Asymmetry in prefrontal resting-state EEG spectral power underlies individual differences in phasic and sustained cognitive control

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A B S T R A C T

In our daily life, we constantly exert sustained and phasic cognitive control processes to manage multiple competing task sets and rapidly switch between them. Increasing research efforts are attempting to unveil how the brain mediates these processes, highlighting the importance of the prefrontal cortex. An intriguing question concerns the influence of hemispheric asymmetries and whether it may be generalized to different cognitive domains depending on lateralized processing. Another currently open question concerns the underlying causes of the observed huge inter-individual variability in cognitive control abilities. Here we tackle these issues by investigating whether participants' hemispheric asymmetry in intrinsic (i.e., resting-state-related) brain dynamics can reflect differences in their phasic and/or sustained cognitive control abilities regardless of the cognitive domain. To this aim, we recorded human participants' resting-state electroencephalographic activity and performed a source-based spectral analysis to assess their lateralized brain dynamics at rest. Moreover, we used three task-switching paradigms involving different cognitive domains to assess participants' domain-general phasic and sustained cognitive control abilities. By performing a series of correlations and an intersection analysis, we showed that participants with stronger left- and right-lateralized intrinsic brain activity in the middle frontal gyrus were more able, respectively, to exert phasic and sustained cognitive control. We propose that the variability in participants' prefrontal hemispheric asymmetry in the intrinsic electrophysiological spectral profile reflects individual differences in preferentially engaging either the left-lateralized, phasic or the right-lateralized, sustained cognitive control processes to regulate their behavior in response to changing task demands, regardless of the specific cognitive domain involved.

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Introduction

Humans constantly cope with demands of an increasingly complex, multitask environment, requiring frequent switching between different operations. Cognitive control processes involved in this ability are commonly investigated using task-switching paradigms, with participants performing two tasks either in isolation (in single-task blocks) or intermixedly (in mixed-task blocks, composed by switch and repeat trials). The basic findings are the so-called switching (Monsell, 2003) and mixing (Rubin and Meiran, 2005) costs, representing respectively the difference in performance between switch and repeat trials and between repeat and single-task trials.

It is increasingly evident that switching and mixing costs might reflect distinct executive functions. On the one hand, the switching cost would reflect specific/phasic cognitive control processes required to switch between different tasks, such as the transient activation of appropriate rules or stimulus-response mappings in place of the recently activated but inappropriate ones, or task set reconfiguration processes (e.g., Kiesel et al., 2010). On the other hand, the mixing cost would reflect global/sustained cognitive control processes required in performing mixed- vs. single-task blocks, such as the increased active maintenance demands due to keeping multiple task sets active and the management of competition between them (Rubin and Meiran, 2005). Empirical dissociations support this conclusion (Rubin and Meiran, 2005) and different neurophysiological mechanisms have been shown to mediate switching and mixing costs (Wylie et al., 2009).

Moreover, switching and mixing costs would depend on complementary executive functions that are dissociable not only functionally and temporally, but also anatomically. Different models have been proposed about the anatomical basis of executive functions and, in particular, of the transient vs. sustained cognitive control processes, with a particular attention to the organization of the prefrontal cortex (PFC). The idea that different sub-regions of the PFC may participate in a specialized manner to different executive functions is supported by findings showing synaptic (Medalla and Barbas, 2009, 2010), cytoarchitectonical (Petrides, 2005), and connectivity (Dosenbach et al., 2008; Tanji and Hoshi, 2008) differences in the anatomo-functional organization of the PFC. Consistent with these distinctions, different theories emerged in

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the last years proposing gradients of functional specialization within the PFC along the three anatomical axes, that is, the ventro-dorsal (Owen, 1997; Petrides, 2005), rostro-caudal (Badre and D'Esposito, 2009; Koechlin et al., 2003), and left–right (Kelley et al., 1998) axes.

In particular, the domain-based left–right organizational principle of the PFC functions, according to which the left and right hemispheres are the locus of verbal and spatial processing, respectively (Kelley et al., 1998; Wagner et al., 1998), is perhaps the first distinction suggested and it is clearly the more intuitive one. Indeed, it is based on the fact that the evolution provided us with two cerebral hemispheres that are functionally lateralized, or asymmetrically specialized, according to a verbal vs nonverbal axis (Corballis, 2009), with the verbal and visuospatial cognitive domains involving left- and right-lateralized processing (Hellige, 1993).

