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How time shapes cognitive control: a high-density EEG study of task-switching

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HIGHLIGHTS

- Repetition and switch trials elicit distinct neural signatures
- Switch trials engage positive-negative spatiotemporal neural signatures
- Switch-cost is reduced as a function of time-on-task effects
- Time-on-task effects are mediated by an increase of prefrontal activity through the task

Abstract

Task-switching is one of the most popular paradigms to investigate cognitive control. The main finding of interest is the switch cost: RTs in switch trials are longer than RTs in repetition trials. Despite the massive amount of research in these topics, little is known about the underlying temporal dynamics of the cortical regions involved in these phenomena.

Here we used high density EEG to unveil the spatiotemporal neural dynamics associated with both the switch cost and to its modulation through the task (time-on-task effect), as two markers of cognitive control reflecting effortful and procedural mechanisms, respectively. We found that, as a function of task practice, the switch cost decreased and both the switch-positivity and the switch-negativity event-related responses increased, although the latter showed a larger modulatory effect. At a source

level, this effect was revealed by a progressively higher activation of the left middle and superior frontal gyrus.

Keywords: Task-switch, hdEEG, time-on-task effects, source reconstruction

1. Introduction

Since its original introduction in the psychological literature (Jersild, 1927), the task-switching paradigm has constantly gained popularity as a tool for exploring cognitive control (see Monsell, 2003; Kiesel et al., 2010). Usually, task-switching paradigms include repetition and switch trials. In repetition trials, participants are instructed to perform the same task a variable number of times, while in switch trials they are required to perform a different task. Each trial typically involves a speeded response, recorded by means of reaction time (RT). The most remarkable finding is the “switch cost” (SC): RTs in switch trials are longer than those observed in repetition trials. It is widely held that SC reflects the so-called task-set reconfiguration, that is attributed to the time taken to abandon a particular stimulus–response mapping rule demanded for the execution of one task and load a different stimulus–response mapping rule demanded for the execution of a different task (Rogers & Monsell, 1995). Although task-switch is traditionally recognized as a standard paradigm to investigate top-down cognitive control processes (Diamond, 2013; Miller & Cohen, 2001), recent experimental evidence suggested that this task is strongly susceptible to low-level mechanisms as well. These include associative learning (i.e., stimulus-stimulus or stimulus-response contingency), conditioning by reward, congruency sequence effects and other bottom-up mechanisms that have been demonstrated to drive cognitive flexibility (see Braem et al., 2019 and Braem & Egner, 2018 for a deeper discussion on this topic). An additional source of bottom-up variability in adapting cognitive control over time regards the practice effect, a form of procedural learning that instantiates

progressively over time as a function of experience on task execution (Donovan & Radosevich, 1999).

Several studies demonstrated that practice may affect a wide variety of computational processes at perceptual, decisional and response-related stages. In the case of task-switch, the main effect of practice seems to modulate task-activation levels, enhancing the representation of task-relevant items while decreasing activation for the irrelevant ones (Steyvers et al., 2019). Although there is consensus that the training can significantly reduce - but not completely eliminate - the switch cost across consecutive experimental blocks (Berrhyll and Hughes, 2009; Kray and Eppinger, 2006; Sicard et al., 2020), the neural bases underlying the practice effect on task-switch are not clear yet. Nevertheless, uncovering the neural mechanisms underlying time on task effect is essential for linking implicit and procedural learning to functional neuroplasticity, paving the way for future applicative outcomes. In this regard, it is well known that cognitive control training is a potential approach to foster cognitive functioning in typically-developing children (Diamond et al., 2007) but also to compensate for cognitive impairments associated to neurodevelopmental disorders (Otterman et al., 2019) or pathological aging (Wang, Chang & Su., 2011). Hence, understanding the functional brain changes associated with practicing control tasks in healthy adults may disclose new multidisciplinary research lines.

Overall, neuroimaging studies have highlighted the involvement of both frontal and parietal regions (e.g., Brass & Cramon, 2004; Kim, Cilles, Johnson, & Gold, 2011; Philipp, Weidner, Koch, & Fink, 2013). The dorsolateral prefrontal cortex (DLPFC) is thought to be specifically engaged in the representation of task-set rules during task-switching (Crone, Wendelken, Donohue, & Bunge, 2006; Cutini et al., 2008). The left superior frontal gyrus (sFG) seems to be involved in interference detection and

suppression (Langenecker, Nielson & Rao, 2004; Jamadar, Hughes, Fulham, Michie, & Karayanidis, 2010). Furthermore, the parietal cortex seems to be involved to some degree in both task-set reconfiguration and rule representation (Crone, et al., 2006). Surprisingly, despite the massive evidence provided by neuroimaging studies about the identification of the neural substrates underlying task-switching, less is known about the temporal dynamics of the cortical regions involved in the cognitive operations required by such task. In a similar vein, little is known about how the task practice impacts on the spatiotemporal dynamics of the task-switch core functional brain regions. Nevertheless, one recent study provided intriguing results: Tayeb and Lavidor (2016) found that the application of transcranial direct current stimulation (tDCS) over the DLPFC enhances the task-switching by reducing SC across time. It is worth noting that this effect was stronger when stimulating the left than right DLPFC, suggesting that the time on task improvement due to practice may be supported by a greater recruitment of left prefrontal neural resources. However, since the tDCS has a relatively low temporal resolution, it is not possible to infer the functional locus of practice effect; thus, the question whether time-on-task effects operate by selectively enhancing perceptual, decisional or motor computational stages underlying cognitive flexibility, remains unanswered. This gap exists mainly because both brain stimulation (tDCS) and classical neuroimaging methods based on the investigation of hemodynamic activity are severely limited by the lack of fine-grained temporal resolution. In this regard, electroencephalography (EEG) has been traditionally employed to track the temporal dynamics of the cognitive processes underlying task-switch but there is little knowledge about the time course of the brain regions underlying the event related potential (ERP) modulations. At least two different scalp ERP components with specific timings have been found to be involved in task-switching paradigms: i) the switch positivity response

