task transitions (i.e., congruent cue-task repetitions). The repetition priming and task-set reconfiguration hypotheses both predict the largest behavioral costs and brain activations in response to cue-task transitions conveying the largest amount of novelty (i.e., congruent cue-task switches). In turn, these two hypotheses make opposite predictions regarding incongruent cue-task transitions, with the former hypothesis predicting smaller – and the latter hypothesis larger – mean RTs in the incongruent cue-repeat/task-switch condition compared to the cue-switch/task-repeat condition. In this study we analyzed local cue/task novelty effects in two-trial sequences (trials $n - 1$ vs. n ; cf., Schneider & Logan, 2007), while keeping constant the global probabilities of switch and repeat cues, and of task alternations, since these influence the local effects of cue-task transitions² (Baldi, 2005; Squires et al., 1976). In order to pit the global probability of two-trial sequences against higher n -order sequential effects, the two congruent conditions in our study occurred slightly less frequently than the two incongruent conditions (with 0.2 and 0.3 global probability each, respectively). This was intended to offset repetition priming effects by making incongruent transitions slightly more frequent and expected than congruent trials over the experiment. Hence, if incongruent cue-task transitions were to elicit larger RTs and brain activations than congruent trials, these should be less likely attributable to overall novelty or sensory priming, while favoring the alternative hypothesis of higher-order task-set reconfiguration mechanisms.

The task-set reconfiguration hypothesis predicts switch-specific control mechanisms such as the preparatory remapping of stimulus–response associations, without denying the existence of concurrent low-level control, such as associative cue-task retrieval (Jost et al., 2008; Monsell, 2005, p.187). In order to infer preparatory control processes, we manipulated the time allowed for anticipatory task-set reconfiguration – and hence, also the temporal decay

² A local change in sensory cue (or task) at the 100th trial will result in different behavioural and brain responses depending on whether its prior (global) probability was 0.10 or 0.90 in the block of trials (cf., Duncan-Johnson & Donchin, 1977; Kleinsorge et al., 2004).

of cue representations – with the prediction that larger task-switch costs will be found with short (800 ms) compared to long (2000 ms) cue-target intervals (CTI) (Meiran, 1996; Monsell, 2003). However, a similar prediction could be made from the competing hypothesis of sensory priming. Thus, smaller cue-switch costs with long – relative to short – CTIs could also be attributed to a more complete dissipation of a previous cue in the former condition, resulting in lesser sensory priming on cue-repeat trials (cf., Forstmann et al., 2007; Logan & Bundesen, 2003). Therefore, the presence of anticipatory brain responses in different CTI conditions may be critical for deciding among these competing views. For instance, the hypothesis of task-set reconfiguration predicts qualitative differences between cue- and target-locked P300 activations, as reflecting distinct task preparation and execution mechanisms, and contrary to the sensory priming and compound learning hypotheses (cf., Jost et al., 2008, p.75; Logan & Bundesen, 2003). In line with two previous studies (Forstmann et al., 2007; Schneider & Logan, 2007), we also predicted an interaction between Cue- and Task updating for behavioral switch costs, which is also a central tenet of the proposal that the anticipatory control of task-switching can be modeled as the *mutual information* between sensory and task representations estimated over the course of the experimental session (Koechlin & Summerfield, 2007). More specifically, both sensory and task novelty were expected to enhance cue-locked novelty P3 responses, and to reduce target-locked P3 activity (cf., Barceló et al., 2008).

Finally, most previous ERP studies have employed simple perceptual *oddball* tasks that are ill-suited to discern the brain responses during task preparation from those related to task execution (Barceló, 2003; Rubinstein et al., 2001). As a consequence, brain potentials to unexpected targets in *oddball* tasks likely reflect a mixture of preparatory resolution of task uncertainty (*novelty P3*) together with task execution (*target P3*) mechanisms (Barceló, Escera, Corral, & Periañez, 2006; Donchin, 1981). Here we measured the brain responses to both anticipatory cues and targets in order to clarify whether the observed changes in cue-locked early and late novelty P3 and target-locked P3 activity could be best explained in terms of sensory updating mechanisms (i.e., bottom-up control of sensory priming; Logan & Bundesen, 2003), or else, they should be attributed to the anticipatory updating of task representations in preparation for the next target response (i.e., top-down control of task-switching; Barceló et al., 2002; Monsell, 2005). A series of correlation and regression analyses served to explore the behavioral significance of the accompanying brain activations.

2. Materials and methods

2.1. Participants

Forty-one university students (27 female, 14 male; mean \pm S.D. age: 20.1 \pm 2.3 years) with a high educational level (mean \pm S.D. years of education: 13.6 \pm 1.8) took part in the experiment. They all had normal or corrected-to-normal visual acuity, and presented no history of neurological or psychiatric disorders. Participants signed a consent form in agreement with the Declaration of Helsinki, and were informed about the purpose of the investigation prior to the experimental session.

2.2. Experimental task and procedures

All testing was performed using a PC with a 17-in. monitor that was controlled by Presentation[®] software (<http://www.neurobs.com>). We used a version of a task-cueing protocol inspired by the Wisconsin Card Sorting test, and adapted for measuring cognitive brain potentials (Barceló, 2003). Our WCST analogue used 24 out of the original 64 choice cards that can be unambiguously matched with the key cards based on one stimulus dimension only (i.e., either the color, shape, or number of items in the card; Fig. 1a). The colored geometrical shapes were outlined in black upon a white background to improve visual contrast. Cards were matched in luminance and displayed upon a grey background. Each trial consisted of a tonal cue followed by a visual target display with four key cards on top of one choice card, all centered on the computer screen (Fig. 1a). The target stimulus subtended a visual angle of 4° horizontally and 3.5° vertically, and remained on display until a response was given. Participants were instructed to match the choice card with

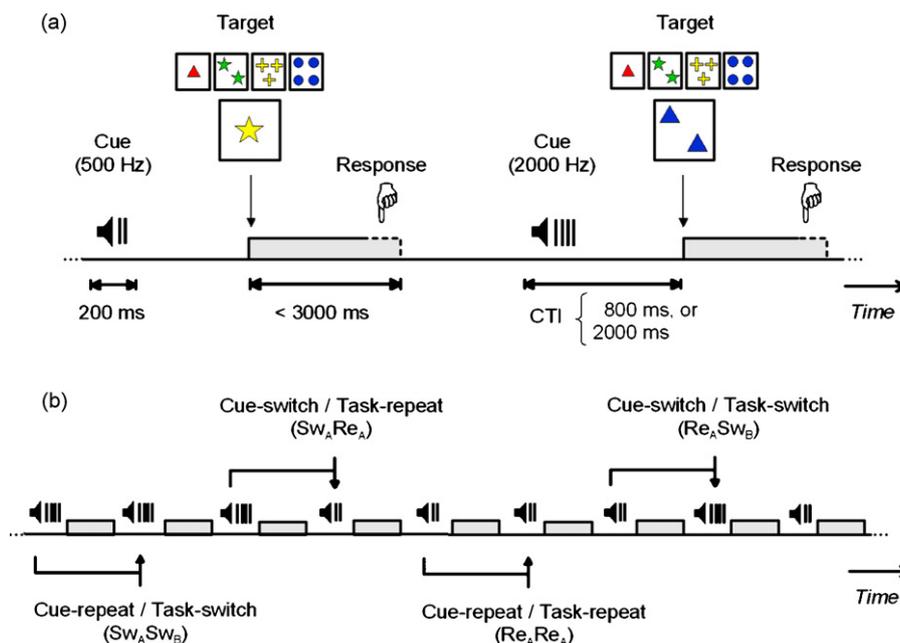


Fig. 1. Stimulus material and experimental design. (a) Each trial consisted of a tonal cue followed by a visual target display with four key cards on top of one choice card. Participants were instructed to sort target cards according to either their color or their shape. Before target onset, a transition cue (2000 Hz or 500 Hz tones) informed whether to switch or to repeat the previous task. The meaning of these tones was counterbalanced across participants. Cue-target intervals were manipulated between-participants (CTI = 800 ms or 2000 ms). (b) Schematic of trial sequences illustrating the four experimental conditions resulting from the orthogonal manipulation of two main factors: (1) whether the cue indicated a task-switch or a task-repeat (*Task updating* factor); and (2) whether the cue switched or repeated between trials $n-1$ and n (*Cue updating* factor). For simplicity, the four possible two-trial sequences are also labeled with the notation $Sw_A Re_B$; where *Sw* and *Re* denote switch and repeat cues in trials $n-1$ and n , respectively; and the subscripts A and B denote the two tasks. In the example, 2000 Hz tones denote a switch in task, and 500 Hz tones indicate a task-repetition.

