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Early reduction of sensory processing within the visual cortex when switching from internal to external attention

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ABSTRACT

The neurocognitive process underlying attention switches between external (perception-based) and internal (memory-based) attention is poorly characterized. Previous research has found that when participants switch attention either between two perception-based tasks (within-domain switches) or between a memory- and a perception-based task (between-domain switches), a substantial and similar processing cost was observed compared to the repetition of the same task (Verschooren, Schindler, De Raedt, & Pourtois, 2019). Here, we recorded 64-channel EEG while participants carried out within- versus between-domain switches of attention. ERP results showed that during early sensory processing, a marked P1 attenuation was associated with both switch types, suggesting that switching was associated with an early bottleneck during information processing. This early gating effect was stronger when switching from an internal to an external task, compared to switching between external tasks, suggesting different top-down requirements for them. These findings are in line with earlier proposals in the literature.

1. Introduction

Attentional flexibility is indispensable to navigate complex environments, selecting currently relevant pieces of information based on dynamic behavioural goals (Marois & Ivanoff, 2005). In advanced mammals such as humans, this challenge is even greater, as we simultaneously have an internally represented environment to monitor (Mesulam, 1998). Consequently, competing demands from both environments, external and internal, need to be resolved on an overarching level of flexibility and control.

Available models of attentional flexibility have nonetheless either been concerned with switches between different external stimuli or switches between different internal representations (for a recent review, see Verschooren, Schindler, De Raedt, & Pourtois, 2019). Moreover, these two research domains have developed almost entirely independently. On the one hand, models of external attention flexibility mostly rely on research with paradigms such as the Posner task (Posner, 1980), in which costs associated with reorientation of spatial attention can be investigated. On the other hand, models of internal attention flexibility rely mostly on task-switching paradigms, where costs associated with switching between internal task representations are studied (Vandierendonck, Liefooghe, & Verbruggen, 2010, for a review).

A consistent finding is that participants are slower and more error-prone on trials where they need to switch (external or internal) attention than trials where repetitions occur. In task-switching, this switch cost has been interpreted as reflecting both the need for enhanced control when moving from one task context to another and interference caused by the activation of the previous task-set when processing the current stimulus (Monsell, 2003; Vandierendonck et al., 2010). Reconfiguration and interference likely also play a role when switching between external and internal attentional states (Verschooren, Pourtois, & Egner, 2020; Verschooren, Liefooghe, Brass, & Pourtois, 2019). However, the similarities and differences between switching within a domain (e.g., external spatial attention or internal task switch) and switching between domain (e.g., a switch from an internal to an external task) are currently not clearly understood.

To fill this gap, we have previously validated a paradigm on which the cost associated with these between-domain attention switches can be reliably measured (see Fig. 1; Verschooren, Schindler et al., 2019). Participants perform a Baseline Task requiring external attention sporadically interrupted by either an external or internal task, requiring external or internal attention, respectively. After this interruption,

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returning to the Baseline Task results in a within-domain (external-to-external attention) or between-domain (internal-to-external attention) switch. Using this procedure, we can directly compare the cost associated with these two types of switches, as the Baseline Task is identical for both. For clarity, it is important to emphasize here that this procedure only uses a single instantiation of the within- and between-domain: we compare external-to-external to internal-to-external switches, but not internal-to-internal or external-to-internal (see 'Constraints on generalizibility' section in the Discussion). Our previous study found that these two switch costs were of equal size in reaction times over a series of four experiments (Verschooren, Schindler et al., 2019).

These identical costs at the behavioral level are compatible with a single neural mechanism that controls within- and between-domain switches (Verschooren, Schindler et al., 2019). However, attentional control mechanism can be dissociated for internal and external attention (e.g., Esterman, Chiu, Tamber-rosenau, & Yantis, 2009; Tamber-Rosenau, Esterman, Chiu, & Yantis, 2011), which suggests that switches between them might rely on distinct processes as well (but see Burgess, Dumontheil, & Gilbert, 2007). Behavioral results are limited in this respect as dissociable neural processes could give rise to equivalent behavioural costs. The present study investigates this question, and determines whether similar or partly dissociable neural processes account for these two switch types.

To address this question, we capitalized on this new paradigm (see Fig. 1) and recorded high-density (64 channels) EEG in healthy adult participants to gain insight into the spatio-temporal dynamics of the between- relative to the within-domain switch cost. We compared the amplitudes of well-defined early visual ERP components (i.e. P1, N1) on the baseline trials immediately preceding (Pre) and succeeding (Post) the interrupting task. As a control analysis, we compared both with baseline trials sampled in the middle of the run (Mid), i.e., preceded by at least two Baseline trials and followed by at least one (see Supplementary Materials). Moreover, in order to disentangle the effects of task difficulty from attentional flexibility to the observed ERP results, we used an easy and hard version of both the external and internal tasks across different blocks (see Fig. 1).

We primarily focused on early visual ERPs time-locked to the onset of the exact same external event for all conditions (i.e., a simple visual cue, see Fig. 1) and compared their amplitudes (as well as latencies) between the four main conditions embedded in this factorial design (between- vs. within-domain switch cost, for each of the two difficulty levels). The P1 component is well suited to explore the dynamic of early attention effects following stimulus onset, including those involved in attentional control (Desimone & Duncan, 1995; Hillyard & Anllo-Vento, 1998; Luck, Heinze, Mangun, & Hillyard, 1990, 1994). It is usually interpreted as reflecting sensory gain control effects taking place in the extrastriate visual cortex (Hillyard, Vogel, & Luck, 1998). Put differently, a reduced P1 amplitude at the cue level likely could reflect attentional inertia (Longman, Lavric, Munteanu, & Monsell, 2014), i.e., reduced availability of attention due to ongoing top-down processes. We additionally analyzed the subsequent N1 component, as previous ERP studies found that top-down endogenous attention factors also influenced it (Hopfinger & Mangun, 1998; Mangun & Hillyard, 1991; Woodman, Vogel, & Luck, 2001). As we previously did not observe any differences at the behavioral level for the within- and between-domain switches (Verschooren, Schindler et al., 2019), we could assume that potential differences in P1 amplitude at the cue level between conditions might be compensated at the target level, for example during the N1, which reflects visual discrimination. In other words, even though more attentional inertia might be present for between-domain switches early on following stimulus onset (cue level), it could be compensated by additional processing occurring later in time, at the target level.

As explained here above, our main ERP analysis focused on cue-related effects. This cue provided the same physical stimulus across all conditions and corresponded to the first visual event informing participants about the return to the Baseline Task after having performed a switch to either another external or internal task. In addition, we analysed these ERP components time-locked to the onset of the subsequent target (see Fig. 1) to investigate potential compensatory processes between cue and target. Moreover, to corroborate the assumption that these attention control effects involved dynamic changes in sensory processing taking place mainly in the extrastriate visual cortex (P1, N1), we supplemented the classical ERP analysis with a distributed source localization method (see Supplementary Materials).