More recently, on the basis of extensive neuropsychological investigation, the ROBBIA (ROtman-Baycrest Battery to Investigate Attention) model of executive functions (Shallice et al., 2007, 2008; Stuss, 2011; Stuss and Alexander, 2007) has been proposed, positing that the left–right prefrontal specialization may be process-based and not only domain-based. In particular, the ROBBIA model proposes a prefrontal hemispheric specialization of two distinct executive functions: the left-lateralized criterion-setting (or task-setting), which can be defined as the phasic, transient cognitive control processes needed to form or select task-relevant rules (Stuss and Alexander, 2007) and suppress the task-irrelevant criteria and operations (Vallesi et al., 2012), and the right-lateralized monitoring, which can be defined as the tonic, sustained cognitive control processes needed to actively maintain abstract coded representations of events and monitor their relative status in relation to each other and the intended plan for behavioral adjustments (Petrides, 2005; Stuss and Alexander, 2007; Vallesi et al., 2012).

On the basis of these proposals, the switching and mixing costs would depend, respectively, on transient, left-lateralized criterion-setting processes and sustained, right-lateralized monitoring processes. Compatible with this view, neuroimaging studies revealed a functional double dissociation in left and right PFC regions supporting, respectively, transient and sustained cognitive control processes during task switching (Braver et al., 2003; Wang et al., 2009). However, despite accumulating evidence supporting the proposed function-based prefrontal hemispheric asymmetry (e.g., Vallesi and Crescentini, 2011), it is still unknown whether this asymmetry is simply related to task features and different cognitive domains known to depend on lateralized processing (e.g., verbal, left-lateralized, vs. visuospatial, right-lateralized; Hellige, 1993) or, rather, to "general" executive control abilities (Chein et al., 2011), that is, abilities that do not depend on either the cognitive domain or the specific requirements of the task. Indeed, previous studies have mostly investigated prefrontal asymmetries by focusing on either the cognitive process (Braver et al., 2003) or the domain (e.g., McCarthy et al., 1996), but their interplay remains underinvestigated. Thus, how prefrontal asymmetries relate to distinct executive functions regardless of task features remains an unresolved enigma.

To complicate the issue further, there are huge individual differences in executive control performance (Miyake et al., 2000) related to differences in task-evoked brain activity (Kim et al., 2011) and even brain structural organization (Gold et al., 2010). However, despite the rising interest in what determines individual differences in executive functioning (Braver et al., 2010), it is currently not known whether they may in part depend on differences in intrinsic (i.e., resting-state-related) brain dynamics (Laufs et al., 2006; Mennes et al., 2010) and related hemispheric asymmetries.

Here, we sought to fill this gap by investigating whether hemispheric asymmetries in intrinsic brain dynamics (as assessed by source-based electroencephalography spectral analysis) are associated with behavioral measures of domain-general phasic and sustained cognitive control (as assessed, respectively, by switching and mixing costs in three task-switching paradigms involving different cognitive domains; see

Fig. 1). In doing this, we also aimed to verify the hypothesized prefrontal hemispheric asymmetry of executive functions causing mixing and switching costs (Braver et al., 2003; Vallesi, 2012).

Materials and methods

Participants

Fifty-six university students (41 females; mean age = 22.9 years, $SD = 2.1$) voluntarily took part in the experiment. All participants gave informed consent prior to their recruitment. They were reimbursed 20€ for their time. All had normal or corrected-to-normal visual acuity and reported having normal color vision. The study was approved by the Bioethical Committee of the Azienda Ospedaliera di Padova and was conducted according to the guidelines of the Declaration of Helsinki (World Medical Association, 2013).