one of the four key cards following one of two possible task rules, namely, either “sort by color” or “sort by shape”. Participants were told that the task rule would change after totally at random, and that they would have to shift tasks frequently. Before target onset, a tonal cue informed whether to switch or repeat the previous task (200 ms duration, 10 ms rise/fall times, 65 dB SPL, 500 Hz and 2000 Hz binaural tones for switch and repeat cues, respectively; the meaning of the cues was reversed for half the participants). Tonal switch and repeat cues occurred with 0.5 probability each, and they signaled each of the two tasks also with equal mean probability. Trial series were arranged semi-randomly with the following constraints: (1) there were a maximum of four consecutive repetitions of the same tonal cue, and (2) there was a slight offset in the relative frequency of occurrence of congruent and incongruent cue-task transitions over the experimental session (see below). Target responses were given with the index and middle fingers of both hands, using a four-button panel arranged in correspondence with the layout of the four key-cards. 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 (Fig. 1a). The number of random repetitions of each of the 24 target cards was balanced within each task condition, and so were the response buttons for correct sorts. This randomization was intended to equalize any subjective expectancy for target displays and motor responses over the block of trials. Immediately after responding, the word “right” or “wrong” was displayed for 200 ms. Also the words “too fast” or “too slow” appeared whenever the button was pressed either before, or after 3 s from target onset, respectively.

The cue-target interval was either 800 ms or 2000 ms, and was manipulated between-participants to prevent that random variation of preparation intervals within subjects could discourage anticipatory task-set reconfiguration (cf., Rogers & Monsell, 1995). Each participant performed a single block of trials, with the number of trials adjusted in the long (200 trials; 100 switch and 100 repeat), and short CTI conditions (366 trials; 183 switch and 183 repeat). This yielded a total duration ranging between 17 min and 20 min per block of trials. This is a common procedure to keep time-on-task constant in task-switching studies (Meiran & Chorev, 2005). Response-to-cue intervals randomly adopted the values of either 500 ms or 1500 ms within subjects, but this variable will not be considered in the present analyses.

Upon arrival to the laboratory, participants were randomly assigned to the short or long CTI conditions ($N=22$ and 19 , respectively). Prior to the experimental session participants read the instructions on the computer monitor and performed one block of practice trials lasting about 10 min, during which they received verbal instructions and feedback from the experimenter. These practice trials did not enter the analyses. In both the practice and experimental sessions, participants received instructions that switch and repeat trials would occur totally at random, and that they should respond as fast and accurately as possible. The experimen-

tal session lasted about 1 h, including debriefing and the arrangements for the ERP recordings.

2.3. ERP recordings

The electroencephalogram (EEG) was recorded from 28 tin electrodes positioned at Fp1, Fp2, Fz, F3, F4, F7, F8, FCz, FC3, FC4, Cz, C3, C4, CP3, CP4, Pz, P3, P4, TP7, TP8, FT7, FT8, T3, T4, T5, T6, O1, and O2, and referenced to the left mastoid. The EEG signal was amplified (band pass, 0.01–30 Hz, 12 dB/octave roll/off), digitized at 500 Hz/channel, and stored for off-line analysis and averaging. Electrode impedances were kept below 5 k Ω . The vertical and horizontal electrooculogram (EOG) were also recorded for eye blink correction (Gratton, Coles, & Donchin, 1983). Trials with EEG above or below $\pm 75 \mu V$ in amplitude, signal clipping, with muscle, or with any other artifacts in the recording epoch were removed from the ERP analyses. Trials with wrong classifications, false alarms, and omissions were also discarded from the ERP analyses.

2.4. Data analyses

2.4.1. Behavioral data

Reaction times (RTs) were measured from correct trials only, and then classified as a function of whether or not the auditory cue had changed from the previous trial (*Cue updating*), and whether it informed about a switch or a repetition in the previous task rule (*Task updating*), resulting in four orthogonal conditions: cue-repeat/task-switch, cue-switch/task-switch, cue-switch/task-repeat, and cue-repeat/task-repeat (see Fig. 1b). The total number of trials for the short and long CTI groups was 366 and 200, respectively. As mentioned before, the global probabilities for switch and repeat cues/tasks were kept constant across both CTI groups, and the task design focused on the sequential effects of second-order local probabilities comparing trials $n-1$ and n (cf., Squires et al., 1976). The frequency distribution of two-trial sequences in each CTI group was such that the two congruent conditions (i.e., cue-switch/task-switch and cue-repeat/task-repeat) occurred slightly less frequently (with 0.2 probability each) than the two incongruent conditions (i.e., cue-repeat/task-switch and cue-switch/task-repeat, with 0.3 probability each). This was intended to preclude that congruency effects, if present, could be simply attributed to a lower global expectancy for incongruent cue-task transitions developed over the course of the experiment (cf., Forstmann et al., 2007; Squires et al., 1976).

This orthogonal design allowed us to estimate behavioral costs specifically related to Cue updating (cue-switch vs. cue-repeat trials), independent from those related to Task updating (task-switch vs. task-repeat trials). The influence of CTI duration on both cue- and task-switch costs was also examined. This yielded a mixed $2 \times 2 \times 2$ ANOVA with two within-subject factors: Cue updating (switch vs.

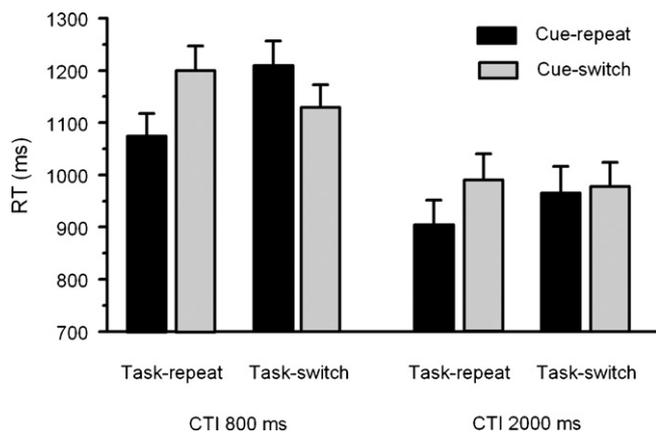


Fig. 2. Behavioral results. Mean reaction time (RT) in milliseconds (\pm S.E.M.) for the Task updating (switch and repeat) and Cue updating (switch and repeat) factors, and for the two groups of participants with short (800 ms) and long (2000 ms) cue-target intervals (CTI).

repeat), Task updating (switch vs. repeat), and CTI as the between-subject factor (800 vs. 2000 ms). The percentage of correct and error trials within each experimental condition was also obtained as a measure of accuracy.

2.4.2. ERP data

Individual ERP averages for each cell of the $2 \times 2 \times 2$ ANOVA design for the behavioral data were computed off-line using a linked-mastoid reference. ERP waveforms were computed time-locked both to the onset of the tonal cues, and to the onset of the target cards. The window of analysis for both cue- and target-locked ERP waveforms was 900 ms, including a 100 ms pre-stimulus baseline. The number of clean EEG epochs that contributed to individual ERP waveforms in each task condition was larger than 38 and 40 for cues and targets, respectively. The analysis of brain activity encompassed several components of the auditory ERP (i.e., N1, early P3, N2, late P3) as well as target-locked P3 responses to visual targets because of their distinct sensitivity to task-switching manipulations as shown in previous studies (cf., Barceló et al., 2002; Nicholson et al., 2005). Mean ERP amplitudes were measured at those electrodes where ERP components showed maximal intensity in the grand averages. Cue-locked N1 (115–145 ms post-cue onset), early P3 (180–220 ms), and N2 amplitudes (255–295 ms) were measured at the vertex (Cz), whereas cue-locked late P3 (300–340 ms post-cue onset) and target-locked P3 amplitudes (310–730 ms post-target onset) were measured at the mid-parietal (Pz) electrode (Fig. 3c and d). Mean ERP amplitudes were submitted to a three-way mixed ANOVA with Task updating (switch vs. repeat) and Cue updating (switch vs. repeat) as the within-subject factors, and CTI (800 vs. 2000 ms) as the between-subject factor.

2.4.3. Correlation and regression analyses

A series of Pearson product-moment correlations were conducted to explore the association between behavioral and brain measures. Mean RTs and the corresponding RT costs were submitted to a series of Pearson product-moment correlation analyses with the mean amplitudes of cue-locked N1, early P3, N2, late P3, and target-locked P3 components for each of the four cue-task transitions. Those ERPs that were significantly correlated with any behavioral measures then entered a multiple regression analysis in order to assess their joint and unique contributions as predictors of behavior.