We predicted, firstly, reduced ERP activity at the cue level following the switch, possibly already occurring at the P1 level. This effect has previously been reported in studies on task-switching (Lange, Seer, Müller, & Kopp, 2015) and can be interpreted as the result of ongoing reconfiguration associated with the switch (Meiran, 1996; Monsell,

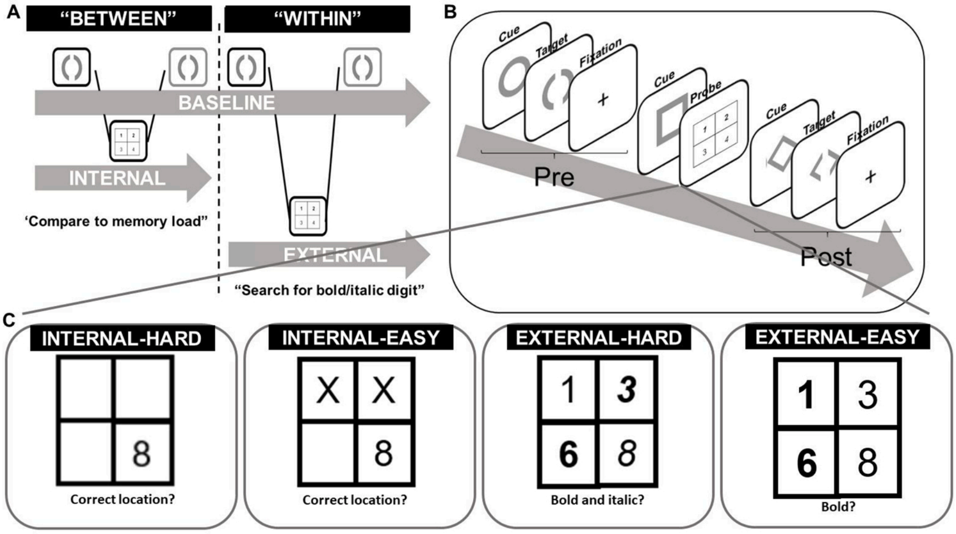

Fig. 1. Presentation of the paradigm. A. A perception-based Baseline Task was interrupted unpredictably on every few trials by a trial from a different memory- (Internal Task) or a perception-based task (External Task) in a block design. When returning to the Baseline Task, potential differences in behavioral and ERP measures could be explained in terms of the interrupting task being memory- or perception-based (i.e., between- or within-domain switches, respectively). **B.** Trial sequence producing Pre and Post trials. On Baseline trials, a cue was presented for 500-800 ms, followed by a target that was presented for 250 ms, and a fixation cross until response. The task consisted of discriminating whether the largest opening in the target was above or below. Trials for the External and Internal tasks started with the same (one of three) cue, after which a square with one to four digits was presented until response (see C). **C.** In the Internal-Hard Task, participants had to decide whether the presented digit was in the correct location when compared to the four-digit memory load they memorized at the beginning of the task. In the Internal-Easy Task, participants performed the same task, but the load consisted of only two digits. In the External-Hard Task, participants had to locate the digit presented in bold and italic and decide whether it was on the left or the right side of the display. In the External-Easy Task, this had to be done for the two bold digits.

2003; Vandierendonck et al., 2010). Second, we assessed whether this early gating effect was comparable for the within- and between-domain switches. We expected that reconfiguration demands would be higher for switches from an internal to an external task than for those between two external tasks. A more pronounced early gating effect for between-domain switches could result from a larger attentional inertia (Longman et al., 2014) in this condition, as different top-down control requirements are present compared to within-domain switches (see Verschooren, Schindler et al., 2019).

2. Methods

2.1. Participants

Thirty-one participants (77 % female) with a mean age of 24.48 (SD = 5.95) were recruited using Experimetrix, an online platform provided by Ghent University. After exclusion (see further), 23 participants remained. Our sample size was based on our earlier work with this paradigm (Verschooren, Schindler et al., 2019) and in line with earlier task-switching experiments where early visual ERP components were investigated (Lange et al., 2015). Participants gave written informed consent and received monetary compensation for participation. The study was reviewed and approved by the local ethics committee.

2.2. Stimuli and procedure

Participants were seated in a dimly lit, electrically shielded experimental room, with their head restrained by a chin rest, which was placed approximately 60 cm away from a 19” CRT screen with a 1280 × 1024 pixels resolution. The experiment was programmed in E-Prime (version 2.0). There were four main experimental conditions (Between-Hard (B_H), Between-Easy (B_E), Within-Hard (W_H), Within-Easy (W_E)) with one practice block (with feedback) and 10 test blocks for each. We used a block design with consecutive Order (e.g., $B_H - B_E - W_H - W_E - B_H - \ldots$), counterbalanced across participants. Each block contained 24 trials from the Baseline Task and three to five trials from the Internal or External Task, in which the digit-related task needed to be carried out (40 in total per condition). At the beginning of each block, participants had to commit to memory a number of digits, which were presented in a square with four compartments. This memory load was used for the Internal Task but was included for blocks with External Task as well, in order to control for potential effects caused by the presence of this memory load. The digits were pseudo-randomly selected, excluding repetitions and incrementing or decrementing sequences (e.g., 6−5 or 5–6). At the end of each block, an empty square appeared, and participants had to retrieve the digits from memory and insert them using the numerical pad of the keyboard. The Baseline Task consisted of a visual discrimination task (see Fig. 1B). In this task, participants had to judge whether the largest opening in a geometric figure (either a square, a diamond, or a circle) was on the top or in the bottom (see Janssens, De Loof, Pourtois, & Verguts, 2016). These figures were presented pseudo-randomly, with an equal number of squares, diamonds, and circles over the entire experiment. Each trial started with a cue (500−800 ms), which was identical to the target figure but contained no openings. Immediately after the cue, the target figure appeared for 250 ms, after which a fixation cross replaced it for 700 ms, or until response.

The trials from the Internal or External Tasks interrupted the Baseline Task with three to five trials. These interrupting trials started with the same cues as the baseline trials (for 500−800 ms) but were followed by a square with four compartments in which digits were presented. This square was presented for 2500 ms (corresponding to the average RT + 2 SDs extracted from Verschooren, Schindler et al., 2019) or until a response occurred (i.e., self-paced stimulus presentation). Even though the stimuli for the Internal and External Tasks were practically identical, i.e., a square with four compartments in which digits were presented, the respective instructions for each task prompted either a switch to a memory-retrieval task or a switch to a different visual discrimination task (see Fig. 1C). In the Internal-Hard and -Easy Task, participants were asked to decide whether the presented digit was in the correct location compared to their memorized locations. In the Hard version, participants needed to memorize four digits, whereas they only needed to memorize two in the Easy one (with the other two locations in the square marked with X’s). In the External Task, participants had to visually search for the digit(s) meeting the criteria (i.e., the two bold ones in the Easy and the one in bold and italic in the Hard version). After they had located this digit (these digits), they had to respond whether they were on the right or the left side of the square.