(see Karayanidis et al., 2010; Karayanidis & Jamadar, 2014; for reviews; Kieffaber & Hetrick, 2005; Miniussi et al., 2005; Nicholson, Karayanidis, Poboka, Heathcote, & Michie, 2005; Li, Wang, Zhao, & Fogelson, 2012; Kopp, Lange, Howe, & Wessel, 2014), which consists in an enhanced positive ERP response to switch trials. Due to its posterior scalp distribution, this ERP marker has been suggested to mainly reflect the involvement of parietal lobes, which may play a core role in task-set reconfiguration (Nicholson et al., 2005; Karayanidis et al., 2010); ii) the later switch-negativity, which exhibits fronto-central scalp distribution and has been suggested to be strictly related to interference detection and suppression, a process typically grounded in prefrontal cortex (Capizzi, Ambrosini, Arbula, Mazzonetto, & Vallesi, 2016). It is worth noting that these two ERP components have been consistently reported in either cued or uncued task-switching paradigms (Karayanidis et al., 2010; Capizzi et al., 2016; Perianez & Barcelo, 2009). This indicates that they may reflect two neural markers tracking the temporal involvement of distinct cortical regions within the executive fronto-parietal network regardless of the presence of anticipatory information allowing to prepare for task-set reconfiguration (Rushworth., Hadland, Paus, & Sipila, 2002; Astle, Jackson, & Swainson, 2006, 2008). Nevertheless, the vast majority of ERP studies does not provide precise information at the source level, because of the poor resolution of standard EEG. However, bridging the gap between spatial and temporal information might allow to provide a richer picture of the neurocomputational processes involved in task-switch, as shown by a recent EEG study (Capizzi et al., 2016). Stemming from these premises, in the present study we sought to exploit the potential offered by high-density EEG (hdEEG), Geodesic 128-channels, to investigate the electrophysiological and cortical correlates of task-switching. The spatial resolution of the estimated cortical activity is strictly dependent on the number of EEG sensors

(Lantz, Grave de Peralta, Spinelli, Seeck, & Michel, 2003; Michel & Murray, 2012). Furthermore, Geodesic electrodes locations allow an even scalp coverage, improving the spatial resolution of inferior cortical sources (Song et al., 2015). In light of this, to reliably investigate through the EEG the cortical activation related to the task-switch, we purposely chose to use an hdEEG system. Furthermore, one of the main purposes of the present study is the investigation of the cortical activity underlying the experience-dependent changes of the switch-cost across time (time-on-task effects). In this scenario, in order to trace the temporal dynamics of different brain areas, the EEG reconstructed source represents one of the best analysis tools. In the present work, we adapted a task-switching paradigm that has been already successfully employed by our lab (Cutini et al., 2008) in a functional near-infrared spectroscopy (fNIRS) experiment. The task-switching paradigm was specifically devised to equate working memory load across the task chosen in the present investigation, because switch trials (compared to repetitions, see Method) require a simple reversal of S-R mapping, that is, an alternation of the response set for the very same stimulus set. This type of paradigm is typically considered as a task-switching procedure (see Monsell, 2003, for a review); having the same working memory load through the whole task, regardless of the instruction at hand, is an advantage that has been exploited in several studies (e.g., Rushworth et al., 2002). As a first result, we expected to replicate previous findings (Capizzi et al., 2016) showing that switch trials elicit two temporally distinct ERP signatures (i.e., switch positivity and switch negativity).

As above mentioned, an additional relevant feature introduced in our study concerns the focus on the temporal evolution of the task-switching performance across the task (time-on-task effect) and the relation with its electrophysiological counterpart. In this way we aimed at addressing the role of procedural processes (i.e., the practice effect)

in adapting cognitive control over time (Braem et al., 2019). Time-on-task behavioural effects have been already investigated in task-switching (e.g., Bherer et al., 2008; Minear & Shah, 2008), showing that practice can reduce SC. In our experiment, we aimed at combining hdEEG methodology with the analysis of time-on-task in order to have an in-depth understanding of the neurocognitive mechanisms subserving task-switching and how these change as a function of task practice.

Crucially for this purpose, we adopted an uncued task-switching variant (Capizzi et al., 2016; Cutini et al., 2008; Crone et al., 2006), because of two specific reasons: first, we wanted to exacerbate SC. A cued version of task-switch typically elicits smaller SC (Karayanidis et al., 2010), mainly because they are specifically designed to underline the residual SC (i.e., the cost observed even when the participant is informed about the switch). Second, we wanted to obtain longer RTs. Typically, the behavioural effect in tasks involving cognitive control and interference increases with slower responses: for instance, the spatial numerical association of response codes (SNARC) effect, which is considered a classical interference paradigm, increases with longer RTs (e.g., Basso Moro, Dell'Acqua, & Cutini, 2017). Larger RTs and stronger SC allowed us to explore in more detail the temporal dynamics of the task, in particular the time-on-task effects, generally defined as a wide range of dynamic changes (both behavioural and neural) occurring throughout the execution of the task (Mento, 2013; Mento, Tarantino, Sarlo, & Bisiacchi, 2013; Mento & Valenza, 2016; Möckel, Beste, & Wascher, 2015).

Our study included several hypotheses. From a behavioural point of view, we hypothesized that the most noticeable time-on-task effect should consist in a decrease of SC. More specifically, we should observe a differential pattern of RTs in switch and repetition trials across time, supported by a differential electrophysiological modulatory engagement of the aforementioned regions. From a neurophysiological

perspective, we wanted to mirror previous neuroimaging evidence (e.g., Crone et al., 2006; Cutini et al., 2008; Brass & Cramon, 2004; Kim et al., 2011; Philipp et al., 2013), that highlighted both parietal and frontal regions as crucial for task-switching performance. The added value provided by the excellent temporal resolution of EEG enables to test further predictions, since i) parietal regions are involved in task-set reconfiguration whereas ii) sFG seems to be involved in interference detection and suppression, we hypothesized that parietal regions might be recruited prior to frontal regions.

In this regard, the high temporal resolution allows validating the prediction about the different dynamics of the fronto-parietal circuit involved in task-switching at both electrode and source level. We aimed at unveiling the sources of the two ERP components elicited by task-switching, and how and to what extent they are differentially modulated by time-on-task effects. This finding would allow to gain further knowledge about the spatiotemporal interplay between those core regions for task-switching.

2. Materials and Methods

2.1. Participants.

Twenty healthy, right-handed volunteers with normal or corrected-to-normal vision participated in the experiment. Three participants were discarded from analyses due to technical problems. The final sample included 17 participants (mean age: 25.2 ± 4 years; range: 21-39 years; 11 females). All volunteers provided informed written consent to the study protocol, which had been approved by the ethical committee of the School of Psychology of the University of Padua (Protocol No. 1351) and was conducted according to the principles expressed in the Declaration of Helsinki.