SPSS v14.0 statistical software was used for all analyses. A significance level of $p < .05$ was adopted for all contrasts. The degrees of freedom were adjusted where appropriate using the Greenhouse-Geisser (*G-G*) correction, as a precaution against inhomogeneities in the variances of the means. A Bonferroni-corrected significance level of $p < .05$ was adopted for all tests of simple effects involving multiple comparisons.

3. Results

3.1. Behavioral results

3.1.1. Accuracy

Accuracy was high, averaging 89.5% (S.D. = 6.9%) across all participants and conditions, and it did not trade off with mean RTs in this study (see Fig. 2 and Table 1). False alarms (“too soon”) and delayed responses (“too late”) occurred in less than 0.2% and 0.6% of all trials, respectively. Therefore, the analyses of behavior focused on the mean RTs.

Table 1

Mean \pm S.E.M. reaction time (RT) in milliseconds and percent error rates (% Errors) for the four combinations of Task updating and Cue updating and the two cue-target intervals (CTI).

	CTI = 800 ms		CTI = 2000 ms	
	Task-switch	Task-repeat	Task-switch	Task-repeat
RT				
Cue-switch	1132 \pm 42	1204 \pm 45	981 \pm 45	992 \pm 49
Cue-repeat	1212 \pm 46	1079 \pm 42	969 \pm 49	907 \pm 45
%Errors				
Cue-switch	11.2 \pm 1.3	20.4 \pm 2.1	3.6 \pm 1.4	4.4 \pm 2.3
Cue-repeat	6.1 \pm 0.7	3.2 \pm 0.4	1.5 \pm 0.8	0.4 \pm 0.5

3.1.2. Reaction times (RTs)

Fig. 2 shows the mean RTs for the four types of cue-task transitions and each of the two CTI conditions. A main effect of Cue updating indicated longer RTs following a cue-switch compared to a cue-repeat ($F(1,39) = 14.0, p < .001$; 1077 ms and 1041 ms, respectively). A main effect of Task updating indicated longer RTs in task-switch trials compared to task-repeat trials ($F(1,39) = 4.8, p < .035$; 1073 ms and 1045 ms, respectively). The interaction between Cue- and Task updating ($F(1,39) = 40.4, p < .0001$; Fig. 2), revealed reliable cue-switch costs under task-repeat conditions ($p < .001$), and task-switch costs under cue-repeat conditions ($p < .0001$). Moreover, ‘paradoxical’ cue- and task-switch benefits were observed when comparing conditions with incongruent cue-task transitions. Thus, longer RTs were found for task-repeat compared to task-switch trials when the cue switched, resulting in a paradoxical task-switch benefit ($p < .0001$). Likewise, longer RTs were found for cue-repeat compared to cue-switch trials when the task switched, resulting in a paradoxical cue-switch benefit ($p < .0001$; Fig. 2). As will be described next, these two ‘paradoxical’ effects were found in the short CTI condition only.

A main CTI effect ($F(1,39) = 10.1, p < .003$) revealed slower RTs in the short compared to the long CTI (1156 vs. 962 ms, respectively). Importantly, the three-way interaction between CTI, Cue- and Task updating ($F(1,39) = 9.1, p < .005$; Fig. 2) revealed that differences in the interplay of Cue updating and Task updating were a function of the cue-target interval. In the short CTI, there were reliable task-switch costs when the cue-repeated (task-switch minus task-repeat = 133 ms; $p < .0001$), as well as reliable cue-switch costs when the task repeated (cue-switch minus cue-repeat = 125 ms; $p < .0001$). Likewise, task-switch benefits were found under cue-switching (task-switch minus task-repeat = -71.2 ms; $p < .001$), and cue-switch benefits occurred when the task-switched (cue-switch minus cue-repeat = -79.6 ms; $p < .0001$). In the long CTI, the two congruent cue-task conditions presented the predicted pattern of task-switch costs under cue-repeat conditions (task-switch minus task-repeat = 62 ms; $p < .029$), and reliable cue-switch costs under task-repeat conditions (cue-switch minus cue-repeat = 85.3 ms; $p < .0001$). These costs were reduced compared to the short CTI condition. Importantly, the paradoxical switch benefits were absent from the long CTI condition (Fig. 2).

3.2. ERP results

Fig. 3 illustrates the main effects for Cue updating and Task updating on the ERP waveforms for the two CTI conditions. Fig. 4 presents the grand ERP waveforms from the four different cue-task transitions, illustrating the interaction between Cue updating and Task updating in each of the two CTI conditions. The analyses focused on the early and late aspects of novelty P3 to the cues and the target-locked P3, as these were the focus of our interest regarding the context-updating hypothesis of the P300 potential, and in relation to our previous task-switching studies.

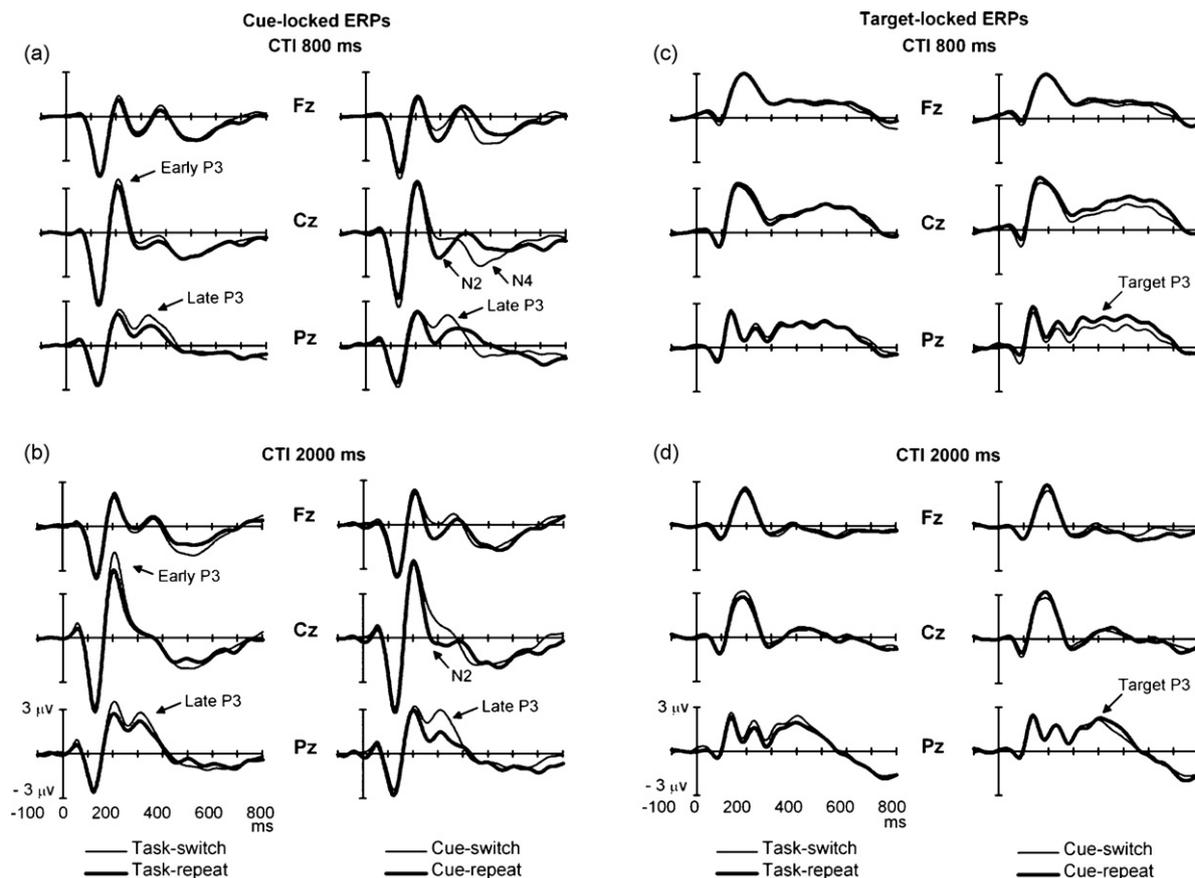


Fig. 3. Grand mean ERPs at three midline electrodes (Fz, Cz, Pz) illustrating the ANOVA's main effects and two-way interactions. (a) Grand cue-locked ERPs elicited by Task updating (left panel) and Cue-updating (right panel) conditions in the short CTI (800 ms) group. (b) The same as (a) for the long CTI (2000 ms) group. (c) Grand target-locked ERPs elicited by Task updating (left panel) and Cue-updating (right panel) conditions in the short CTI (800 ms) group. (d) The same as (c) for the long CTI (2000 ms) group. CTI: cue-target interval.

3.2.1. Cue-locked ERPs

Mean N1 amplitudes were not modulated by the present manipulations of Task updating, Cue updating, CTI, nor by their interactions ($ps > .1$).