Finally, we used two different response mappings, counterbalanced across participants. For half of the participants, responses were made with keypresses “q” and “s” for the largest opening being up or down, respectively, in the Baseline Task. For the External and Internal Tasks, participants responded with numerical pad presses “7” and “4” for match/left or mismatch/right respectively (i.e., when the digit (mis) matches the memorized digit in that location or when the bold/italic figure is on the left/right side in the Internal and External Task, respectively). For the other half, “4” and “5” in Task A and “q” and “w” for match/left and mismatch/right, respectively.

2.3. EEG recording and analyses

EEG was recorded from 64 BioSemi active electrodes (www.biosemi.com). The recorded sampling rate was 512 Hz, online low-pass filtered at 100 Hz. The electrodes were fitted into an elastic cap following the BioSemi position system (i.e., electrode positions are radially equidistant from *Cz*; www.biosemi.com/headcap.htm). Two separate electrodes were used as ground electrodes, a Common Mode Sense active electrode (CMS) and a Driven Right Leg passive electrode (DLR), which form a feedback loop that enables measuring the average potential close to the reference in the A/D-box (www.biosemi.com/faq/cms&drl.htm). Four additional electrodes (EOG) measured horizontal and vertical eye-movement. These were placed at the outer canthi of the eyes and below and above the left eye.

EEG preprocessing was performed using BESA (www.besa.de). Offline, data were re-referenced to the average reference and then filtered with a forward 0.01 Hz high-pass (6 dB/oct). The use of causal high-pass filters is recommended since they do not smear effects back in time (see Acunzo, MacKenzie, & van Rossum, 2012; Rousselet, 2012). Further, a 30 Hz low-pass zero-phase filter (24 dB/oct) was used. Filtered data were segmented from 100 ms before stimulus onset until 600 ms after it for cues and targets, separately. The 100 ms before stimulus onset were used for baseline correction. Eye-movements were corrected using the automatic eye-artefact correction method implemented in BESA (Ille, Berg, & Scherg, 2002). Here, a predefined source model was applied to the data, combining three topographies accounting for EOG activities, consisting of horizontal and vertical eye-movement and blinks (HEOG, VEOG, blink) with 12 regional sources modeling the different brain regions. The adaptive artifact correction method then performed a principal component analysis (PCA) for segments where the correlation between data and artifact topography exceeded the HEOG (150 μV) or VEOG (250 μV) thresholds. All PCA components explaining more than the minimum variance were maintained. The recorded data were decomposed using all topographies into a linear combination of brain and artifact activities (Ille, Berg, & Scherg, 2002). The remaining artifacts were rejected based on an absolute threshold (<120 μV), signal gradient (<75 μV/∂T), and low signal (i.e., the *SD* of the gradient, >0.01 μV/∂T). Overall, 6.3 percent of all electrode measurements were interpolated using spline interpolation, with a total of nine electrodes within the sensor ROIs. For each condition, 40 trials in total were presented before preprocessing, but trials were only selected when probe and cue responses were correct. For cues, on average, 82 percent of all trials were kept, with no differences between Type, Difficulty, and Order, as well as no interaction of these factors (Fs < 1.30, ps $> .266$, see Table 1). For targets, 83 percent of all trials were kept. There were no differences between Type, Difficulty, and Order, or interactions between these factors (Fs < 2.07, ps $> .164$, see Table 1).

2.4. Statistical analyses

For the behavioural data, preprocessing and visualization were carried out in R Studio (version 1.1.383), and statistical analyses were performed in JASP (version 0.8.4). We removed four participants that did not follow the instructions (accuracy 1.5 times lower than the .25 quantile) and four others that had a low signal-to-noise ratio for the EEG recording (>50 % unusable trials). Hence, the final sample included 23 participants whom all had normal or corrected-to-normal vision. However, to be sure that these excluded participants did not bias the results, we also ran statistical analyses including these four subjects with poor performance and found that the main results obtained remained unchanged (results not reported here).

Error trials on the Baseline, External, and Internal Tasks were removed. In addition, we excluded the preceding and the following trial on the Baseline Task. Our analyses were focused on the RT data, as with this paradigm, they are more sensitive than the error rate (ER) data (Verschooren, Schindler et al., 2019). Outliers on RTs, defined for each condition within each subject as 1.5 times lower than the .25 quantile and 1.5 times larger than the .75 quantile, were removed as well. The main variables of interest were the RTs on the Baseline Task trials right before (Pre) and right after (Post) the Internal or the External Task, as this comparison allowed us to quantify the switch cost. We used a 2 × 2 × 2 Repeated-Measures Analysis of Variance (RM ANOVA) with Type (Between, Within), Order (Pre, Post), and Difficulty (Hard, Easy) as within-subject factors. As an estimate for the effect size, we reported omega squared (ω^2) values, which are less biased than eta squared (η^2) estimates (Albers & Lakens, 2018). Significant main or interaction effects were followed up by two-sided Paired Sample T-Tests, for which the standardized difference scores Cohen's d effect size is reported (d_z). When Mauchly's Test detected a violation of sphericity, degrees of freedom were corrected according to Greenhouse-Geisser. Finally, we reported a Bayesian model comparison, to compare the amount of evidence gathered in favor of H_0 (no difference for between- and within-domain cost) and H_1 (difference between them, see also Verschooren, Schindler et al., 2019).

For ERP data, we extracted the mean amplitude in specific time windows and for specific electrodes, which were defined using a collapsed localizer approach (e.g., see Luck & Gaspelin, 2017 and Fig. 2 for ERP component identification). First, time windows were identified based on changes in global field power (see Fig. 2). For the cue, a clear P1, but no N1, component was visible, whereas at the target level, the P1 was strongly attenuated, and mainly a subsequent N1 component was identified (see Fig. 2). Accordingly, for cue-related activations, we segmented time windows for the cue from 115 to 155 ms for the P1 component. Further, for the target, we identified the N1 peak from 140 to 180 ms (see Fig. 2**a, right panel**). Based on the collapsed topography (see Fig. 2), a parieto-occipital cluster of seven electrodes was selected for the P1 and N1 components (PO7, O1, Oz, O2, PO8, PO3, POz, PO4). The mean amplitudes extracted from these time windows and electrodes were submitted to an RM ANOVA. For the cue and target, separate 2 × 2 × 2 RM ANOVAs with Type (Between, Within), Order (Pre, Post), and Difficulty (Hard, Easy) were used to analyze the ERP data extracted in the specific time windows and electrode clusters identified based on the collapsed localizer approach (see here above). ω^2 was estimated to describe effect sizes (Albers & Lakens, 2018; Cohen, 1988). We used Greenhouse-Geisser correction when applicable.

Table 1
Number of kept trials per condition.