2.2. Stimuli and Task.

A modified version of the task-switching paradigm employed by Cutini et al., (2008) was used. Stimuli were presented on a 17-inch monitor at a resolution of $1,280 \times 1,024$ pixels. Participants were seated comfortably in a chair at a viewing distance of ~60 cm from the monitor. During the experiment, each participant was instructed to rest the index and middle fingers of the right hand on the 'M' and 'N' keys of the computer keyboard throughout the entire experiment. As shown in Fig.1, each trial began with the central presentation of a '+' or '-' on a black screen. These stimuli could be displayed in red or green color. The color of the stimuli served as a task-relevant information indicating which particular stimulus-response mapping rule participants had to adopt to provide a correct response to a given stimulus. Upon the presentation of a green stimulus, participants had to press the 'N' in response to a '+', or the 'M' key in response to a '-.' Upon the presentation of a red stimulus, participants had to use the reversed mapping, pressing 'M' in response to a '+', and 'N' in response to a '-'. Each stimulus was presented for a maximum of 1.5 s, and replaced with a blank screen upon detection of a response. The Inter Stimulus Interval (ISI) was varied randomly between 1,000 and 3,000 ms. After a 5 min of practice, participants performed a sequence of 480 experimental trials. Stimulus type (+ or -) and color (red or green) were varied orthogonally, in order to include in the sequence an equal number of repetition trials (i.e., 240 trials in which the responses were repeated in accordance with a given stimulus-response mapping rule) and switch trials (240 trials in which a given stimulus-response mapping rule had to be reversed). This paradigm provides several methodological advantages: the frequency with which participants had to execute

switch and repetition trials was the same, thereby ruling out odd-ball effects (e.g., Dove, Pollmann, Schubert, Wiggins, & Von Cramon, 2000); trials with red or green stimuli could have been both repetition or switch trials, depending on the color of the stimuli shown in the previous trial, thus avoiding color as a possible confound; task order was totally unpredictable, so as to reduce to a minimum the possibility to anticipate and/or prepare for a task-switch. Finally, as already mentioned in the introduction, the working memory load was the same for both repetition and switch trials. The order of repetition trials and switch trials was randomized, and was different for each subject.

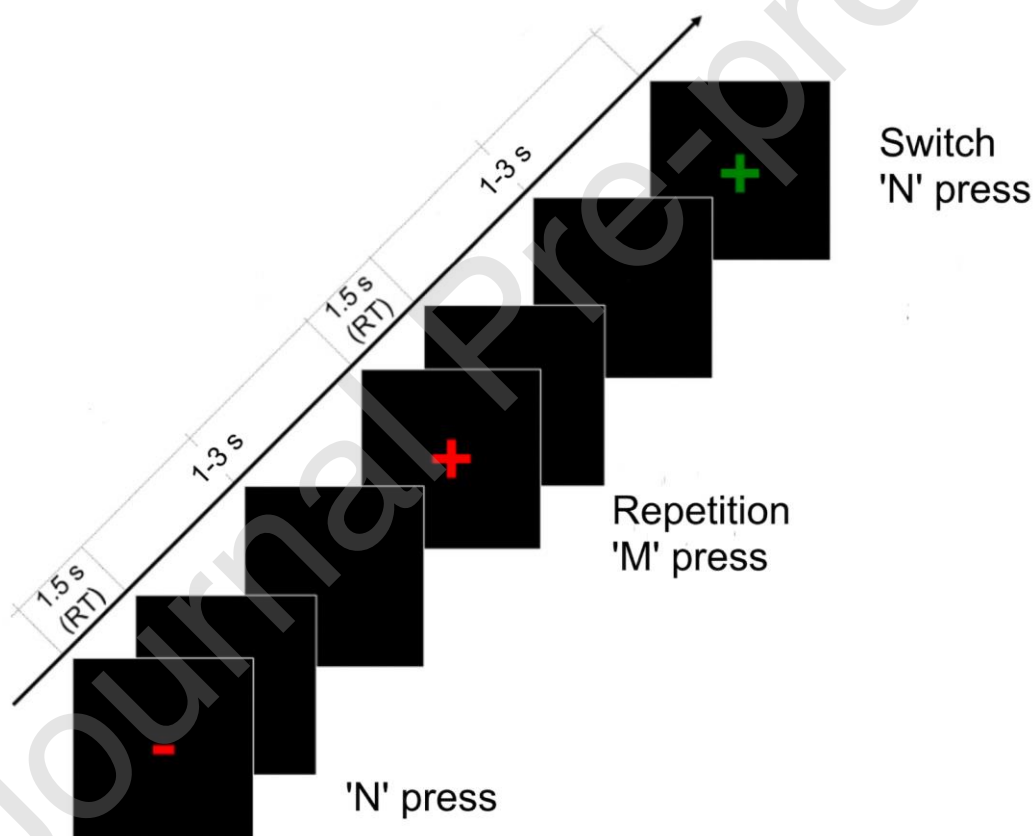


Figure 1. The picture shows the experimental paradigm. A schematic illustration of the sequence of events in the present paradigm.

2.3. EEG Recordings

During the entire task, the EEG was continuously recorded and amplified using a geodesic EEG system (EGI GES-300), through a pre-cabled high-density 128-channel HydroCel Geodesic Sensor Net (HCGSN-128) and referenced to the vertex. The sampling rate was 500 Hz. The impedance was maintained below 30 K Ω for each sensor. To reduce the presence of EOG artifacts, all participants were instructed to limit both eye blinks and eye movements as much as possible.

2.4. Data Analysis

2.4.1. Behavioural Analysis.

Reaction times (RTs) to repetition/switch stimuli were recorded. RTs below 200 ms or above 3000 ms were discarded. SC was classically assessed by comparing RTs and accuracy for repetition and switch trials through t-tests. Furthermore, the presence of time-on-task effects, - defined as the dynamic changes occurring during the task (Mento et al., 2013, Mento, 2013; Mento & Valenza, 2016) - was investigated in both behavioural and ERP data. For each participant, trials were divided according to trial type (i.e., switch and repetition) and then sorted separately into three temporal clusters, defined as early, middle and late bin, each one with an equal number of trials. A total of 145 ± 15 correct and artefact-free trials were included in each bin. Temporal order was the sorting criterion: the early bin included the trials performed in the first phase of the experiment, the middle bin included the trials performed in the intermediate part of the experiment, while the late bin included the trials performed in the last part of the experiment. The presence of significant bin-by-bin behavioural effects on RTs for both

repetition and switch trials was assessed by means of a 2×3 repeated-measure ANOVA, with trial type (switch *vs.* repetition) and bin (early *vs.* middle *vs.* late) as the main factors. The Bonferroni post hoc test was used to correct for multiple comparisons. Effect size was calculated by using the partial eta square (η_p^2).

2.4.2. ERP Analysis.

All EEG recordings were processed offline using the MATLAB toolbox EEGLAB (Delorme & Makeig, 2004), separately for each participant. The data were first band-pass filtered between 0.1 and 30 Hz using a Hamming windowed sinc finite impulse response filter (filter order = 8250) and segmented into epochs starting 200 ms before stimulus onset and ending 1,000 ms after it. Epochs related to trials containing premature or incorrect responses were rejected. Epochs were then visually inspected to interpolate bad channels and remove rare artefacts. Artefact-reduced data were then subjected to Independent Component Analysis (ICA) (Stone, 2002) to isolate highly characteristic artefacts (e.g., eye blinks and eye/muscle movements). A mean of 5.44 ± 2.44 artifact components per subject were discarded, and the remaining components were projected back to the electrode space to obtain cleaner EEG epochs. The remaining epochs containing excessive noise or drift ($\pm 100 \mu\text{V}$ at any electrode) were further rejected. Data were then re-referenced to the average of all electrodes and the signal was aligned to the baseline by subtracting the mean signal amplitude in the pre-stimulus interval (-200 to 0 ms). Subject average and grand average ERPs were generated for each electrode site and experimental condition. For the seventeen participants, a mean of 110 ± 13 epochs per condition were accepted. There were no significant differences ($F(1,16) = 0.92$; $p > .9$) between the percentage of epochs rejected in all conditions.