Larger early P3 mean amplitudes were found in response to task-switch compared to task-repeat cues, as revealed by a main effect of Task updating ($F(1,39) = 4.3, p < .05$; see Figs. 3 and 4, left panels). A main effect of CTI ($F(1,39) = 4.9, p < .04$) indicated larger early P3 amplitudes in the long – rather than short – CTI condition (see Fig. 3a and b). No other main effects or interactions reached significance for early P3 amplitudes.

Mean N2 amplitudes were more negative for cue-repeat compared to cue-switch trials as revealed by a main effect of Cue updating ($F(1,39) = 37.6, p < .0001$; Fig. 3a and b). The main effect of CTI ($F(1,39) = 25.7, p < .02$) revealed larger N2 amplitudes in the short as compared to the long CTI condition. No other main effects or interactions reached significance for this component (see Figs. 3a, b and 4).

Mean late P3 amplitudes revealed a main effect for Cue updating ($F(1,39) = 40.5, p < .0001$), whereby cue-switches yielded larger late P3 amplitudes than cue-repetitions. The main effect for Task updating was marginally significant ($F(1,39) = 3.4, p < .07$). Post-hoc analyses revealed enhanced late P3 amplitudes for task-switch as compared to task-repeat trials ($p < .035$, one-tailed). Neither the main effect for CTI, nor any other interactions reached significance (Figs. 3 and 4, left panels). This outcome suggested an additive contribution from Cue updating and Task updating to late P3 amplitudes in both CTI conditions (Fig. 5a). These additive effects still held after removing the influence from the previous

N2 component using analysis of covariance. Thus, when mean N2 amplitudes measured at Pz were entered as covariates in the analysis of late P3 activity, the main effects of both Cue updating and Task updating still held ($F(1,39) = 4.1, p < .05$, and $F(1,39) = 10.2, p < .003$, respectively). Post-hoc tests of effects confirmed the significant enhancement of cue-locked late P3 amplitudes for cue-switch vs. cue-repeat trials ($ps < .01$) across all levels of the Task updating and CTI factors (see Fig. 5a).

3.2.2. Target-locked ERPs

The analysis of target-locked P3 amplitudes did not yield any significant main effects, but there was a marginal interaction between Cue updating and Task updating ($F(1,39) = 3.3, p = .08$), indicating larger target P3 amplitudes in cue-repeat/task-repeat trials compared to all other trials (Figs. 3c and 4a). This effect was dependent on preparation times, as revealed by a significant Cue updating by Task updating interaction for the short CTI group only ($F(1,21) = 6.6, p = .02$). Pairwise comparisons among the four cue-task transitions revealed that this effect was due to the significantly larger target P3 amplitudes for cue-repeat/task-repeat trials compared to cue-switch/task-repeat trials ($p = .05$, Bonferroni-corrected). No other contrasts reached significance for target P3 amplitudes measured at Pz (see Figs. 4 and 5b).

To sum up this section, the largest ERP modulations were observed during the cue-target interval consistent with the existence of several distinct preparatory adjustments triggered by both cue-switches and task-switches. These preparatory adjustments seemed time consuming, since they influenced target-locked brain responses and behavior only with short preparation intervals.

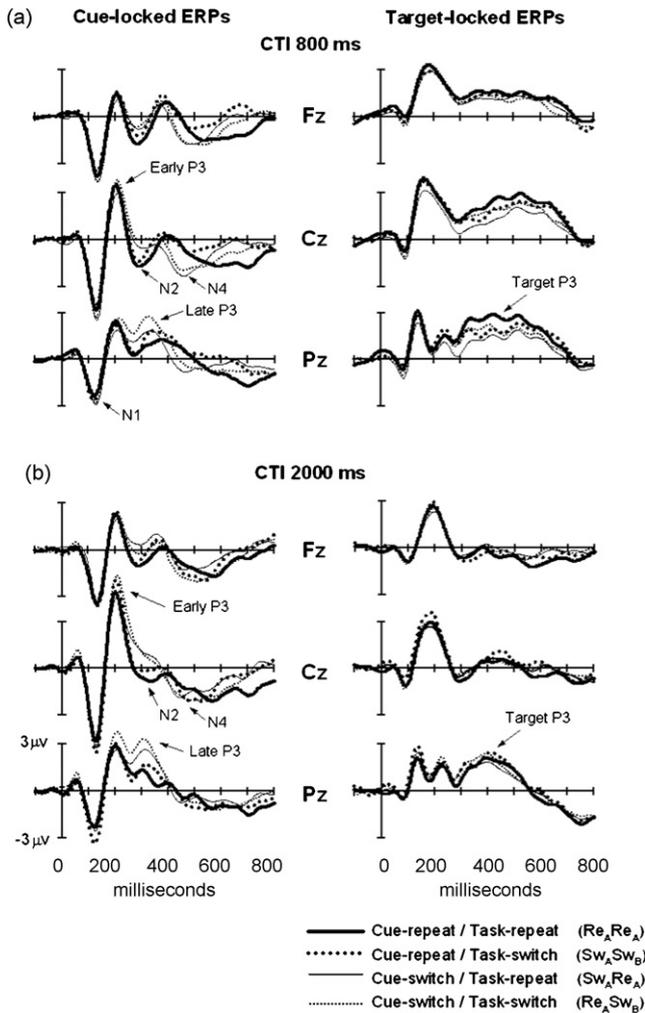


Fig. 4. Grand mean ERPs at three midline electrodes (Fz, Cz, Pz) illustrating the ANOVA's significant three-way interaction. (a) Grand cue-locked (left panel) and target-locked (right panel) ERPs elicited by each of the four possible combinations of the Task updating and Cue-updating factors in the short CTI (800 ms) group. (b) The same as (a) for the long CTI (2000 ms) group. CTI: cue-target interval.

Importantly, although Cue- and Task updating showed dissociable effects on several cue-locked ERP components, they contributed additively to the amplitude of cue-locked late P3 responses in both CTI conditions. In contrast, target P3 amplitudes were influenced by both Cue- and Task updating only with short cue-target intervals (Figs. 3–6).

3.3. Correlation and regression analyses

A series of correlation analyses examined the association between behavior (both mean RTs and RT costs) and various ERP indexes (mean amplitudes for cue-locked N1, early P3, N2, late P3, and the target P3 components). Mean RTs did not generally correlate with ERP amplitudes when the Task updating and Cue updating conditions were tested separately ($N = 41$, $ps > .1$). The only exception was one negative correlation found between mean RTs and mean target P3 amplitudes to task-switch trials ($r = -.32$, $p < .05$). In a second series of correlations, we examined the relationship between behavioral task-switch costs and cue-switch costs, and their corresponding ERP measures. We only found two significant correlations between task-switch costs (task-switch minus task-repeat trials) and the mean amplitudes of both cue-locked late P3 ($r = -.37$, $p < .05$) and target P3 ($r = -.32$, $p < .05$) in task-switch trials.

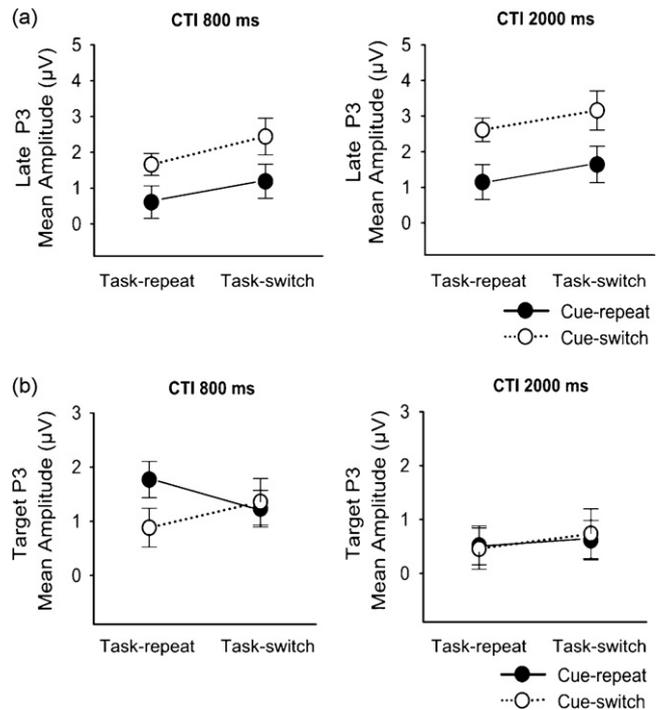


Fig. 5. (a) Mean amplitudes (\pm S.E.M.) for cue-locked late P3 (novelty P3) activity measured at Pz, showing the additive relationship between Cue updating and Task updating at both the short and long CTI conditions. (b) Mean amplitudes (\pm S.E.M.) for target-locked P3 activity measured at Pz, showing the significant interaction between Cue updating and Task updating only at the short CTI condition. CTI: cue-target interval.