General procedure

For each participant, testing took place in three separate sessions during a 1-month period. The order of administration was: 1) resting-state electroencephalography (rsEEG) recording, 2) the verbal and spatial task-switching paradigms, and 3) the color–shape task-switching paradigm. The order of administration of the three sessions was fixed for all participants to minimize any error due to participant by order interaction (Miyake et al., 2000), but the verbal and spatial task-switching paradigms were administered in randomized order during the second session. In the last session, participants performed additional behavioral tasks tapping into different executive functions, which were not the object of the present study and whose results will be reported elsewhere. Similarly, after the recording of the rsEEG, participants took part in an event-related potential experiment, which will also be reported elsewhere. Participants were tested in a quiet and normally illuminated room. They were seated in front of a 17″ computer screen (refresh rate: 60 Hz, resolution: 1366 × 768) at a distance of approximately 60 cm.

Behavioral tasks and procedure

Since our aim was to investigate whether brain dynamics at rest in prefrontal cortex (PFC) can specifically predict general executive function abilities, that is, the performance in phasic and sustained cognitive control tasks regardless of both task features and cognitive domain, we chose to use three different behavioral paradigms sharing the same underlying executive functions and then, based on participants' performance in these three paradigms, computed a compound measure of the target executive process.

First, we chose to use the color–shape task-switching paradigm, as it was frequently used in previous studies investigating switching and mixing costs (Friedman et al., 2006, 2008; Garbin et al., 2010; Gold et al., 2013; Prior and MacWhinney, 2010). This paradigm makes use of non-verbal stimuli, requiring participants to indicate either the color or the shape of a simple visual stimulus, and thus it is supposed to involve right-lateralized cognitive processing related to the visuospatial domain. However, a closer examination suggests that it would not be well suited to investigate whether possible PFC asymmetries are truly function-based or, rather, domain-based, as contrasting findings exist about the hemispheric lateralization of color categorical perception (Franklin et al., 2008), which recently has even been questioned (Witzel and Gegenfurtner, 2011). Moreover, the performance in both color and shape tasks could be influenced by the use of lexical codes, which would rather involve left-lateralized verbal processes. Finally, the color–shape task-switching paradigm shares a potential drawback with previous studies suggesting the existence of distinct, but paradigm- and domain-general executive function abilities (e.g., Friedman et al., 2006, 2008; Miyake et al., 2000). Indeed, the paradigms used in most of the
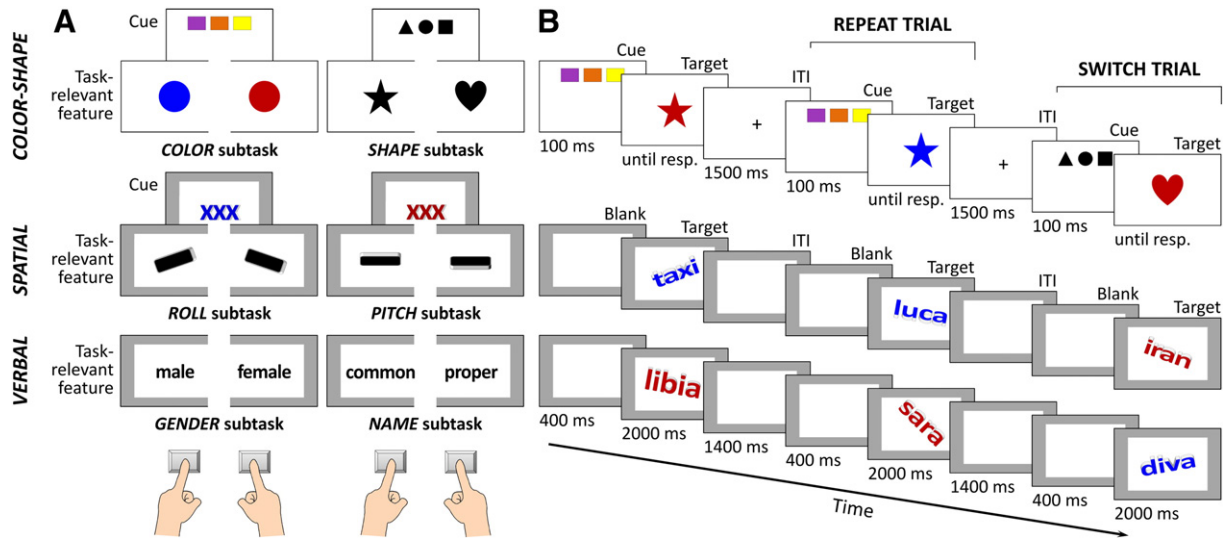
Fig. 1. Task-switching paradigms. A, Task cues and task-relevant features of the stimuli in the three task-switching paradigms. In each paradigm (depicted in the rows), depending on the specific task cue, the participants were asked to perform two different subtasks (depicted in the columns) in which they had to categorize the stimuli according to two orthogonal task-relevant features. B, Temporal structure of the trials in the mixed-task blocks (see the Behavioral Tasks and Procedure section) in the three paradigms and exemplar stimuli. In all the paradigms, tasks were either repeated (repeat trials) or switched (switch trials) from trial to trial on the basis of a pseudorandom sequence. See the The Color-Shape Task-Switching Paradigm and The Verbal and Spatial Task-Switching Paradigms sections for details.