	Cues Mid *M (SD)*	Cues Pre *M (SD)*	Cues Post *M (SD)*	Target Pre *M (SD)*	Target Post *M (SD)*
Within Hard	32.96 (3.31)	33.65 (3.17)	33.09 (4.41)	33.91 (3.58)	32.39 (4.60)
Within Easy	32.87 (4.08)	33.00 (3.23)	32.52 (3.26)	34.09 (3.10)	33.04 (3.25)
Between Hard	33.13 (2.83)	32.35 (3.08)	32.61 (3.64)	32.91 (2.75)	32.61 (3.85)
Between Easy	32.43 (3.29)	32.61 (3.64)	33.04 (3.27)	33.22 (3.28)	33.26 (3.29)

Note: Standard deviation appears in parentheses behind means.

Additionally, we ran two control analyses with the Mid trials. A first control analysis focused on the Mid trials (see Supplementary Materials). We ran 2 × 2 × 2 RM ANOVAs with Type (Between, Within), Difficulty (Hard, Easy), and Order (Mid, Pre) and another one where we compared Mid to Post trials using the same statistical model. Second, Analyses of Covariance (ANCOVAs) with RTs on the Interruption Task as covariates were carried out to assess whether the ERP modulations found for the Baseline Task were related to systematic variations in RT speed across conditions or not. We entered the respective RT data per condition as a within-subject covariate as implemented in ezANOVA from the R-package "ez" (see Lawrence & Lawrence, 2016).

3. Results

3.1. Behavior

Accuracy was high for all conditions (i.e., around 90 % correct; see Fig. 3C), indicating that participants were able to perform the task adequately. The ANOVA for the RTs (see Fig. 3D) showed a significant main effect of Order ($F_{1,22} = 40.20$, $p < 0.001$, $\omega^2 = 0.11$) and an Order x Difficulty interaction ($F_{1,22} = 6.18$, $p = 0.021$, $\omega^2 = 0.002$). Follow-up Paired Sample T-Tests confirmed that participants were slower on the Post compared to the Pre trials ($ts_{22} > [4.28]$, $ps < 0.001$, $Cohen's\ ds_z > [0.893]$, 95 % $CIs > [0.400;1.371]$). For both the Hard and the Easy trials, there was a significant Pre-Post difference ($t_{22} = 5.72$, $p < 0.001$, $Cohen's\ d_z = 1.192$, 95 % $CI = [0.646; 1.723]$; $t_{22} = 6.31$, $p < 0.001$, $Cohen's\ d_z = 1.316$, 95 % $CI = [0.746; 1.871]$, respectively), but this difference was larger in the Hard compared to the Easy condition ($t_{22} = 2.412$, $p = 0.025$, $Cohen's\ d_z = 0.503$, 95 % $CI = [0.063; 0.933]$).

Crucially, a Bayesian model comparison for the RT data demonstrated that the best model for explaining the data was the one with Order only, 5.47 times better than the model including Type + Order (BF_{01} for the Type + Order model compared to the Order only model, see Table 2). This demonstrated a lack of difference between the two Types of switch cost and the two Difficulty levels.

Accuracy was high for the External and Internal Tasks (see Fig. 3B). As expected, a 2 × 2 RM ANOVA on the RTs with Type (Between, Within) and Difficulty (Hard, Easy) revealed a significant main effect of Difficulty ($F_{1,22} = 158.67$, $p < 0.001$, $\omega^2 = 0.379$), with faster RTs in the Easy compared to the Hard conditions (see Fig. 3A). However, we also found a significant main effect of Type ($F_{1,22} = 5.00$, $p = 0.036$, $\omega^2 = 0.053$). This main effect was qualified by a significant interaction with Difficulty ($F_{1,22} = 6.77$, $p = 0.016$, $\omega^2 = 0.023$). Follow-up Paired Sample T-Tests revealed significantly slower RTs for the Internal-Easy compared to the External-Easy Task ($t_{22} = 3.07$, $p = 0.006$, $Cohen's\ d_z = 0.641$, 95 % $CI = [0.185;1.085]$), a difference which was not present for the Internal-Hard and External-Hard Task ($t_{22} = 0.95$, $p = 0.350$, $Cohen's\ d_z = 0.199$, 95 % $CI = [-0.216;0.610]$). To account for the potential influence of these RT differences on the ERP amplitudes, we ran an ANCOVA with these RTs entered as covariates (see below).

3.2. ERP results: cue related activity

A clearcut P1 component was elicited in response to the cue (see Fig. 4). However, this P1 appeared to be substantially altered when

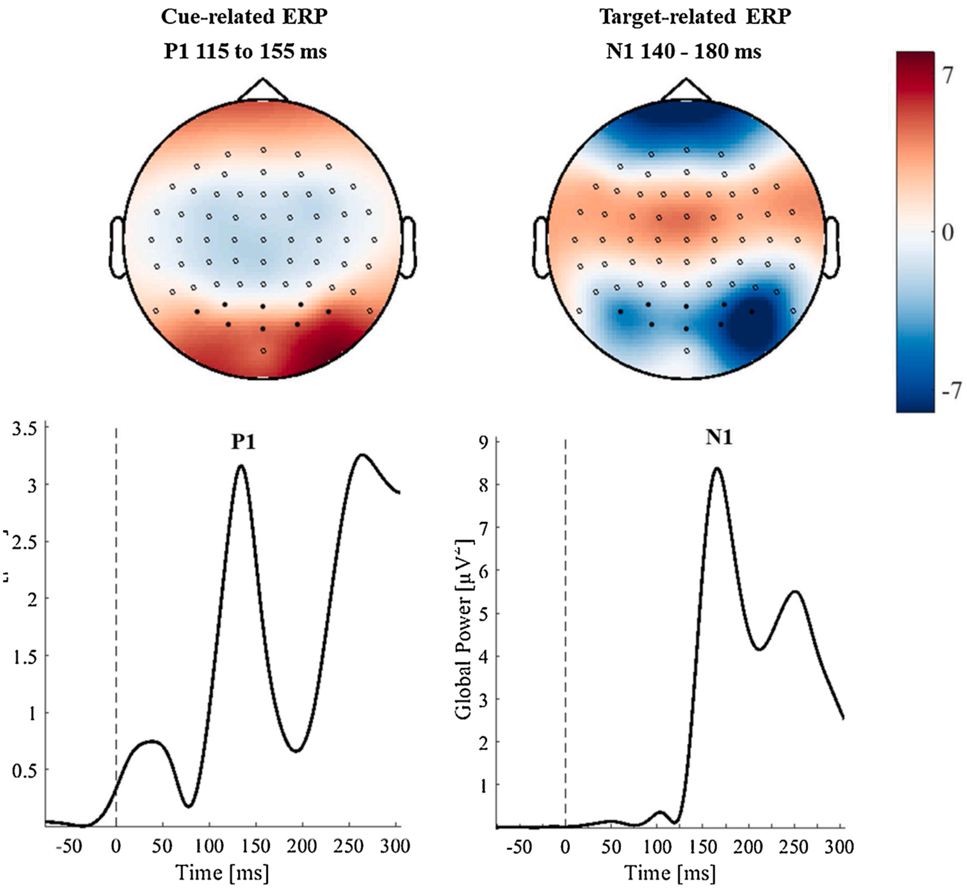

Fig. 2. Identification of cue-related (left panel) and target-related (right panel) ERP components based on a collapsed localizer approach (i.e., average amplitudes for all four conditions). Global field power changes following stimulus onset are shown for the cue and target separately. Selected electrodes for the occipito-parietal cluster for cue- and target-related ERPs are highlighted on the corresponding scalp topographies (voltage maps) for the selected time windows.

comparing Pre to Post trials, suggesting their sensitivity to switches of attention with the elected design. In addition, this change was different when comparing the between- and the within-domain condition, despite the use of identical stimuli (see Fig. 4). These observations were corroborated by the statistical analyses performed for each ERP component separately.