No significant correlations were found between task-switch costs and ERP amplitudes in task-repeat trials, nor between cue-switch costs and mean ERP amplitudes to cue-switch and cue-repeat trials.

Multiple regression analyses were conducted only for those two ERP indexes that had shown a significant association with behavior in the previous analyses. When cue-locked late P3 and target P3 mean amplitudes from task-switch trials were entered as predictors in a multiple regression model with behavioral task-switch costs as the criterion, they explained a significant 17% of variance in RT costs ($Adj R^2 = .13$, $F(2, 38) = 4.0$, $p < .026$), with 7.3% and 3.6% of unique contribution from late P3 and target P3, respectively (Table 2). When cue-locked late P3 and target P3 were sequentially entered into the model, late P3 explained 14% of variance in RT costs (R^2 Change = .14; $F(1, 39)$ change = 6.3, $p < .016$), with target P3 adding a non-significant 4% to the prediction of RT costs (R^2 Change = .04, $F(1,38)$ change = 1.6, $p = .2$).

4. Discussion

In this study we aimed to dissociate the behavioral and ERP correlates of sensory updating (cue-switching vs. cue-repetition) and Task updating (task-switching vs. task-repetition) employing an intermittent task-cueing paradigm inspired in the Wisconsin Card Sorting test (Barceló, 2003; Rubinstein et al., 2001). The orthogonal manipulation of Cue updating and Task updating, together with

Table 2

Results from the multiple regression analysis with cue-locked late P3 and target P3 as predictors of behavioral task-switch costs.

	B	S.E.	β	t	Partial	Semipartial
Late P3	-11.8	6.4	-.29	-1.84*	-.29	-.27
Target P3	-9.8	7.8	-.20	-1.28	-.20	-.19

* $p < .05$.

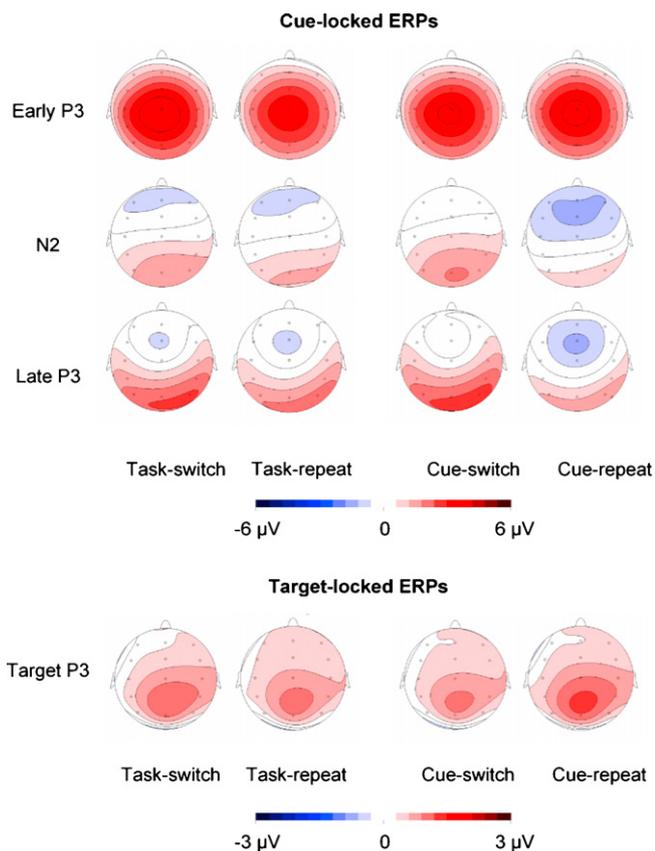


Fig. 6. Scalp topography of cue-locked early P3, N2, late P3 activity (top panel), and target-locked P3 activity (bottom panel) collapsed across both CTI groups. Maps are built up from the task-switch, task-repeat, cue-switch, and cue-repeat grand ERP averages shown in Fig. 3. The maps were computed from the grand mean amplitudes of the corresponding ERP components.

our use of transition cues, and two different cue-target intervals was intended to segregate the relative contribution from exogenous and endogenous sources of information to the behavioral task-switch costs. Our results revealed a complex interplay among these factors, since both the updating of sensory and task representations jointly contributed to the behavioral costs and ERP modulations during the stages of task preparation and execution. Next we discuss the implications of these results for current models of task-switching, and for the context-updating hypothesis of the P300 component of the human brain potential.

4.1. Behavioral costs of switching sensory versus task representations

The present behavioral results replicate two recent task-cueing studies (Forstmann et al., 2007; Schneider & Logan, 2007), and also lend partial support to both the sensory priming and task-set reconfiguration hypotheses. Firstly, we found longer RTs in cue-switch trials as compared to cue-repeat trials (a main effect of Cue updating), supporting an encoding advantage of sensory representations when the cue repeats from trial to trial (Logan & Bundesen, 2003). Second, the presence of task-switch costs (a main effect of Task updating), also lent support to the existence of anticipatory task-set reconfiguration processes (Meiran, 1996; Rogers & Monsell, 1995).

The interaction between Cue updating and Task updating partly reiterated the main effects that switching one level of representation (either cue or task) results in behavioral switch costs only when the other level of representation remains constant from trial $n-1$ to n . Most importantly, though, we found paradoxically increased

mean RTs not predicted by current models in the two conditions with incongruent cue-task transitions (i.e., when the cue repeated and the task switched, or vice versa; see Figs. 1b and 2). These results replicate the cue-switch benefits found by Forstmann et al. (2007), who attributed them to the formation of *bindings* between cues and tasks over the course of the experiment. These bindings were assumed to interfere with overt behavior in incongruent trials (i.e., as in the second trial of a $Sw_A Re_A$ sequence; where Sw and Re denote switch and repeat cues in trials $n-1$ and n , respectively, and the subscripts A and B denote the two tasks). Forstmann et al. (2007) argued that “when the cue changes but the task needs to be repeated, the previously established cue-task binding creates interference because the same task is now indicated by a different cue, which requires a new task activation or task-retrieval process” (cf., Forstmann et al., 2007, p. 398). However, it is unclear how this proposal could also explain our task-switch benefits when a cue-repetition signaled a switch in task (i.e., as in the second trial of a $Sw_A Sw_B$ sequence; see similar results by Schneider & Logan, 2007). Instead, an alternative interpretation becomes plausible in the light of the three-way interaction with cue-target intervals, and also the accompanying ERP results.

The interaction between Task updating, Cue updating, and CTI suggested that increased RT costs in incongruent cue-task transitions could reflect proactive interference from previous task-switching operations, whenever there was not enough time to prepare (CTI = 800 ms). It should be noted that what Forstmann et al. (2007) defined as “incongruent combinations of cue and task transitions” corresponded with two-trial sequences where the $n-1$ trial was a task-switch trial (i.e., trial sequences $Sw_A Re_A$ and $Sw_A Sw_B$ in Fig. 1b). In such conditions, it could be argued that a short CTI favored proactive interference from a previous task-switch in trial $n-1$, and some residual control operations might have been carried over to the next trial, even if this was a task repeat trial. Analogous proposals of long-term carry over of task-set activation and/or inhibition following a switch in task have been put forward by several authors (Altmann, 2004; Allport & Wylie, 2000; Barceló et al., 2008; Hsieh & Cheng, 2006; Mayr & Keele, 2000; Nicholson, Karayanidis, Bumak, Poboka, & Michie, 2006; Swainson et al., 2006). The hypothesis of proactive interference could explain our paradoxical cue-switch benefits because interference from a task-switch in trial $n-1$ may add up extra RT costs to the next task-repeat trial (as with incongruent $Sw_A Re_A$ sequences). Likewise, such proactive interference could also explain our paradoxical task-switch benefits, because interference from task B in trial $n-1$ may facilitate re-engagement of the same task B in trial n of $Sw_A Sw_B$ sequences. In turn, no such delayed control of interference would be expected in two-trial sequences starting with a task-repetition (as in $Re_A Sw_B$ and $Re_A Re_A$ sequences in Fig. 1b). The absence of switch benefits with longer preparation times suggests that such proactive interference probably disrupted task-set reconfiguration operations at trial n . The hypothesis of proactive interference would be compatible with the presence of backward inhibition during the CTI of trial n (Mayr & Keele, 2000; Mayr & Kliegl, 2003), but also with the existence of higher n -order sequential effects along the stimulus sequence (Duncan-Johnson & Donchin, 1977; Remington, 1969; Squires et al., 1976).