previous studies, including the color–shape paradigm, embedded only tasks requiring semantic decisions or decisions based on stimulus identity, thus involving exclusively the ventral visual stream of processing (Goodale and Milner, 1992; Yehene and Meiran, 2007).

Based on these considerations, we developed a verbal and a spatial task-switching paradigm that makes use of the same experimental stimuli that were matched for a number of experimental features, thus maximizing the likelihood of detecting possible common cognitive control processes. In particular, we used words shown in three-dimensional text as stimuli in both paradigms. This allowed us to investigate both the left-lateralized verbal processes required to identify lexico-grammatical features of the presented words and, importantly, the right-lateralized visuospatial processes required to identify the spatial properties (orientation) of the three-dimensional stimuli and to mentally rotate them, which involve the dorsal visual stream of processing (Goodale and Milner, 1992; see Hugdahl, 2000). However, since we wanted to assess executive control processes that were not only independent from (lateralized) cognitive domains, but also from the specific task features of the novel paradigms, we also took the performance in the color–shape paradigm into account in assessing the paradigm- and domain-general executive function abilities of our participants.

The color–shape task-switching paradigm

The paradigm was adapted from Prior and MacWhinney (2010). Target stimuli consisted of a heart or a star shape (visual angle: 2.1° by 2.1° and 1.8 by 1.8°, respectively) that were presented at the center of the screen in either red or blue (Fig. 1). A graphic cue (3.8° by .9°) located 2.1° above the center of the screen served as task cue stimulus, signaling the task to be performed by the participants (see below). There were two types of task cues: the color task cue, consisting in a color gradient formed by a row of three colored rectangles (purple, orange, and yellow), and the shape task cue, consisting in a row of three small black shapes (a triangle, a circle, and a square, see Fig. 1). We chose to use graphic task cues to limit the use of linguistic information. Eight different combinations of stimuli were thus available by mixing the two possible shapes, two colors, and two cues.

A trial started with the presentation of a black fixation cross (.5° by .5°) for 1500 ms, followed by the presentation of the task cue stimulus. After a cue-to-target interval of 100 ms, the target stimulus was presented until a response was produced by the participant (Fig. 1). In

case of an erroneous response, a sound stimulus was presented via headphones (duration: 916 ms, error-onset delay: 50 ms) providing direct error feedback. Stimulus presentation and data recording were controlled by the Presentation software (Neurobehavioral Systems, Inc., Albany, CA) running on a Windows 7 operating system.

In the single-task condition, participants were required to perform two types of subtasks, one at a time in different blocks. In the color-type and the shape-type subtasks, participants were asked to respond to either the color or the shape of the stimulus, respectively, by pressing either the left or the right arrow button on the computer keyboard using two index fingers. The four possible response-to-button mappings were counterbalanced across participants and preserved throughout the single-task and mixed-task blocks. In the mixed-task block, the task cue stimulus instructed participants about the specific subtask they had to perform on any given trial.