To detect reliable between-condition ERP differences, we applied a whole-scalp analysis approach at all electrode sites using a paired two-tails t-test ($\alpha = .05$) permutation approach to control the family-wise error rate (Groppe, Urbach, & Kutas, 2011). A similar technique was employed in previous ERP studies (Duma et al., 2019; Mento, Astle, Scerif, 2018; Mento, 2017; Strauss et al., 2015; Capizzi et al, 2016). To control for the Type I error we performed 2,000 Monte-Carlo permutations and applied cluster-based correction over all 128 electrode locations using the Fieldtrip functions (Maris & Oostenveld, 2007; Oostenveld, Fries, Maris, & Schoffelen, 2011), accessible via Brainstorm (Tadel et al., 2011). The effect size was estimated by computing Cohen's d of the effect averaged over all the electrodes included in the significant clusters for each comparison (Buiatti et al., 2019; Duma, Granzio & Mento, 2020). We investigated time-on-task effects for ERP data, similarly to the behavioural analysis, by dividing trials according to the trial type (i.e., switch and repetition) and then sorted separately into three temporal clusters, obtaining in this way three temporal bins, namely, early, middle and late. In order to test for the presence of time-on-task effects, statistics were further performed by considering pair-wise comparisons amongst the three temporal bins. We are aware of the possible methodological limitations related to our sample size however we want to highlight two main points. First, the present study adopts the same experimental paradigm of a previous fNIRS study (Cutini et al., 2008) from our lab, in which we observed an effect size of $d = .94$ in relation to the modulation of the neural activity in the left superior frontal gyrus. This suggests that this paradigm is likely to elicit a massive recruitment of neural resources. As a consequence, it is reasonable to argue that our sample size could be sufficient to isolate an experimental effect of this kind of magnitude. Second, to overcome potential issues deriving from a potentially low sample size we purposely use a cluster-based permutation analysis,

which is one of the most reliable and conservative statistical analysis among mass-univariate approaches for investigating ERP effects, as suggested by Luck & Gaspelin (2017). Therefore, in light of these considerations, we consider the following results as fairly reliable.

2.4.3. ERP-Behaviour Correlational Analysis.

In line with previous studies (Capizzi et al., 2016), in order to investigate the association between behavioural and electrophysiological correlates of task-switching a correlational analysis was conducted between the mean SC in RTs (SC-RT) and the corresponding ERP-SC effects. To this aim, we used the ERP mean amplitudes calculated for the time points and across the channels that resulted significantly modulated by trial type in the cluster-based permutative analysis. Specifically, from the permutation analysis we obtained the significant clusters indicating in which electrodes and in which time points it was possible to find a statistically significant ERP effect. We then extracted the ERP mean amplitude by averaging the ERP activity in the significant time points and electrodes separately for each statistical effect (switch positivity and switch negativity). Finally, we correlated this ERP mean amplitude with the mean switch cost in the reaction time (SC-RT). We performed robust correlation analysis (Pernet, Wilcox & Rousselet, 2012) using the WRS2 package in R (Mair, Wilcox, & Mair, 2020).

2.4.5. Brain Source Reconstruction

Baseline-corrected epochs were imported in Brainstorm (Tadel et al., 2011) to model their cortical generators. We used the ICBM152 anatomical template to approximate the individual anatomy of each participant (Evans, Janke, Collins, & Baillet, 2012). Co-registration of EEG electrodes position was performed via Brainstorm, by projecting

the digitized EEG sensor positions GSN Hydrocel 128 E1 available in Brainstorm on the head surface. We then derived the EEG forward model according to the 3-spheres BERG method (Berg & Scherg, 1994). The source space was constrained to the cortex and modeled as a grid of 15,002 orthogonal current dipole triplets. As a source model we used the weighted minimum norm estimation (wMNE) solution implemented as a routine of the Brainstorm platform, with Brainstorm's default parameter settings. The empirical noise covariance model was obtained from the average of ERP baseline signals. The sources were projected to the standard anatomical template (MNI) and their activity was transformed in Z scores relative to the baseline. Finally, a spatial smooth (FWHM of 3 mm), was applied to each source. The cortical activations were located according to the anatomical Desikan-Killany atlas (Desikan et al., 2006) adapted for cortical space solution.

3. Results

3.1. Behavioural Results

Switch trials were slower than repetitions, $t(16) = 5.52, p < .001$. Accuracy scores followed the same pattern (repetition: .94, switch: .91; $t(16) = 4.77; p < .001$). A summary of the behavioural results is shown in Fig. 2. Analysis on time-on-task effects revealed a main effect of trial type ($F(1,16) = 30.11; p < .001; \eta_p^2 = .65$) and bin ($F(1,16) = 10.09; p < .001; \eta_p^2 = .39$) and a significant interaction between the two factors ($F(2,32) = 8.53, p < .001; \eta_p^2 = .35$). In order to enucleate such interaction, we calculated the SC for each bin, defined as the difference between RTs in switch and repetition trials. These measures were compared with a series of two-tails paired t-tests: the results have shown that the SC for the early bin was significantly larger than the

one observed for both the middle ($t(16) = 2.81$; $p = .006$) and late bins ($t(16) = 3.3$; $p = .002$), while the SC between middle and late bin did not reach significance.

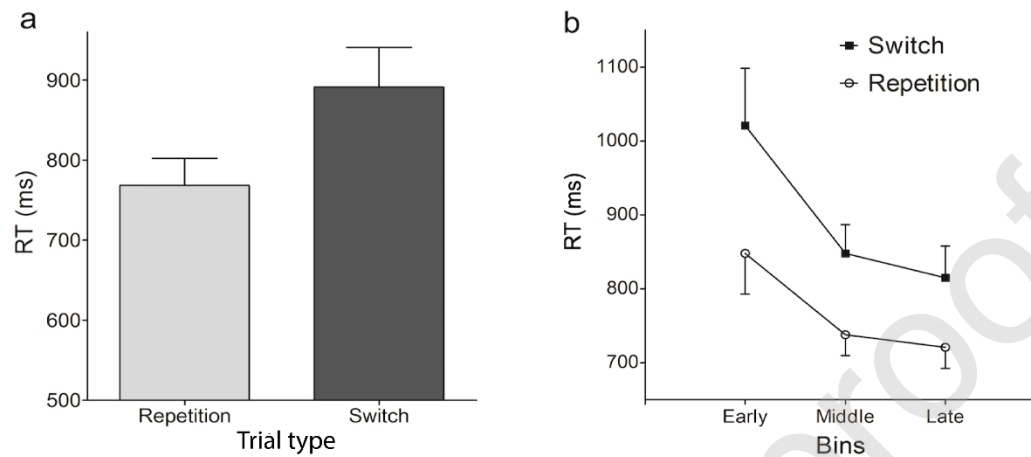


Figure 2. The picture shows the behavioural data. a) Mean RTs for repetition (light gray) and switch (dark gray) trials. b) Time-on-task effects for repetition (circles) and switch (squares) trials.