In line with previous studies, we found the expected task-switch costs under cue-repetition, and the expected cue-switch costs under task-repetition (cf., Forstmann et al., 2007). These switch costs were larger in the short – relative to the long – CTI groups (with 133 vs. 62 ms task-switch costs, and 125 vs. 85 ms cue-switch costs, respectively; see Fig. 2). Taken together, these results are reminiscent of the sequential effects described in serial RT tasks, mostly found with inter-trial intervals of less than 2 s (Remington, 1969). However, our behavioral analyses alone cannot decide among competing hypotheses about the nature of task-switch costs. On the one

hand, we found reduced task-switch costs with longer preparation intervals, as predicted by the task-set reconfiguration hypothesis (i.e., Meiran, 1996; Monsell, 2003). On the other hand, the sensory priming hypothesis also predicts reduced cue-switch costs with longer cue-target intervals, as these favor a more complete memory decay from a previous cue, and hence, lesser cue-repeat benefits due to sensory priming of cue encoding (Forstmann et al., 2007; Logan & Bundesen, 2003; Schneider & Logan, 2007). Moreover, our behavioral analysis of cue and task transitions in two-trial sequences leaves open the possibility of higher *n*-order effects, particularly for incongruous cue-task transitions (cf., Forstmann et al., 2007; Schneider & Logan, 2007). Higher *n*-order sequential effects have been related to the build-up of global event expectancies over extended trial sequences, and were originally linked to context-updating operations indexed by the endogenous P300 complex in simple perceptual tasks (Duncan-Johnson & Donchin, 1977; Squires et al., 1976). Next we explain how the analysis of brain responses helped us to clarify the nature of representations mediating behavioral switch costs, as well as their temporal course of operation.

4.2. Brain responses to Cue updating versus Task updating

One important finding was the absence of any simple one-to-one correspondence between any specific ERP feature and the overall pattern of behavioral costs (Figs. 2–5). Instead, our manipulation of Cue- and Task updating caused significant time-dependent modulations (i.e., relative increments or reductions) in the amplitude of cue-locked early and late P3, as well as on other negativities in the vicinity of the P300 complex. In sharp contrast, target-locked P3 activity was modulated only with short cue-target intervals.

The main features of the brain responses can be summarized as follows. First, task-repetitions resulted in reduced cue-locked early and late P3 potentials, relative to task-switches. Second, cue-repetitions reduced cue-locked late P3, but enhanced cue-locked N2 amplitudes, relative to cue switches. These effects were present in both CTI conditions, although larger early P3 amplitudes were observed with longer intervals. Third, cue-repetitions elicited larger target P3 amplitudes than cue switches, but only for task-repeat and short CTI conditions. Fourth, cue-locked early and late P3 amplitudes did not merely reflect the global probability of occurrence (i.e., the amount of surprise; Donchin, 1981) of congruent versus incongruent cue-task transitions. These results do not support the strong versions of the sensory priming and associative compound learning hypotheses. Instead, they seem consistent with the presence of advance task-set reconfiguration, and higher *n*-order control of trial-by-trial sequences. Finally, cue-locked late P3 (*novelty* P3) and target P3 potentials explained a modest amount of variability in the behavioral measures.

4.2.1. Task updating modulates cue-locked brain responses

Task-repetitions reduced the amplitude of the early and late aspects of cue-locked P3 activity, as compared to task-switches, and these effects partly mirrored the main effects of Task updating for mean RTs (Figs. 2 and 3a, b). These results replicate previous studies showing a reduction of fronto-central and mid-parietal P3 potentials in response to task-repeat cues as early as 150–200 ms post-cue onset (Barceló et al., 2008; Barceló et al., 2002; Jost et al., 2008; Nicholson et al., 2005; Rushworth et al., 2002). These results also agree with the notion that recurrent task representations suppress neural activity at an early processing stage (Grill-Spector et al., 2006). Importantly, the dissociation of early and late P3 responses to cue and task transitions support their distinct functional roles as two sequential and hierarchically organized processes involved in the preparatory control of task-switching, in line with recent ERP evidence (Barceló et al., 2008; Barceló et al., 2002), and theoretical

proposals (Kleinsorge et al., 2004; Lien & Ruthruff, 2004; Schneider & Logan, 2006). Higher-order Task updating operations (i.e., goal setting) seem to precede subordinate Task updating operations (i.e., S–R remapping), consistent with suggestions that prefrontal cortices precede and bias processing at posterior cortical regions during task-switching (Brass et al., 2005). Next we discuss the hypothesis that cue-locked early and late P3 activations observed in task-cueing paradigms index a two-stage process consisting of (1) the re-activation of task-set information, as a pre-requisite for (2) the subsequent re-mapping of stimulus–response (S–R) associations in working memory, respectively (cf., Barceló et al., 2008; Jost et al., 2008).

Cue-locked early P3: The earliest cue-locked ERP signature attributable to Task updating operations was an enhancement of early P3 amplitude to task-switch – relative to task-repeat – cues, which was larger in the long – compared to the short – CTI condition (Fig. 3a, b, left columns). Several lines of evidence indicate that early P3 could reflect the intermittent re-activation of task-set information, rather than any switch-specific operations such as the re-mapping of S–R associations within the active task-set (cf., Altmann, 2004; Barceló et al., 2008). Firstly, early P3 activity was sensitive to Task updating – rather than Cue updating – manipulations, consistent with the notion of cue-based task-retrieval or activation (Altmann, 2004; Forstmann et al., 2007). This outcome also agrees with the activation of neural information at the most general level of representation, such as task goals (Rubinstein et al., 2001), action plans (Schneider & Logan, 2006), or conceptual judgments (Kleinsorge et al., 2004), and probably involves the simultaneous deactivation or inhibition of competing task representations (Mayr & Keele, 2000). Likewise, the reduced early P3 activity to task-repeat cues agrees with the suppression of neural responses to recurrent conceptual representations (Grill-Spector et al., 2006). Secondly, larger early P3 amplitudes were observed with long – relative to short – CTIs, and regardless of trial type because of the null interaction between CTI and Task updating. This outcome is also compatible with the task-set activation hypothesis, since longer intervals would favor forgetfulness of a previous task-set, thus making it necessary stronger subsequent re-activation independent of trial type. Finally, our regression analyses revealed that unlike late P3, early P3 amplitudes did not correlate with switch-specific behavioral costs. This agrees with our previous findings (Barceló et al., 2008), and suggests a critical dissociation between early and late P3 activations towards the overall score of behavioral switch costs.

Other alternative accounts for these early P3 activations are also worth considering. Amplitude modulations of positive-going deflections around 200 ms post-stimulus onset in the auditory modality have been related to changes in the intensity and pitch of the eliciting sounds (Crowley & Colrain, 2004). In our study, the increment of early P3 amplitudes to task-switch cues could not be attributed to changes in pitch or sound intensity, since our two tones had the same intensity, and the mapping of 500 Hz and 2000 Hz tones with the two Task updating conditions was counterbalanced across participants. Most ERP studies have compared early P3 responses to repetitive and novel stimulation using single task-set paradigms like *oddball* tasks (Friedman et al., 2001). In such single task settings, the early P3 response seems insensitive to attentional manipulations (Escera et al., 1998), probably because such conditions do not demand any updating of higher-order task representations. In contrast, our results reveal enhanced early P3 amplitudes with changing task representations that seemed to reflect “a necessary, although not sufficient, step before a P300 can be elicited” (García-Larrea, Lukaszewicz, & Mauguier, 1992, p. 737). One such obligatory, general purpose mechanism could be the intermittent re-activation of task rules necessary for the subsequent re-mapping of S–R associations in memory (cf., Barceló et

al., 2008), consistent with the notion of cue-based task-retrieval or activation (Altmann, 2004; Forstmann et al., 2007).