Participants completed three blocks of trials. The first two blocks were single-task blocks in which only one subtask (i.e., either color or shape) was presented for the entire block. The specific assignment was counterbalanced across participants. Each single-task block consisted of six practice trials and 12 experimental trials. The third block was a mixed-task block in which the two subtasks were equally distributed. This block included 10 practice trials followed by 96 experimental trials with a short rest break administered after half of the trials were completed. Switch and repeat trials were presented in equal proportion in a pseudo-random order (Fig. 1).

The verbal and spatial task-switching paradigms

These paradigms were the same as those used in a recent fMRI study from our laboratory (Vallesi et al., 2015). Briefly, the stimulus material consisted of 18 proper nouns and 18 common nouns, equally subdivided into male and female nouns. All the words were presented in lowercase 80-points Calibri bold font and subtended on average 1.6° of visual angle horizontally and 4.9° vertically. We applied both a three-dimensional effect (depth: 10 points) and a three-dimensional rotation in order to add depth to the shape of the words and manipulate their spatial configuration. As a result, each word assumed both a pitch (upward vs. downward) and a roll (clockwise vs. anti-clockwise) rotation (Fig. 1). Each word could be filled with one of four colors: red, blue, green, or brown. The blue and red colors were associated with the task-switching condition, while the green and brown colors were

used for the single-task condition (see below). The reader is referred to the original study (Vallesi et al., 2015) for a detailed description of the stimulus material.

A trial started with the presentation of a gray blank screen with a light-gray frame for 400 ms (Fig. 1). The word stimulus was then displayed for 2000 ms at the center of the frame. The participants were asked to respond to the word according to the specific task instructions of each condition as outlined below. The inter-trial interval was 1400 ms. Stimulus presentation and data recording were controlled by the E-Prime 2 software (Psychology Software Tools, Pittsburgh, PA) running on a Windows 7 operating system. Participants' responses were recorded using a keyboard.

The verbal single-task condition consisted of two subtasks that were presented in different blocks. In the gender-type subtask, participants were required to identify female and male nouns by pressing, respectively, the "F" and "K" key with the left and right index finger. In the name-type subtask, they had to identify proper and common nouns in the same way. The assignment of categories to response keys was counterbalanced across participants for each subtask condition. In the verbal mixed-task blocks, the color of the word instructed participants about the specific subtask they had to perform on any given trial. The blue and red colors were associated with the name-type and gender-type subtasks, respectively.

The spatial task was similar to the verbal one and it was implemented on the same set of word stimuli. The spatial single-task condition consisted of two subtasks that were presented in different blocks. Specifically, in the roll- and pitch-type subtasks, participants had to classify the words according to either their clockwise/anti-clockwise or upward/downward rotations, respectively. As for the verbal conditions, the response keys were the "F" and "K" key on the computer keyboard, and the assignment of categories to response keys was counterbalanced across participants. In the spatial mixed-task blocks, the participants had to perform either the roll-type subtask or the pitch-type subtask when the color of the word was blue or red, respectively.

After a practice session (see Vallesi et al., 2015 for details), half of the participants started with the verbal switching task, while the other half started with the spatial one. Each of the two switching tasks consisted of six experimental blocks (two single-task and four mixed-task blocks), each comprising 32 trials (a higher number of mixed-task blocks was administered to ensure a sufficient number of switch and repeat trials). The first mixed-task block for each switching task was also preceded by 5 warm-up trials to allow participants to remember the corresponding stimulus-response mapping. For the task-switching blocks, switching trials were presented in a pseudo-random order.

Resting state EEG recording

We recorded rsEEG by using the BrainAmp system (BrainProducts, Munich, Germany) from 64 Ag/AgCl electrodes that were mounted on an elastic cap (EASYCAP GmbH, Germany) according to the 10–10 system. Electrooculographic activity was also recorded with an electrode placed under the left eye. Impedances for each channel were measured and adjusted until they were kept below 10 kΩ before testing. All electrodes were referenced online to FCz during the recording, and an electrode positioned at AFz served as the ground. Continuous electroencephalographic (EEG) activity was digitized at a sampling rate of 500 Hz and band-pass filtered online between 0.1 and 100 Hz.