3.2. ERP Results

3.2.1. Task-Switching effect (Switch vs. Repetition)

The cluster-based permutation analysis revealed two spatiotemporally windows, defined as T1 and T2, which revealed significant amplitude differences (Fig. 3).

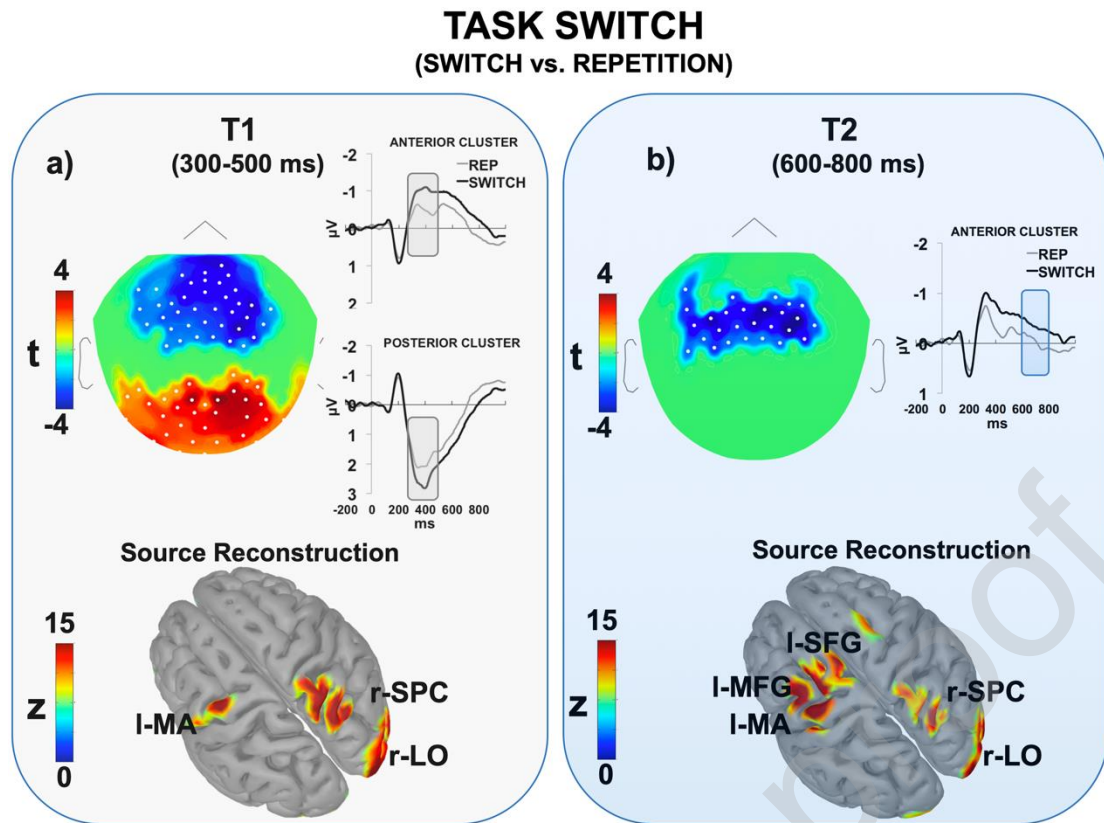


Figure 3. Task-Switching hdERP effects. The upper parts of the picture display the cluster-based results. The electrodes in which the difference in the activity between switch and repetition conditions is statistically significant ($p < .05$) are displayed in reddish or bluish colours, depending on the direction (positive or negative) of the t-test. The waveforms are derived by averaging the activity of the electrodes included in each cluster. The rectangles positioned over the waveforms represent the time windows in which the ERP mean amplitude of switch vs. repetition has been contrasted. The panel a) corresponds to the switch positivity while the panel b) to the switch negativity. The lower panels display the differential cortical source map (i.e., switch minus repetition), averaged between 300-500 ms and 600-800 ms for the T1 and T2 respectively. Data were adjusted using a threshold of 50% of the maximum amplitude and a size of at least 10 vertices.

3.2.2. T1

The first interval, defined as T1, extended between 300 and 500 ms. The ERP activity in this interval consisted of a clear-cut component spatially expressed as a dipolar scalp activity. The analyses identified two clusters of spatiotemporally adjacent electrodes whose signal amplitude exceeded the critical t-score threshold of ± 2.12 (Family-wise error corrected $p = .002$; Cohen's $d = .21$; Fig. 3a). The negative cluster was anteriorly localized over the scalp. By contrast, the positive cluster spread over the posterior portion of the scalp. The morphology, latency and distribution of this component was fully compatible with the switch positivity modulatory effect reported for switch as compared to repetition trials with similar tasks (Capizzi et al., 2016).

The brain source reconstruction of the T1 averaged ERP activity revealed a distributed cortical activation including both posterior and anterior regions. Posterior regions comprised the right lateral occipital (r-LO) and the right superior parietal (r-SPC) cortex. Anterior regions encompassed the left precentral gyrus and in particular the left motor area (l-MA).

3.2.3. T2

The second interval, defined as T2, extended between 600 and 800 ms. The analysis identified a negative cluster localized over fronto-central electrodes ($p = .023$; Cohen's $d = .19$). As compared to T1, the morphology of the T2 ERP activity did not show a sharpen component but rather a sustained negative activity which was larger for switch as compared to repetition trials. According to previous literature (Capizzi et al., 2016) we defined this activity as switch negativity. The brain source reconstruction of the T2 ERP modulatory effect revealed a complex pattern which included the same areas identified in T1 (i.e., r-LO, r-SPC and l-MA) as well as prefrontal areas including the left superior (l-SFG) and middle (l-MFG) frontal gyrus.

Taken together, ERP and source reconstruction findings suggest that the effects identified in T1 and T2 mark distinct neurocognitive mechanisms underlying task-switching. The time course of the reconstructed cortical activity further corroborated this account by showing spatiotemporally dissociable patterns for anterior and posterior regions (Fig. 4). In particular, the r-LO and the r-SPC regions displayed the largest modulatory effect in the T1 range while the left preCentral, the l-MFG and the l-SFG were maximally modulated by condition in correspondence of T2.