Cue-locked late P3: The enhanced cue-locked late P3 amplitudes over mid-parietal scalp regions in response to task-switch – and relative to task-repeat – cues replicates a very consistent finding in the literature (Barceló et al., 2006; Barceló et al., 2008; Barceló et al., 2002; Brass et al., 2005; Jost et al., 2008; Nicholson et al., 2005; Rushworth et al., 2002; Swainson et al., 2006). The main effect of Task updating was reliable after controlling for the influence of the negative N2 component using covariance analysis (Fig. 3a and b). Interestingly, task-repetition did not totally suppress late P3 responses, and these effects could not be simply attributed to the global probability of occurrence of congruent *versus* incongruent cue-task transitions (Figs. 3a, b and 4). Thus, congruent cue-switch/task-switch trials (in $Re_A Sw_B$ sequences) elicited the largest late P3 amplitudes, compared to the equally probable congruent cue-repeat/task-repeat trials (in $Re_A Re_A$ sequences), and relative to the less expected but incongruent cue-repeat/task-switch trials (in $Sw_A Sw_B$ sequences). Therefore, if cue-locked late P3 activity was to index anticipatory task-switching operations at trial n , it seemed also influenced by foregoing task-switching operations (i.e., higher n -order sequential effects; Forstmann et al., 2007; Squires et al., 1976). The comparatively reduced late P3 amplitudes for incongruent cue-task transitions in $Sw_A Re_A$ and $Sw_A Sw_B$ sequences argue for the presence of proactive interference from previous task-switching operations (see Figs. 4 and 5). Thus, the efficient remapping of S–R associations in working memory (putatively indexed by late P3), may first require efficient updating of the ruling task-set (putatively indexed by early P3). Whatever disruption in the latter obligatory process (i.e., incomplete task-set activation, proactive interference, etc.) might also impair any subsequent S–R re-mapping, and disrupt late P3 responses in incongruent cue-task transitions, making them prone to “prediction errors”. The negative correlation found between behavioral task-switch costs and late P3 amplitudes to task-switch cues, and the contribution of late P3 as a predictor of task-switch costs (Table 2) both concur with previous findings that cue-locked late P3 amplitudes are predictive of subsequent task performance (Barceló et al., 2008; Kieffaber & Hetrick, 2005). Taken together, these results suggest that behavioral task-switch costs were inversely related to the efficient updating of S–R mappings in memory, as indexed by enhanced cue-locked late P3. In the next section, we discuss why similar cue-locked late P3 activations, reflecting the putative re-mapping of S–R associations, may be observed following both cue- and task-switches.

4.2.2. Cue updating modulates cue-locked brain responses

The manipulation of Cue updating (*cue-switching vs. cue-repetition*) modulated cue-locked N2 (255–295 ms) and late P3 (300–340 ms) amplitudes, as well as a longer-latency negative N4 waveform in the short CTI condition (Fig. 3a and b). These results are reminiscent of the sequential effects in serial RT tasks, also known to modulate the endogenous P300 complex (Duncan-Johnson & Donchin, 1977; Squires et al., 1976). However, these previous ERP studies used simple *oddball* tasks with only one active task-set, and could not ponder the relative contribution of Task updating to their ERP effects. The present results also suggest that Cue updating operations were chronologically subordinated to Task updating operations.

Cue-locked late P3: Reduced cue-locked late P3 amplitudes were observed in cue-repeat trials, relative to cue-switch trials (Fig. 3a, b, right columns). This result indicates that – unlike early P3 – late P3 responses were modulated by the updating of both sensory and task representations (cf., Barceló et al., 2008). The absence of an interaction between Cue updating and Task updating for late P3 activity may seem paradoxical in the light of the present behav-

ioral results. This null effect was unlikely due to lack of sufficient statistical power for the relevant contrasts, judging by the small standard error of the means for late P3 amplitudes (Fig. 5a). On the contrary, data from Figs. 4 and 5a suggest a truly additive contribution from Cue updating and Task updating to late P3 amplitudes, although the former factor seemed chronologically subordinated to the latter, since Cue updating did not influence early P3 activity. This account concurs with the observed increases in late P3 amplitudes with a change in sensory cue, a change in task, or both, since all these cases seem to demand corresponding adjustments of S–R associations in memory.

The present results are consistent with the proposal that cue-locked late P3 (*novelty P3*) indexes the re-mapping of S–R associations in working memory whenever the current task context needs to be updated in the presence of *contextual novelty*, and regardless of whether this *novelty* is conveyed through exogenous or endogenous sources of information. To support this view, the largest late P3 amplitudes (2.8 μ V at Pz; Fig. 4a, b) were elicited by cue-switch/task-switch events that required both cue and task-switching operations. In contrast, the smallest late P3 amplitudes (0.9 μ V at Pz) were elicited by cue-repeat/task-repeat events that did not require any changes in sensory or task representations (Fig. 4a and b; Grill-Spector et al., 2006). For our equally probable congruent cue-task transitions, the largest late P3 amplitudes corresponded with the largest re-adjustments in the active task-set in the presence of novelty at both the sensory (cue) and task levels of representation. This evidence supports an additive contribution from both Cue- and Task updating to the amplitude of cue-locked late P3 potentials during the resolution of contextual novelty (Fig. 5a; Barceló et al., 2008; Squires et al., 1976). These modulations in cue-locked late P3 activity did not merely reflect the global probability of congruent cue-task transitions, but instead they seemed to reflect a dynamic interaction between local bottom-up inputs and contextual top-down inputs, as can be formally expressed as the *mutual information* between sensory and task representations estimated over the course of the whole experimental session (Barceló et al., 2008; Koechlin & Summerfield, 2007).

For incongruent cue-task transitions, the comparatively reduced late P3 amplitudes could be caused by the presence of task-switching operations in trial $n - 1$ (Figs. 1 and 4). These reduced late P3 amplitudes do not fit simple models based on global stimulus probabilities, or local novelty in two-trial sequences, because incongruent cue-task transitions were comparatively less frequent (more surprising) events (cf., Donchin, 1981). On the contrary, our results are consistent with the presence of higher n -order sequential effects that might have required the deployment of extra contextual control in incongruent cue-task transitions. In these cases, an efficient remapping of S–R associations, and a full-blown novelty P3, could be both compromised by proactive interference from – or backward inhibition of – preceding task-set switching operations (Forstmann et al., 2007; Schneider & Logan, 2007). In these circumstances, the neural/mental representations responsible for such sequential effects in the behavior and brain responses would be more likely related with higher-order contextual control (Koechlin & Summerfield, 2007), rather than with lower level sensory priming (Logan & Bundesen, 2003).

Finally, larger late P3 amplitudes were observed with long–compared to short–CTIs (Fig. 3a and b), but this effect did not interact with other factors. This outcome seems also consistent with the proposal that late P3 activity reflects the preparatory updating of S–R associations, since longer preparation times favor more complete task-set reconfiguration, including a more complete re-mapping of S–R associations in working memory. This proposal gains support from a modest but significant negative correlation found between late P3 amplitudes and behavioral switch-costs (cf., Barceló et al., 2006; Barceló et al., 2008).

Cue-locked long latency negativities: Relative to cue-switch trials, cue-repetitions increased the amplitude of a negative N2 component with a fronto-central scalp distribution (Fig. 6). The reverse was true for a longer-latency negativity (N4; 450–550 ms) that was enhanced in cue-switch compared to cue-repeat trials in the short CTI condition (Figs. 3a and 4a). As we did not have any *a priori* hypotheses about these fronto-central negativities, we will only briefly comment about their putative role based on evidence from this and previous studies. Enhanced N2 amplitudes to cue-repeat trials were reminiscent of a “repetition negativity” described by Näätänen and Rinne (2002) both in terms of its latency, scalp distribution, and response to task variables. In the study by Näätänen and Rinne (2002), the repetition of an auditory stimulus elicited a fronto-central N2 negativity that grew progressively larger over successive repetitions of the same sound. This evidence suggests that stimulus repetition does not always result in the suppression of neural responses (cf., Grill-Spector et al., 2006). On the other hand, and consistent with the hypothesis of cue-repetition benefits in the task-switching literature (Forstmann et al., 2007; Logan & Bundesen, 2003; Mayr & Kliegl, 2003), enhanced N2 amplitudes during cue-repeat trials could reflect sensory priming of cue encoding, leading to an enduring memory for the repeated stimulus (Näätänen & Rinne, 2002). This idea would be supported by the largest N2 amplitudes observed with the shortest CTI, where a lesser decay of sensory memories would lead to a more efficient priming of the next cue. Similar cue-locked N2-like potentials have been reported in previous task-switching studies, even though these could not discern between task-switching and cue-switching operations (Barceló et al., 2006; Brass et al., 2005; Jost et al., 2008; Nicholson et al., 2006).

In sharp contrast with cue-locked N2 amplitudes, a longer-latency N4 negativity was specifically enhanced in response to cue-switch trials in the short CTI condition only (cf., Figs. 3a and 4a). This effect was reminiscent of the re-orienting negativities following novelty P3 responses to sensory deviants in oddball tasks (Escera et al., 1998), and suggests that multiple preparatory processes may be concurrently active during the anticipatory control of task-switching. In line with multicomponent models of task-switching (Monsell, 2005; Nicholson et al., 2005; Shallice, Stuss, Picton, Alexander, & Gillingham, 2008), these results suggest a complex interplay of control operations during the stage of task preparation that are unlikely to be fully captured through any single component process in the ERP waveform. Further research will be needed to clarify the type of control operations indexed by these fronto-central N2 and N4 modulations.