A single rsEEG session was recorded. Participants were required to sit comfortably in a chair in a dimly illuminated, sound-shielded Faraday recording cage properly designed to minimize external stimulations interfering with the participants' resting state. They were instructed to keep their eyes closed, relax as much as possible while trying not to fall asleep, and not think of anything specific. The EEG recording lasted 5 min and was always performed before the behavioral tasks.

Behavioral data analysis

Response times (RTs) from incorrect responses were discarded, as well as trials with RTs shorter than 100 ms, which are treated as guesses. Median accuracy was greater than 89% in all the conditions of all the task-switching paradigms. Since the distributions of the RTs were skewed and/or kurtotic, we log-transformed RTs to improve normality. Moreover, to obtain measures of central tendency that were as robust as possible against aberrant observations, we applied an estimation procedure that is robust to non-normality and sample size (Rousseeuw and Verboven, 2002). For each participants and condition of the three task-switching paradigms, we computed an M-estimator of location with logistic psi-function and median absolute deviation as the auxiliary scale estimate, as implemented by the mlogist and madc functions in the LIBRA Matlab library (Verboven and Hubert, 2005, 2010).

Next, for each of the three task-switching paradigms, we calculated the switching cost as the difference between the M-estimator of location for switch trials and that for repeat trials. Similarly, we computed the mixing cost as the difference between the M-estimator of location for repeat trials and that for single-task trials. After these transformations, the variables measuring switching and mixing costs for the three task-switching paradigms showed acceptable skewness and kurtosis (respectively, mean = .03 and −.23; range = −.52 to .31 and −.70 to 42) (see Fig. 2). The statistical significance of both the switching and mixing costs for each of the three task-switching paradigms was assessed by means of one-sample t-tests against zero. The Cohen's d was used as the measure of the effect size (Cohen, 1977).

General switching and mixing costs

To obtain behavioral indexes of paradigm- and domain-general phasic and sustained cognitive control abilities reflecting, respectively, the commonalities among the three paradigm-specific measures of switching and mixing costs, we computed general switching and mixing cost measures as the average of the three paradigm-specific switching and mixing costs after z-standardization. The zero-order correlations among the three paradigm-specific measures and the corresponding paradigm- and domain-general measure of cognitive control were .77, .59 and .82 for the switching cost and .76, .78 and .67 for the mixing cost in the color–shape, verbal and spatial task-switching paradigm, respectively. It should be noted here that the resulting measures of general switching and mixing costs were virtually identical to the corresponding factor scores obtained from factor analysis, as the respective regression equation (when regressing the latter on the former) were $y = 0 + .96x$ ($R^2 > .98$) and $y = 0 + 1x$ ($R^2 > .88$). Moreover, the subsequent analyses performed on factor scores yielded very similar results to that reported here. However, we preferred not to use factor scores obtained from factor analyses, which at a first sight could seem preferable and more consistent with previous studies (e.g., Miyake et al., 2000), because the characteristics of our data did not fully satisfy the recommendations for performing factor analyses (MacCallum et al., 1999), mainly because of the small sample size and the range of communality values.