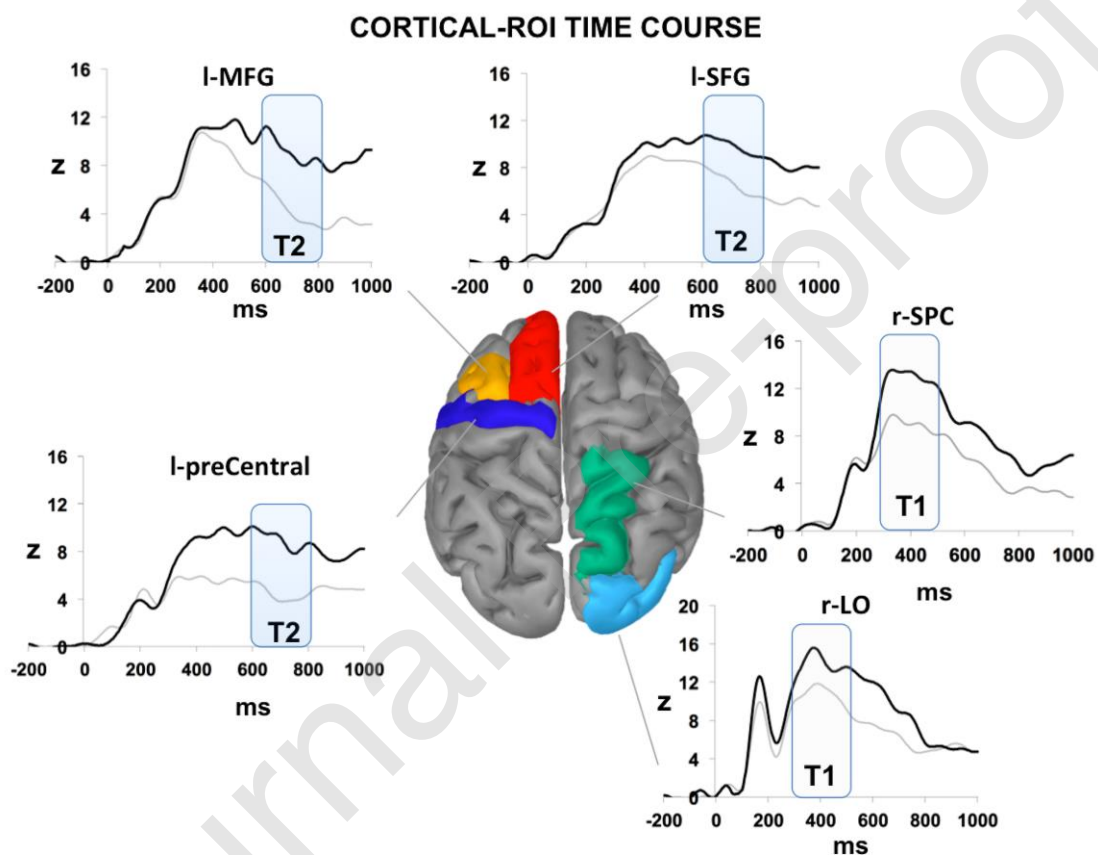


Figure 4. Temporal dynamics of task-switching cortical areas. The picture shows the mean activity time course (in Z scores) of the cortical areas involved in task-switching (orange: l-MFG; red: l-SFG; blue: l-preCentral; green: r-SPC; turquoise: r-LO). The rectangles positioned over the time courses demarcate the T1 and T2 windows, corresponding to the switch positivity and switch negativity, respectively.

3.2.4. Time-on-task ERP Effects

The Fig. 5 displays the waveform morphology and the relative scalp maps of the ERP activity averaged by condition and temporal bin separately for T1 and T2.

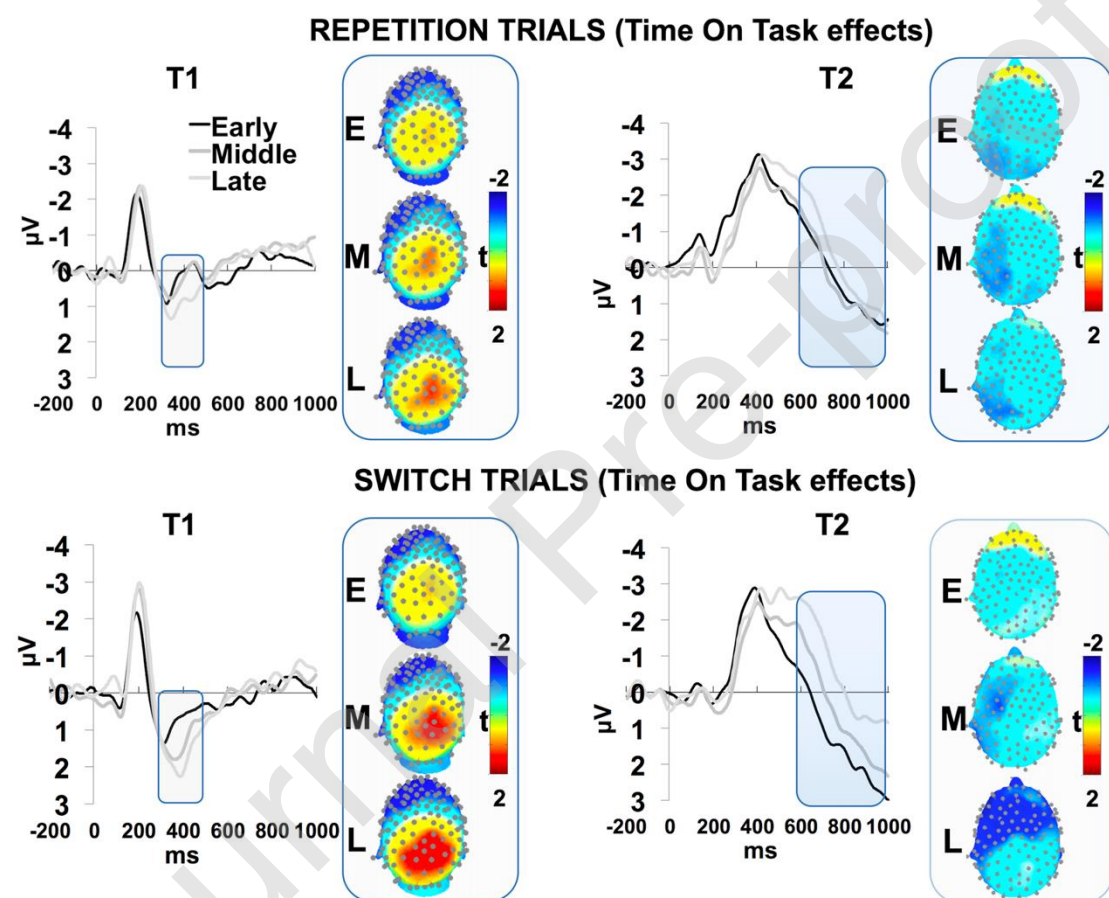


Figure 5. Time-on-task hdERP effects. Top: time-on-task ERP effects for T1 (left panel) and T2 (right panel) for repetition trials. Bottom: time-on-task ERP effects for T1 (left panel) and T2 (right panel) for switch trials. All the waveforms are derived by averaging the post-stimulus ERP activity for the early (E, black), middle (M, dark grey) and late (L, light gray) temporal bin across the electrodes significantly modulated by task-switching (identified by the cluster-based analysis). The rectangles positioned over

the time courses demarcate the T1 and T2 windows, corresponding to the switch positivity and switch negativity, respectively. For each waveform, the corresponding spline scalp map is shown.