3.2.1. P1

The ANOVA (see Fig. 4) showed a significant main effect Order ($F_{1,22} = 53.65, p < 0.001, \omega^2 = 0.399$), as P1 amplitude was significantly smaller for Post compared to Pre trials ($t_{1,22} = 7.31$, $p < 0.001$). Crucially, this main effect was qualified by a significant interaction with Type ($F_{1,22} = 6.95$, $p = 0.015$, $\omega^2 = 0.007$), which demonstrated a stronger amplitude reduction of the P1 for Post trials following a between-domain compared to a within-domain switch ($t_{1,22} = 2.74$, $p = 0.018$). By comparison, P1 amplitude was similar for between-domain and within-domain switches at the Pre trial level ($t_{1,22} = 0.80$, $p = 0.426$). In addition, there was a main effect of Difficulty ($F_{1,22} = 4.90$, $p = 0.038$, $\omega^2 = 0.006$), with a decreased P1 in the hard compared to the easy blocks ($t_{1,22} = 2.21$, $p = 0.038$). This main effect was qualified by the interaction with Order ($F_{1,22} = 6.01$, $p = 0.023$, $\omega^2 = 0.005$). Here, differences between easy and hard conditions were found for Post trials, with larger P1 amplitudes following the hard tasks ($t_{1,22} = 3.25$, $p = 0.005$). Conversely, there were no differences at the Pre trial level ($t_{1,22} = 0.24$, $p = 0.814$). There was no significant main effect of Type ($F_{1,22} = 1.70, p = 0.206, \omega^2 = 0.001$). The interaction between Type and Difficulty, and the three-way interaction were non-significant ($F_s < 0.31$; $ps > 0.583$).

3.3. Target-related ERP activity

3.3.1. N1

The ANOVA showed that whereas effects of Difficulty ($F_{1,22} = 1.20, p = 0.285$, $\omega^2 < 0.001$), and Type were non-significant ($F_{1,22} = 0.21$, $p = 0.655$, $\omega^2 < 0.001$), there was an effect of Order ($F_{1,22} = 18.21$, $p < 0.001$, $\omega^2 = 0.011$). The Order effect was qualified by a significant interaction of Type and Order ($F_{1,22} = 5.12, p = 0.034, \omega^2 = 0.002$). This interaction demonstrated a amplitude increase of the target N1 for Post trials following a between-domain switch ($t_{1,22} = 4.71$, $p < 0.001$), while no Pre Post difference was found for a within-domain switch ($t_{1,22} = 1.76$, $p = 0.188$). All other interaction effects were not significant ($F_s < 0.87$; $ps > 0.360$) (Fig. 5).

3.4. Control analysis

3.4.1. P1

For the P1, the ANCOVA with RTs included as covariates showed that main effects of Difficulty ($F_{1,22} = 6.19$, $p = 0.021$) and Order were significant ($F_{1,22} = 16.22, p < 0.001$). Importantly, the interaction between Type and Order was also significant ($F_{1,22} = 5.96$, $p = 0.023$), demonstrating a stronger amplitude reduction of the P1 for Post trials following a between-domain compared to a within-domain switch when controlling for RT differences between conditions. Further, the Order by Difficulty interaction was not significant ($F_{1,22} = 0.10, p = 0.760$). All other interaction effects were non-significant ($F_s < 0.12$; $ps > 0.728$).

3.4.2. N1

For the N1, the ANCOVA showed that main effects of Order

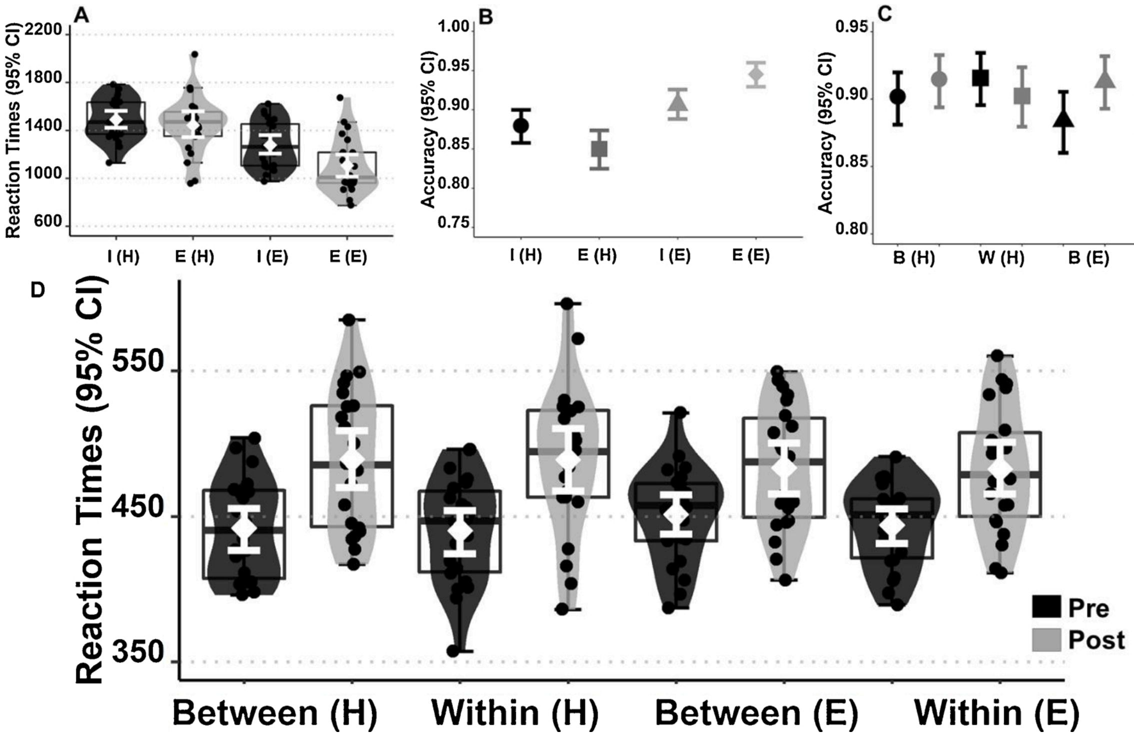

Fig. 3. Behavioral results. **A)** Mean RTs and 95 % confidence interval (CI) (in white) on the Internal-Hard, External-Hard, Internal-Easy, and External-Easy Task. Mean for each participant (black dots) and their distribution. **B)** Mean accuracy on these Tasks. **C)** Mean accuracy on the Baseline Task for Pre and Post Trials for each condition. **D)** Mean RTs and 95 % CI (in white) on Baseline Task comparing Pre and Post trials for each condition separately. Mean for each participant (black dots) and their distribution.