EEG data analysis

EEG preprocessing

Offline EEG processing and analyses were performed using custom Matlab (The MathWorks, Inc, Natick, Massachusetts, USA) scripts using functions from the EEGLAB environment (version 12.0.2b; Delorme and Makeig, 2004). The continuous EEG data were band-pass filtered (.5–45 Hz) using a zero-phase Kaiser-windowed sinc FIR filter (beta = 6.317, transition bandwidth = .01 Hz) as recently recommended (Widmann et al., 2014), and then visually inspected for clearly noisy electrodes. TP9 and TP10 channels showed large fluctuations during the entire experiment in most of the participants (probably because of bad skin contact and/or excessive muscular artifacts) and thus were
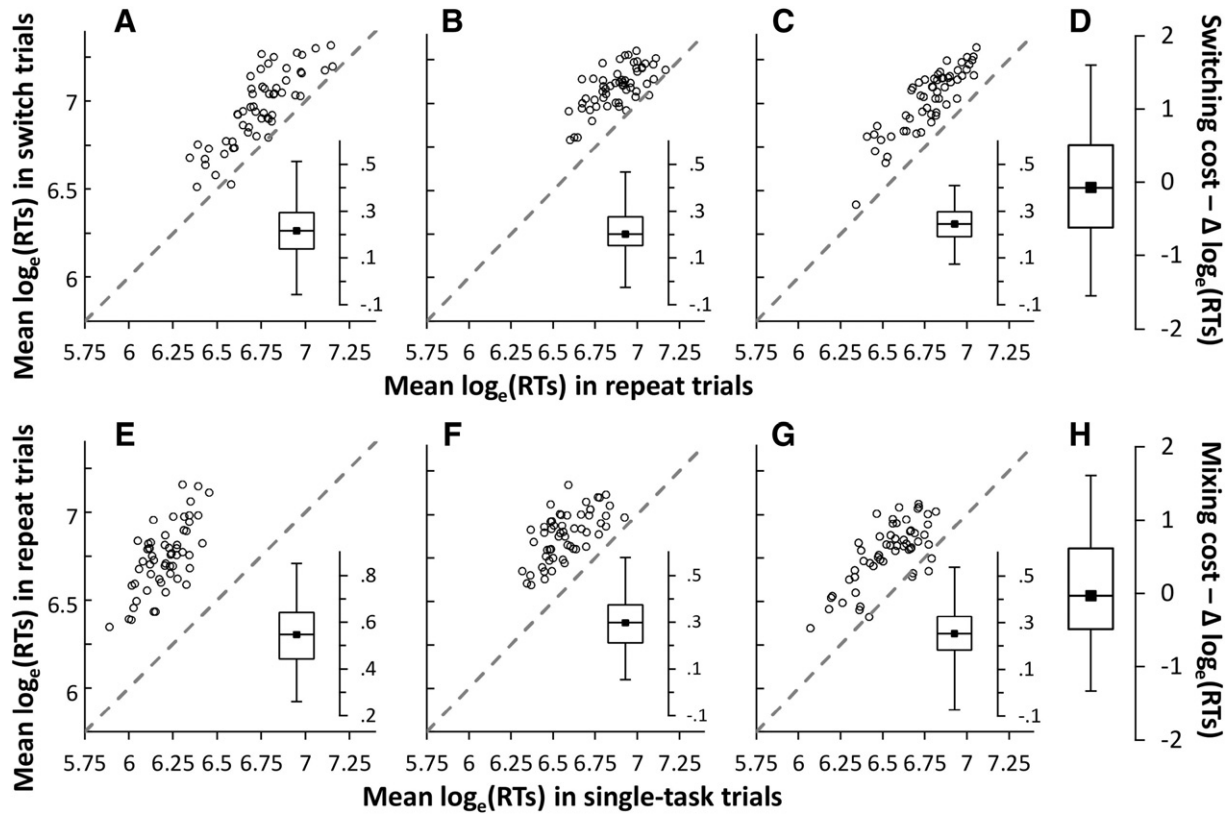
Fig. 2. Participants' behavioral performance in the task-switching paradigms. A–C, Scatterplots showing the participants' mean M-estimates of natural log-transformed RTs in repeat (x-axis) and switch (y-axis) trials for the color–shape (A), verbal (B), and spatial (C) task-switching paradigms. Circles represent data from each participant. The diagonal dashed line indicates the identity line ($y = x$), so that circles above the diagonal represent participants exhibiting a switching cost. The boxplots in the insets show the distribution of the participants' switching costs; the central line/point of the box represents the median, the edges of the box are the first and third quartiles, and the whiskers represent the range of the data. E–G, Scatterplots showing the participants' behavioral performance in single-task (x-axis) and repeat (y-axis) trials for the color–shape (E), verbal (F), and spatial (G) task-switching paradigms. The circles above the diagonal represent participants exhibiting a mixing cost. The boxplots in the insets show the distribution of the participants' mixing costs. Other conventions are as above. D and H, The boxplots show the distribution of the participants' general switching (D) and mixing (H) costs computed from the three respective paradigm-specific costs (see the Behavioral Data Analysis section for details). Other conventions are as above.