As it can be seen, the visual inspection of the grand average ERP activity showed different time-on-task effects for T1 and T2. Specifically, time-on-task effects in repetition and switch trials were comparable over T1 window. By contrast, the modulatory time-on-task effect was larger in switch as compared to repetition trials. This differential time-on-task neural modulation was further expressed in the spatial domain, as illustrated in the three-dimensional scalp maps.

To statistically support these results, we performed two distinct repeated measure ANOVA analyses either on T1 and T2 mean ERP amplitude, including condition (Switch *vs.* Repetition) and temporal bin (Early *vs.* Middle *vs.* Late) as within-subject factors. These analyses revealed a main effect of condition ($F(1,16) = 8.09$; $p < .02$; $\eta_p^2 = .33$) and temporal bin ($F(1,16)=15.01$; $p < .001$; $\eta_p^2 = .48$) in the T1 window, confirming that the switch positivity became gradually larger as the task went on. As a noteworthy consideration, we did not find an interaction between condition and temporal bin, suggesting that the ERPs were equally shaped over time in repetition and switch trials.

Concerning T2, the ANOVA revealed a main effect of temporal bin ($F(2,32) = 7.93$; $p < .01$; $\eta_p^2 = .33$). As a remarkable finding, statistics also yielded a significant interaction between condition and temporal bin ($F(1,16) = 7.86$; $p < .01$; $\eta_p^2 = .32$) effect. These findings are shown in Fig. 6 (top panels).

3.2.5. Time on task source effects

To explore whether the differential time-on-task ERP pattern for T1 and T2 was supported by specific neural signatures, we extracted the mean activity for the cortical regions that showed consistent activity within these two windows. The results are plotted in the bottom part of Fig. 6.

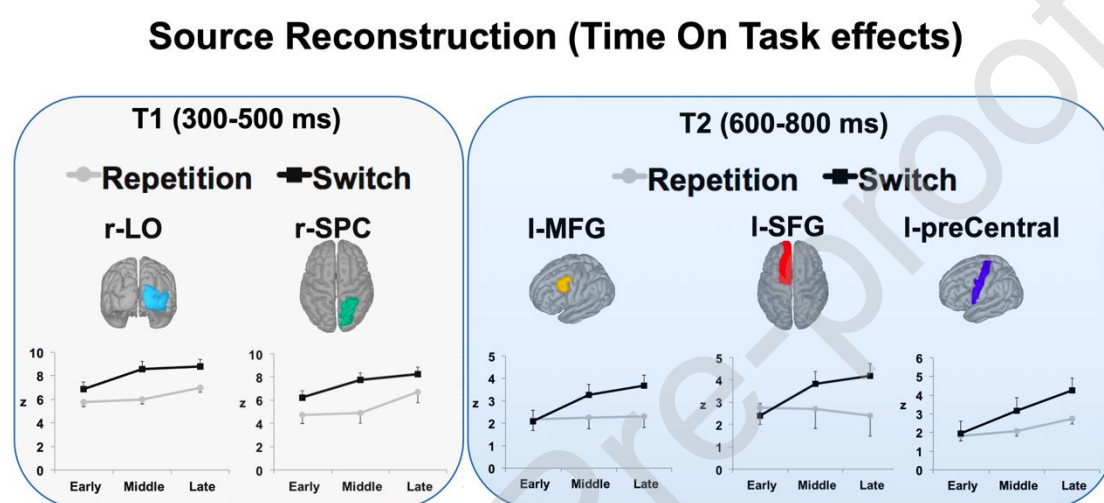


Figure 6. Time-on-task effects on the activity of cortical sources. The picture shows the time-on-task changes in the mean neural activity in relation to T1 (left panel) and T2 (right panel) of the cortical areas underpinning task-switching (orange: I-MFG; red: I-SFG; blue: I-preCentral; green: r-SPC; turquoise: r-LO). For each region, the mean activity is shown for both repetition (grey lines) and switch (black lines) trials, in early, middle and late trials. The bars represent the mean standard error.

As it can be seen, the posterior regions (r-LO and r-SPC) show a comparable boost of neural activity over the task in T1. Conversely, in T2 the anterior regions (I-preCentral, I-MFG and I-SFG) showed a different pattern, characterized by the progressive emergence of time-on-task modulatory effects. More specifically, no condition-related

differences were observable in the early temporal bin. Conversely, in the middle temporal bin these areas were more activated for switch than repetition trials and this effect became even larger in the late temporal bin.

3.2.6. ERP-Behaviour Correlation Analysis

The correlational analyses between behaviour and ERPs revealed that the mean participants' SC was predicted by the amplitude of either the switch positivity ($r = -.50$; $p = .041$) or the switch negativity ($r = .63$; $p = .007$) components (Fig. 7).

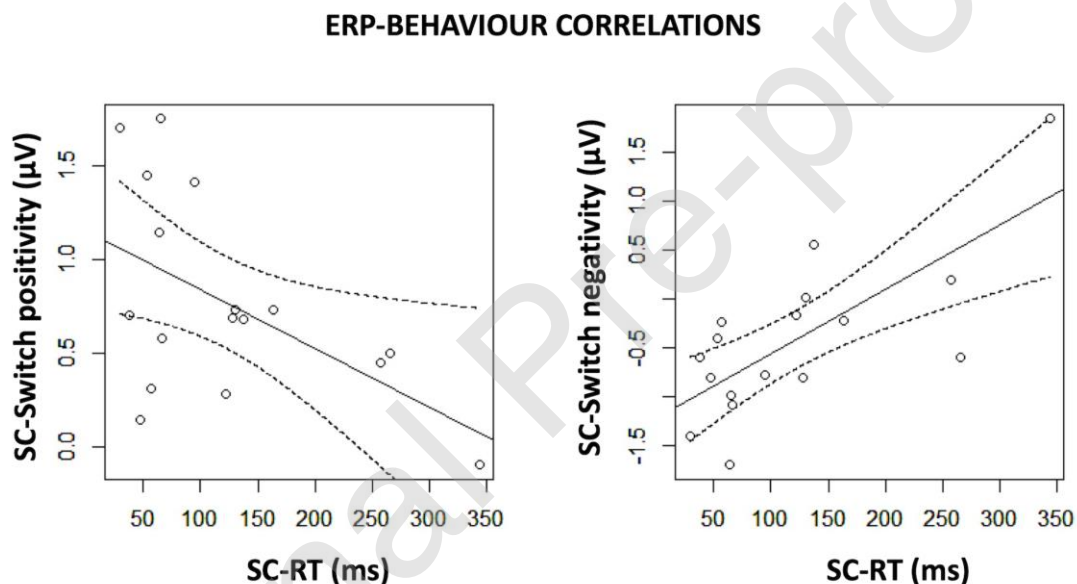


Figure 7. ERP-Behaviour correlations. The picture illustrates the relationship between the mean behavioural (RT switch cost) and neural (ERP switch cost) effects for the switch positivity (left panel) and the switch negativity (right panel) components.