Table 2
Bayesian model comparison.

Models	P(M)	P(M| data)	BF $_M$	BF $_{01}$	error %
Order	0.053	0.637	31.598	1.000	
Type + Order	0.053	0.116	2.373	5.470	5.217
Order + Difficulty	0.053	0.097	1.945	6.534	1.828
Order + Difficulty + Order ∗ Difficulty	0.053	0.066	1.271	9.657	3.449
Type + Order + Type ∗ Order	0.053	0.035	0.648	18.322	2.959

Note. All models include subject. Only the five best models are shown here, ordered from best to worst fit to the data. Bayes Factors (BF_{01}) are compared to the best model.

($F_{1,22} = 18.21$, $p < 0.001$, $\omega^2 = 0.011$), Difficulty ($F_{1,22} = 1.20$, $p = 0.285$, $\omega^2 < 0.001$), and Type ($F_{1,22} = 0.21$, $p = 0.655$, $\omega^2 < 0.001$) were all three significant. However, the interaction between Type and Order was not significant ($F_{1,22} = 3.02$, $p = 0.096$). All other interaction effects were non-significant either ($F_s < 1.09$; $ps > 0.307$).

4. Discussion

Attention flexibility allows us to select the most relevant information in our interaction with the environment (Marois & Ivanoff, 2005). For this interaction to be adaptive, we are oftentimes required to switch between different types of information that do not necessarily share the same code, e.g., between internal representations and external stimuli. Attentional flexibility allows us to operate between these different domains, despite the potential lack of overlap between them (see Tas, Luck, & Hollingworth, 2016, but see Chun, 2011; Kiyonaga & Egner, 2013). Although switches between external and internal attention occur frequently, we still lack a clear understanding of the neurophysiological signature of this type of (between-domain) attentional flexibility. This study's main aim was to fill this gap by exploring the neurophysiological correlates of the processing cost incurred when participants switched attention from internal or external representations to an external task in a controlled experimental setting (Verschooren, Liefooghe et al., 2019; Verschooren, Schindler et al., 2019). The asset of the design was that the processing of the exact same visual cue could be examined at the ERP level in different conditions where we systematically manipulated across different blocks the nature of the attention switch to be performed (either within- or between-domain), as well as the overall level of task difficulty (being either easy or hard).

The behavioral results showed that a substantial switch cost was elicited for within- and between-domain switches, replicating previous findings (Verschooren, Liefooghe et al., 2019; Verschooren, Schindler et al., 2019). This cost is likely associated with a bottleneck emerging on trials where participants switched towards the Baseline Task, as competition emerges between redirecting attention from an internal to an external source and processing the current stimulus. Such a bottleneck has been demonstrated during task-switching, where the updating of the task set on switch trials interferes with task performance (Rubinstein, Meyer, & Evans, 2001; Vandierendonck et al., 2010). If such a bottleneck is present for between-domain switches, it should be reflected in reduced amplitudes of ERP components associated with early sensory processing when participants switch back to the Baseline Task (Post trial).

At the ERP level, we indeed found that the amplitude of the P1 component for the cue manifesting the return to the baseline external visual task after a switch (Post trial) was substantially reduced relative to the same visual cue provided before this switch (Pre trial). The P1 component has been mainly linked to efficient detection of visual stimuli through the recruitment of top-down attentional control (Desimone & Duncan, 1995; Hillyard & Anllo-Vento, 1998; Luck et al., 1990, 1994). The reduction in P1 amplitude observed here is consistent with the switch-cost found at the behavioral level. It confirms the presence of a processing bottleneck arising during attention switches, limiting