4.2.3. Contextual novelty influences target P3 activity

The analysis of target-locked ERPs confirmed a critical functional dissociation between cue-locked late P3 (*novelty P3*) and target P3 activity reported in previous task-switching studies (Barceló et al., 2006; Barceló et al., 2000; Barceló et al., 2002). In brief, target-locked P3 amplitudes were reduced with changing sensory and/or task representations, whereas those same conditions enhanced cue-locked late P3 amplitudes. In other words, the early and late aspects of novelty P3 showed *habituation* with recurrent sensory and task representations (also repetition suppression; cf., Grill-Spector et al., 2006). In turn, target P3 amplitudes showed the opposite phenomenon of repetition enhancement. This has been a very consistent finding in recent ERP studies on task-switching (Barceló et al., 2000; Barceló et al., 2002; Jost et al., 2008; Nicholson et al., 2005; Swainson et al., 2006), and lends support to the *task novelty hypothesis* that cue-locked late P3 (*novelty P3*) indexes preparatory adjustments in task-set representations necessary to resolve contextual novelty for anticipatory response selection (i.e., the updating of novel S–R associations in working memory; Barceló et al., 2006; Philipp, Jolicoeur, Falkenstein, & Koch, 2007). In con-

trast, target P3 amplitudes seemed related to task-set rehearsal or implementation during the stage of response execution, with more practiced task-sets eliciting larger target P3 amplitudes. Whenever the ruling task-set could not be fully updated (i.e., because of lack of time, proactive interference, backward inhibition, etc.), the preparatory resolution of uncertainty about the next response was delayed, possibly overlapping with target onset. The consequences of such delayed control were slower and less accurate behavioral responses, and reduced target P3 amplitudes (Figs. 2 and 4). In turn, larger target P3 amplitudes seemed to index the efficient implementation of the active task-set, whenever it had been fully updated following longer preparation times, or after several repetition trials in a row (Barceló et al., 2002).

The gradual increment of target P3 amplitudes along successive task-repetition trials has been previously interpreted as the neural signature of the growing efficiency in the implementation and consolidation of a task-set with practice (Barceló et al., 2000; Barceló et al., 2002; Jost et al., 2008). The sequential structure of our task design was highly unpredictable because switch and repeat cues occurred with a global probability of 0.5 each, and with the constraint of a maximum of four consecutive task-repeat trials in a row (with only 1.5 trials on average). For such short runs of task-repetitions, consolidation of the task-set would be expected to be weaker than for longer runs, and hence, this aspect of our task design must have limited the increment in target P3 amplitude previously observed over longer runs of task-repeat trials (Barceló et al., 2000; Barceló et al., 2002). Alternatively, these effects could be also described as a sharp reduction in target P3 amplitude following a switch in task, owing to a less efficient task execution in early post-switch trials (Barceló et al., 2000; Jost et al., 2008). The previous confound of cue-switching and task-switching precluded an unequivocal account of this post-switch reduction in target P3 amplitude (and the accompanying behavioral costs), in terms of either sensory or task-set updating mechanisms. Undoing this confound was one of the main objectives of the present study.

The interaction between Cue updating and Task updating for target P3 was a function of preparation time (Fig. 4c and d), and revealed the distinct nature of the underlying processes compared to those responsible for novelty P3 elicitation (Figs. 4 and 5). The largest target P3 (and the smallest cue-locked late P3) amplitudes were elicited by cue-repeat/task-repeat trials, i.e., in $Re_A Re_A$ sequences, which required a minimum of preparatory Cue- and Task updating. Such condition could be thought of as the least surprising and least prone to prediction errors, at either the sensory or task levels of representation. In contrast, the other three types of cue-task transitions involved preparatory task-set re-adjustments, and resulted in comparatively reduced target P3 amplitudes and larger mean RTs. Thus, whatever change in cue or task, at either trials $n - 1$ or n , also motivated some degree of re-adjustment in the active task-set, as indexed by preparatory cue-locked P3 activity. Whenever these re-adjustments could not be completed in advance because of lack of preparation time, they were carried over to the target period, thus reducing target P3 amplitudes. As a consequence, reduced target P3 amplitudes seemed to index lesser efficiency in task-set or response execution, following unfinished task-set reconfiguration (Barceló et al., 2002). This account compares with the diversion of attentional resources away from target processing, and towards surprising sensory changes in behavioral distraction studies (Escera et al., 1998; Friedman et al., 2001). This rationale would also be compatible with the limitations of attentional resources when confronting task novelty in dual task conditions (Barceló et al., 2006). The proposal that disruptions in behavioral efficiency may be caused by both exogenous and endogenous sources of information is also consistent with the hypothesis of a continual interaction between sensory and task-set representations encompassing the stages of task preparation and task execution (cf.,

the perception-action cycle; Fuster, 2002). This putative interaction between sensory and task representations (including motor responses) can be formally expressed as the *mutual information* between cues and tasks over the course of an experiment (Barceló et al., 2008; Koechlin & Summerfield, 2007), and concurs with an intrinsic interplay between local and global control processes (i.e., “a task space”; Kleinsorge et al., 2004) in determining sequential trial-by-trial changes in behavioral and brain responses (Duncan-Johnson & Donchin, 1977; Squires et al., 1976).

The present findings complement and expand previous ERP results from task-switching studies revealing that (1) reduced target P3 amplitudes during task-switching can be caused by changes in both sensory and task representations, because they can both trigger preparatory task-set re-adjustments for the resolution of any contextual novelty in anticipation of the next target response; and (2) the temporal interval between cue and target onset determines whether task preparation will be completed on time, or else, whether the preparatory re-adjustments will interfere with the behavioral and brain responses at target onset.

5. Conclusions

This study provides evidence that both sensory and task representations jointly contribute to the behavioral costs and accompanying brain activations observed during task-switching. Lesser behavioral cue- and task-switch costs with long preparation intervals supported the presence of anticipatory task-set reconfiguration processes during the cue-target interval, partly indexed by early and late cue-locked P3 activity. The analysis of brain responses suggested that task preparation (and novelty P3 potentials) coexisted with additional control processes compatible with the repetition priming of past sensory representations (Grill-Spector et al., 2006; Logan & Bundesen, 2003), as well as with proactive interference (Allport & Wylie, 2000; Rushworth et al., 2002), or backward inhibition of an old task-set (Mayr & Keele, 2000; Mayr & Kliegl, 2003). These additional control processes could well explain the presence of higher *n*-order sequential effects in the behavioral and brain responses, mostly in incongruent cue-task transitions. Further research will be needed to better define these control mechanisms, and to formally model their relationship with the development of subjective expectancies over extended trial sequences or time scales (Baldi, 2005; Mars et al., 2008; Nobre et al., 2007).

Trial-by-trial fluctuations in stimulus expectancy have long been shown to modulate the endogenous P300 complex in simple perceptual tasks (Duncan-Johnson & Donchin, 1977; Squires et al., 1976), although few studies have explored the dynamic interplay between sensory and task representations during the updating of contextual expectancies for the preparatory control of action (Barceló et al., 2006; Barceló et al., 2008). For most purposes in cognitive neuroscience, the information conveyed by any stimulus depends on the *task context* where the stimulus was delivered, and therefore, on an intrinsic interplay between bottom-up inputs and top-down inputs along a putative hierarchy of representations in our brains (cf., Friston, 2005, p. 826). This interaction may be formally expressed as the *mutual information* between sensory and task representations (including motor responses) estimated over the course of an experiment (Koechlin & Summerfield, 2007). One corollary of this proposal is that any general model of cognitive control for task-switching should also consider motor response demands (Mayr & Kliegl, 2003; Philipp et al., 2007), and response congruency effects (Meiran et al., 2000; Philipp et al., 2007), as important sources of switch costs. Future research should address the relative contribution from these factors to the information content of sensory stimuli for task and response selection (cf., Barceló et al., 2008; Koechlin & Summerfield, 2007).

In sum, the present ERP results suggest a chronological and hierarchical organization of control processes in response to anticipatory task cues in a task-switching paradigm, whereby three successive features of the P300 complex (early P3, N2, and late P3) seemed to index: (a) the intermittent re-activation of task-set information; (b) the priming of sensory memories; and (c) the additive contribution of sensory and task-set information to the updating of S–R mappings in working memory, respectively. In contrast, target P3 activity seemed related to task rehearsal or implementation (Barceló et al., 2006; Barceló et al., 2008). In line with multicomponent models of task-switching (Monsell, 2005; Nicholson et al., 2005; Shallice et al., 2008), our findings suggest that the cognitive control of task-switching depends on a complex interplay between exogenous and endogenous sources of information whenever these need to be integrated over time for goal-directed behavior (Fuster, 2002; Nobre et al., 2007).

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