4. Discussion

In the current study we sought to unveil the spatiotemporal neurodynamics underlying task-switching, by exploiting the high-density EEG, which provides an optimal balance between temporal and spatial resolution. We pursued two main goals: the first one was

to depict the temporal course of the cortical generators of the main switch-related ERP components, namely, the posterior switch positivity and the anterior switch negativity (Karayanidis et al., 2010). The hdEEG enabled us to unravel the temporal interplay between frontal and parietal areas in their contributions to task-set reconfiguration and interference detection and suppression. The second aim was to unveil the neural underpinnings of the behavioural changes that take place in task-switching performance through time. Being able to connect behavioural time-on-task effects with their electrophysiological counterpart might be fundamental for understanding the role of procedural processes (i.e., the practice effect) as a potential source of cognitive control adaptation over time (Braem et al., 2019). Here too, we monitored brain activity with hdEEG while observing the time-on-task effects during task-switching, in order to enucleate the role of distinct cortical regions in task-switching by observing their activity throughout the task. Behavioural data confirmed results from previous experiments showing a large switch cost in terms of both accuracy and RTs (Monsell, 2003). Furthermore, we replicated previous electrophysiological evidence showing that task-switching is associated with two different modulatory ERP effects, namely, a posterior switch positivity and a following frontal switch negativity. Specifically, this pattern mirrors the findings by previous studies using either cued (see Karayanidis et al., 2010 for a review) or, more recently, uncued (Capizzi et al., 2016) task-switching paradigms. In our study, the uncued version of the paradigm is likely to elicit larger ERP responses given that the cognitive control required to reconfigure the task-set is not attenuated by knowledge of prior information.

We can speculate that these two ERPs components are associated with two different neurocomputational stages underlying task-switch. The origin of the switch positivity might reside in the task-set reconfiguration (Monsell, 2003), consistently with previous

evidence (see Karayanidis & Jamadar, 2014). Interestingly, we show that switch positivity can be triggered even by the mere reversal of S-R mapping that differentiates repetition and switch trials, as in previous studies (Astle, Jackson, & Swainson, 2008; Rushworth et al., 2002). On the other hand, the switch negativity might be related to the task-driven interference. This interpretation is consistent with a previous EEG/fMRI investigation (Jamadar, et al., 2010), who found a positive correlation between the amplitude of the switch-negativity and the fMRI activity in the anterior cingulate cortex, a core region for interference detection and suppression (e.g., Botvinick et al., 2004). The positive correlation between the ERP components and switch costs found in our study nicely dovetails with the aforementioned results: a larger switch negativity is associated with smaller switch costs, suggesting that the stronger frontal activity, the better the coping of the interference. We also found a negative correlation between the switch positivity and switch costs; this result can be interpreted accordingly: a larger switch positivity is associated to a more efficient task-set reconfiguration, which triggers a reduction of switch costs. In addition to electrode-level findings, the source reconstruction provided clear-cut information about the cortical origin of the ERP effects. Specifically, the posterior switch positivity induced by task-switching was supported by a recruitment - between 300 and 500 ms from switch onset - of a circumscribed frontal activity around the left motor area and the right occipito-parietal cortices. These brain areas were still engaged in the following temporal interval - between 600 and 800 ms - although spreading over additional prefrontal regions, including the caudal portion of the middle and superior frontal gyrus. Noteworthy, this pattern replicated previous neuroimaging data (Crone et al., 2006; Cutini et al., 2008), with the additional value of supplying high temporal resolution information. In fact, we clearly show that not only task-switching engages distinct occipito-parietal and frontal

cortical regions, but that the latter comes into play at least 200 ms after the recruitment of parietal regions, confirming its high-order role in cognitive control (Astle et al., 2008). Our study attempted to provide an integrated framework, bridging current electrophysiological and neuroimaging evidence. Our experimental investigation strongly suggests that the core regions for task-switching performance might have distinct properties, as shown by the heterogeneous temporal modulation emerging from the behavioural time-on-task effects. In this regard, RTs exhibited a different pattern for switch and repetition trials: the decrease observed across bins for switch trials was much steeper than the one observed for repetition trials. Coherently, the switch positivity and the switch negativity components exhibited a different time-on-task pattern in relation to repetition and switch trials.

Specifically, we observed that both these two components displayed a clear-cut modulation (i.e., more positive and negative amplitudes, respectively) as far as participants went throughout the task. Yet, this effect was significantly larger for the switch negativity, which showed higher differences in response to switch trials than those observed in the switch positivity. This interaction can be interpreted by assuming that the process targeted by the switch negativity is more sensitive to time-on-task effect.

This ERP signature, which originated mainly from prefrontal areas, is associated with interference detection and suppression (Capizzi et al., 2016). This led us to argue that the learning effect –that has been already reported to occur in task-switching paradigm (Bherer et al., 2008; Minear & Shah, 2008 – might be triggered by a more efficient task suppression of interference, as a function of task procedural experience. This account is in line with recent theoretical framework positing that cognitive control can indeed

be guided by learning processes (Braem & Egner, 2018; Crump & Logan, 2010; Sali, Anderson & Yantis, 2015; Farooqui & Manly, 2015).

This view is supported by the visual inspection of time-on-task effects on cortical source activity that displayed a different pattern for these two core regions. In occipito-parietal areas, the time-on-task increase in activity was comparable across repetition and switch trials. In the prefrontal areas, a different pattern emerged: the activity in repetition trials did not exhibit a specific trend across time, while neural activity in switch trials constantly increased through time, especially in the left middle and superior frontal gyrus. This pattern confirms that left prefrontal areas are strongly involved in cognitive control, corroborating previous evidence coming from a wide range of neuroimaging techniques (Capizzi et al., 2016; Cutini et al., 2008; Vallesi, 2012). Evidence coming from brain stimulation is consistent with the present findings: stimulating the left prefrontal cortex induces a stronger practice effect as compared to the contralateral homologue region or sham stimulation (Tayeb & Lavidor, 2016). Finally, the significant correlation between behavioural and neural data calls for further investigation to explore the topic in terms of intra- and inter-individual differences in cognitive control, paving the way for a deeper investigation of peculiar populations (often characterized by high inter-variability), such as typical and atypical development and aging. In the present work we used distributed source reconstruction with a wMNE inverse solution. We decided to apply this analytic approach since it was successfully adopted in previous cognitive and methodological studies (Serget, Baillet & Dehaene, 2005; Florin, Bock, & Baillet, 2014; Strauss et al., 2015; Tadel et al., 2019). However, we are aware that this is not the unique method to perform source reconstruction. Future studies might not only investigate the stability of the present results, but also comparing

different source analysis approach, as for example dipole fitting, or non-linear distributed methods for source estimation (e.g., maximum entropy on the mean).

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