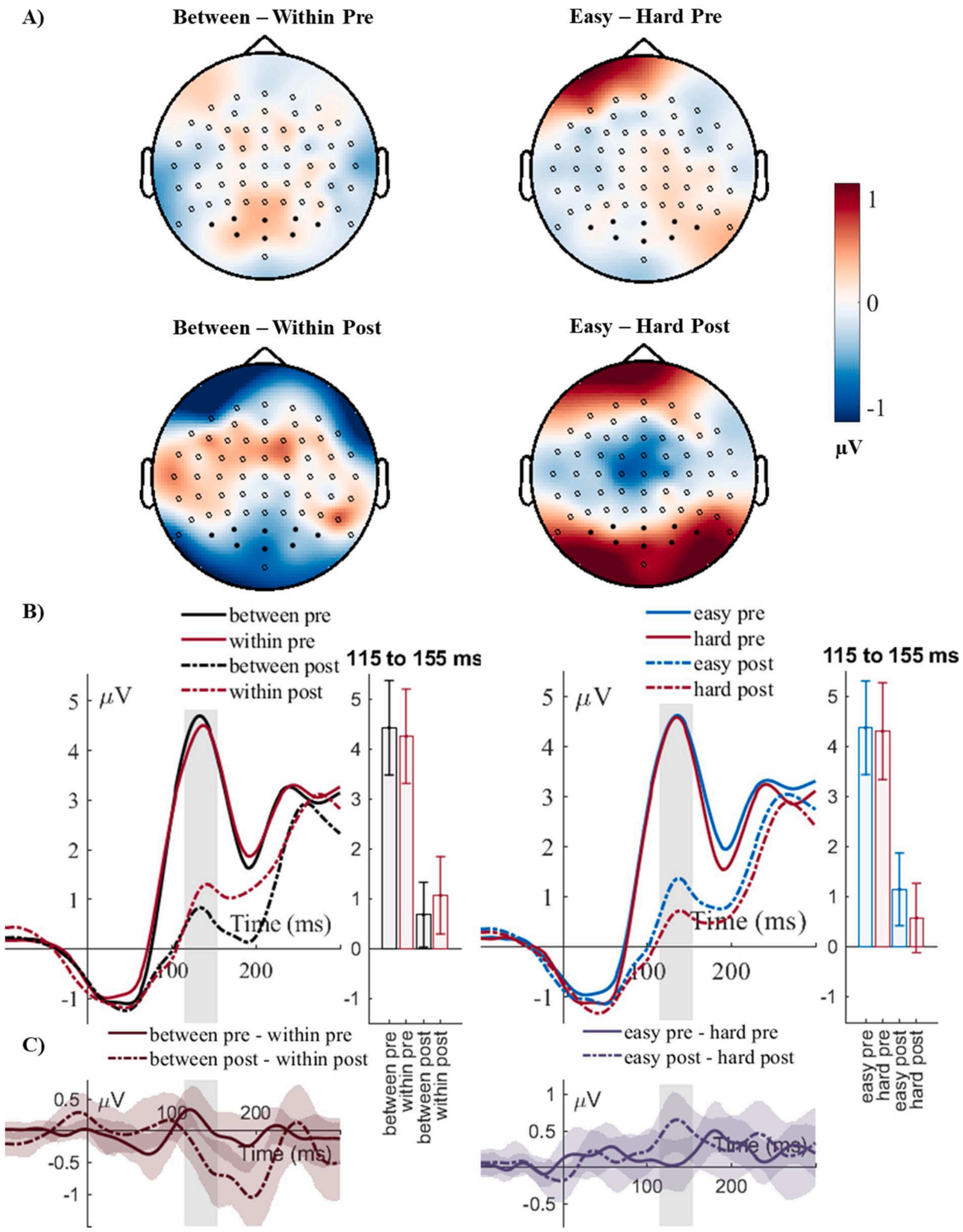

Fig. 4. Cue-related switch effects for the P1 component. A. Difference topographies showed a larger reduction of the P1 (Post trial level) for between- than within-domain switches. Difference topographies showed a larger reduction of the P1 (Post trial level) for hard than easy trials. **B.** Grand average ERP waveforms (collapsed for electrodes PO7, O1, Oz, O2, PO8, PO3, POz, PO4) for the four main experimental conditions, separately. The gray area indicates the time interval used to compute the amplitude of the P1. A significant Type x Order interaction effect was found for the P1. **C.** Difference waves are computed, together with the 95 % bootstrap confidence interval of intra-individual differences.

processing of the immediately following stimulus (see also Lange et al., 2015). That is, when regarding the P1 as the locus where top-down attentional control can be exerted during sensory processing (Klimesch, Sauseng, & Hanslmayr, 2007), our results show such early top-down control effect during switches of attention between two tasks sharing the same domain (external stimuli), and two tasks belonging to two different ones (external stimuli and internal representations). In both cases, the amplitude of the P1 component decreased and RTs increased. The supplementing source localization results (see Supplementary Materials) confirmed that the extrastriate visual cortex mostly contributed to the generation of this P1 at the scalp level, lending support to the assumption that these complex attention control processes did gate early sensory processing there (Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2001).

Critically, in spite of similar processing costs at the behavioral level, we found an asymmetry in this dynamic change in early sensory processing at the P1 level between the two switch types. More precisely, the P1 reduction was stronger for the between- than within-domain switch, which could not be explained easily by higher or different task demands (see control analyses). As we already briefly alluded to in the Introduction, the stronger reduction of the P1 for the between-domain switch could reflect enhanced attentional inertia. This explanationis motivated by the different control requirements likely needed for between- and within-domain switches. Burgess and colleagues (Burgess et al., 2007; Gilbert, Frith, & Burgess, 2005) have previously argued that the “supervisory attentional gateway” (SAG) arbitrates the continuous competition between external and internal attention. This top-down control mechanism, implemented within the rostral prefrontal cortex (rPFC), gates either external or internal information based on salience and/or current goals. Our new ERP findings are compatible with this theoretical account, and moreover, they extend it by showing how this gating mechanism can affect the dynamics of early attentional processes. More precisely, our results show partly dissociable effects of swichting from internal to external versus from external to external at an early stage following cue onset, mostly corresponding to bottom-up sensory processing in the extrastriate visual cortex. Put differently, our new ERP results add to the existing literature on attention flexibility and cognitive control (Burgess et al., 2007; Gilbert et al., 2005) by revealing, using a

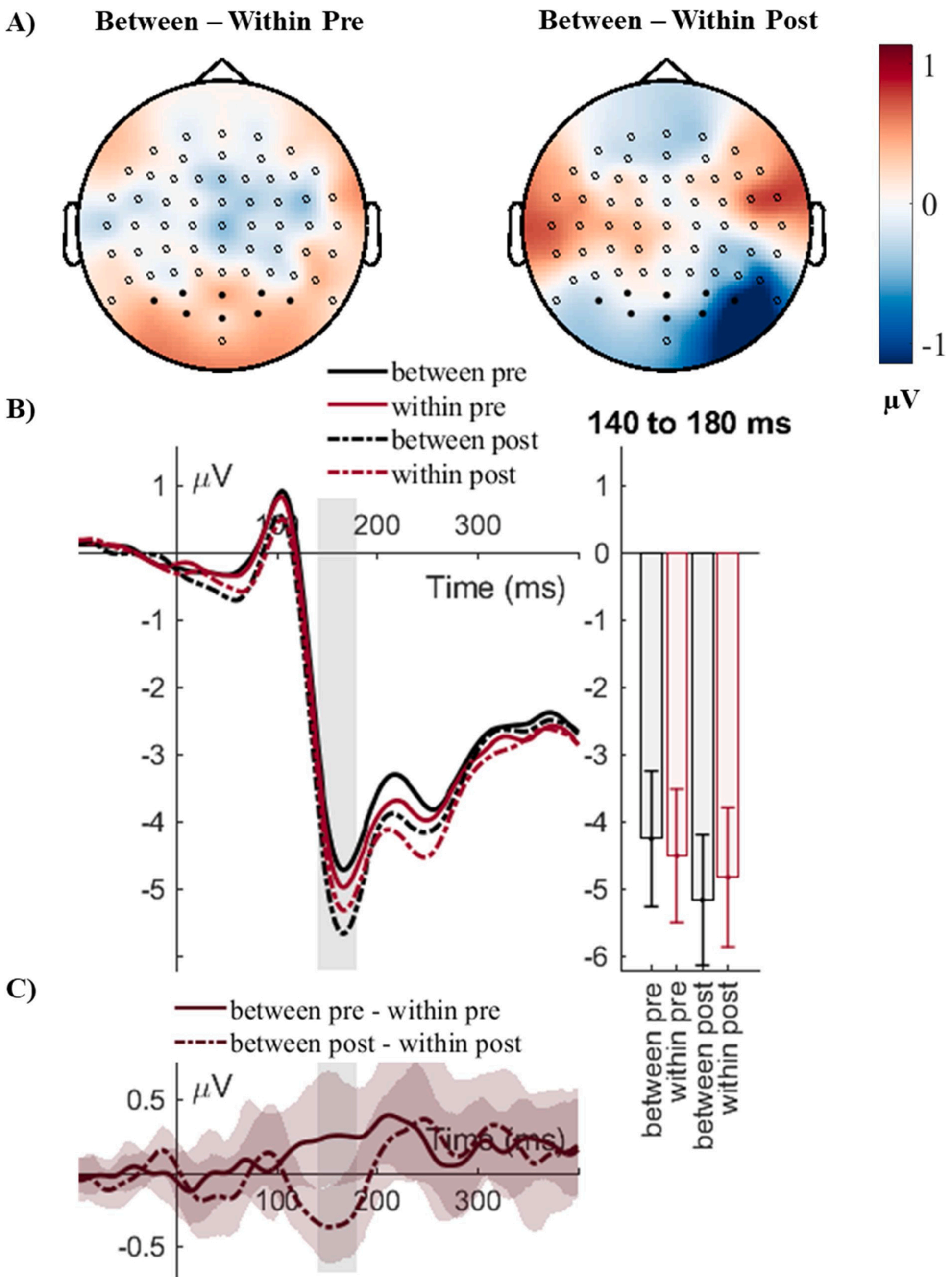

Fig. 5. Target-related switch effects for the N1 component. A. Difference topographies showed a larger reduction of the N1 (Post trial level) for between- than within-domain switches. **B.** Grand average ERP waveforms (collapsed for electrodes PO7, O1, Oz, O2, PO8, PO3, POz, PO4) for the four main experimental conditions, separately. The gray area indicates the time interval used to compute the amplitude of the N1. A significant Type x Order interaction effect was found for the N1. **C.** Difference waves are computed, together with the 95 % bootstrap confidence interval of intra-individual differences.

time resolved neurophysiological method, an early perceptual locus for the competition between external stimuli and internal representations. This competition is likely resolved by the involvement of a top-down attention control mechanism that gates early sensory processing in the extrastriate visual cortex (Pratt, Willoughby, & Swick, 2011).

However, an alternative interpretation is possible as well. According to the inhibition timing hypothesis (for a review, see Klimesch, 2012), the P1 ERP component is strongly related to alpha-band oscillations, and could reflect an inhibitory filter during access to knowledge. More specifically and translated to our new paradigm, during a switch of attention, it is likely that inhibition of the task-irrelevant network (i.e., interruption task) as well as activation of the task-relevant one (i.e., Baseline Task) are required, which could alter (i.e., reduce) the amplitude of the P1 time-locked to the cue in Post- compared to Pre trials. While the activation of the task-relevant networks is the same in both cases, the inhibition of the task-irrelevant network could be weaker for between- than within-domain switches, possibly due to the above discussed attentional inertia occurring during the transition between the internal task and the Baseline Task. Hence, instead of a mere sensory gain control effect (Hillyard et al., 1998), the present P1 ERP results could be interpreted as reflecting a complex change in the attentional state of the participant depending on the Type of switch encountered, and best captured by posterior alpha band oscillations that give rise to this early visual ERP component (Klimesch, 2012). We note however that this interpretation remains speculative at this point as appropriate time-frequency analyses (with a focus on alpha ERD/ERS) should be performed in order to corroborate it more directly at the empirical level.

Further, one might also argue that the reported difference at the P1 level actually reflect an imbalance in task difficulty, with the between-domain switches being more difficult than the within-domain ones. More difficult tasks usually result in a lower P1 amplitude, both when increasing the perceptual (de Fockert, Rees, Frith, & Lavie, 2001; Lavie, 2005; Lavie, Hirst, de Fockert, & Viding, 2004; Lavie & De Fockert, 2005; Schindler, Tirloni, Bruchmann, & Straube, 2021) or memory load

(Pratt et al., 2011). This amplitude reduction of the P1 with task difficulty has been explained by the additional demands imposed on memory when load is increased. Such an increase taxes the PFC, weakening top-down attention control of early sensory processing in the visual cortex (de Fockert et al., 2001; Krawczyk & D`Esposito, 2013; Pratt et al., 2011). RT differences, albeit remaining modest (see Fig. 3), between hard and easy conditions for the two different switch types could potentially drive this interaction effect. This alternative interpretation is highly unlikely, however. We used a factorial design where we included and modeled the effect created by task-difficulty per se, and while we validated that this influenced early sensory processing at the P1 level, it did so independently of the effect created by within or between-the domain switches. To test this assumption, we ran an ANCOVA including the RTs for the external or internal task as covariates. This control analysis showed that even though the main effect of Difficulty remained significant, the interaction of Difficulty with Order disappeared. Crucially, however, the interaction between Type and Order did remain significant (i.e., a larger reduction in P1 amplitudes following between- compared to within-domain switches). This finding suggests that the P1 effect following between-domain switches cannot be attributed to task difficulty only.

In addition to the cue-locked ERPs, we also investigated the target-locked ERPs to test whether some kind of compensation could take place, i.e. a strong reduction of the P1 at the cue level might be offset by a large N1 at the target level. In agreement with this view, we found that the N1 was larger for Post trials compared to Pre trials, suggesting that additional top-down control was probably exerted following the early reduction in sensory gain at the cue level (Hopfinger & Mangun, 1998; Mangun & Hillyard, 1991; Woodman, Vogel, & Luck, 2001). Interestingly, this main effect for Order (i.e. larger N1 on Post than Pre trials) interacted with Type, showing that this N1 increase was larger following a between-domain than within-domain switch. However, caution is needed in the interpretation of this N1 effect given that it became non-significant in an ANCOVA with RTs as coviariates. Accordingly, it appears parsimonious to conclude that whereas some compensation took place at the N1 level on Post trials, we could not ascertain however whether it was different for between- compared to within-domain switches. Since this compensation effect at the N1 level could reflect specific top-down attention control effects during switches of attention, additional research that seeks to address this question more directly would be desirable.

4.1. Constraints on generalizibility

Last, a limitation warrants comment. The task design of the current study does not test both directions of the between-domain switch, as we used a Baseline Task always requiring external attention. That is, we compared external-to-external (within-domain) to internal-to-external (between-domain) switches. Therefore, caution is required to generalize to both directions. That being said, the stronger attentional inertia effect observed here for the between-domain switches is likely bi-directional, as it should reflect a general property of attention control. Future ERP research is needed to assess whether the current results could generalize to conditions where attention has to switch between internal and external representations without the use of a predefined and fixed direction for these changes. In this context, it is notewothy that we have recently validated at the behavioral level a new experimental paradigm in which participants have to switch on a trial-by-trial basis between external stimuli and internal representations, yielding all possible combinations of switches and repetitions for these two domains (see Verschooren et al., 2020; Verschooren, Liefooghe et al., 2019). This paradigm appears suited to assess the generalizability of the ERP results found in this study.

5. Conclusion

In sum, we report novel neurophysiological evidence suggesting that task switching is associated with an early change following stimulus onset at the P1 level and likely has a perceptual locus. Crucially, despite similar processing costs at the behavioral level, we found that between and within-domain switches could be dissociated from each other at the ERP level; mostly at the level of the P1 component following the switch that was more strongly reduced for the former compared to the latter case. These dissociable attention flexibility effects were different from the gating effect created by task difficulty only.

Open practices statement

The raw behavioral data (https://osf.io/auw57/, experiment 4), raw EEG data and experimental script (https://osf.io/bku24/) can be found on OSF. The experiment was not preregistered.

Declaration of Competing Interest

The authors declared that they had no conflict of interest with respect to their authorship or the publication of this article.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.biopsycho.2021.108119.

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