excluded from further data analysis. Automatic rejection of noisy EEG channels was then performed on continuous data and confirmed by visual inspection. Rejection thresholds were $SD > 4$ for the improbability and spectral test, and $SD > 7$ for the kurtosis test. The resulting contaminated channels (one channel in seven participants, two channels in one participant) were interpolated using spherical splines (Perrin et al., 1989). Continuous EEG data were then segmented into non-overlapping 2048 ms epochs and re-referenced to the average of all EEG electrodes. The length of the epochs was chosen so as to maximize the efficiency of the automatic artifact detection method (see below) without excessive loss of data while being able to compute the rsEEG spectral power for low (≈ 1 Hz) frequencies (since we aimed to compute the total spectral power in the 1–45 Hz frequency range, see the Spectral Power Analysis section).

We then performed automatic detection and rejection of artifactual and/or outlier EEG data epochs by applying five different methods (see Delorme et al., 2007) according to the following criteria, which were determined on the basis of preliminary examination to optimize artifact rejection in our sample: i) ± 125 µV for the standard extreme values thresholding (± 75 µV for the EOG channel); ii) current drifts larger than ± 50 µV and $R^2 > .10$ for the linear trend test; iii) $SD > 5$ (for each channel) and $SD > 3$ (for all channels) for the improbability test; iv) $SD > 7$ (for each channel) and $SD > 4$ (for all channel) for the kurtosis test; and v) $SD > 4$ for the spectral pattern test in the 30–80 Hz band. Epochs containing data points exceeding at least two of these criteria were excluded from further data analysis. As a result, a mean of 21% of the epochs ($SD = 14$%) were rejected. For each subject, 30 artifact-free epochs were randomly selected for the estimation of sensors

variance, and the remaining epochs (mean = 85, $SD = 20$) were selected for the source analysis.

Source analysis

Cortical EEG source imaging was performed on selected epochs of individual participants using Brainstorm (Tadel et al., 2011), which is documented and freely available for download online under the GNU general public license (http://neuroimage.usc.edu/brainstorm). A distributed source model consisting in 15,002 elementary current dipoles was used to estimate the cortical current source distribution. These dipole sources were distributed at each node (i.e., vertex) of a tessellated cortical mesh template surface (brain model) derived from the standard 1 mm resolution brain (Colin27) of the Montreal Neurological Institute provided in Brainstorm. Dipole orientations were constrained to be normal to the cortex surface. The EEG forward modeling of volume currents was completed with a symmetric boundary element model generated with OpenMEEG (Gramfort et al., 2011; Kybic et al., 2005) using the adaptive integration method. This volume conduction model of the head uses three realistic layers corresponding to the surface of the head (1082 vertices, relative scalp conductivity = 1), the outer skull (642 vertices, relative skull conductivity = .0125), and the inner skull (642 vertices, relative brain conductivity = 1).

To estimate the current strength dynamics of cortical sources of the EEG time series, we used the depth-weighted minimum norm estimation approach (Baillet et al., 2001), implemented in Brainstorm, with default parameter settings. This technique has been shown to be robust to noise in recorded data and head model approximations with fair spatial resolution (Baillet et al., 2001), and the depth weighting used in this

approach alleviates the natural bias of basic minimum norm estimation approaches toward superficial currents. A diagonal noise covariance matrix computed for each participant on 30 randomly selected artifact-free epochs was used as an estimate of sensors variance. Finally, the recorded EEG time series at each electrode were multiplied by the depth-weighted minimum-norm estimate inverse operator to yield the estimated source current strength, as a function of time, at each of the 15002 vertices composing the cortical surface. Given that this is a linear transformation, it does not alter the spectral properties of the underlying sources and it is thus possible to perform time–frequency analysis directly on the source space (Billeke et al., 2013).

Spectral power analysis

For spectral power analysis of the estimated activity of the cortical sources, a parcellation of the cerebral cortex into anatomical regions of interest (ROIs) was derived in Brainstorm from the cortical atlas by Destrieux et al. (2010), which was modified by i) subdividing the original gyral ROIs that were composed by more than 200 vertices into smaller ($\approx$100 vertices) ROIs on the basis of anatomical criteria, and ii) excluding original sulcal ROIs that were composed by less than 40 vertices. For example, the left superior frontal gyrus ROI, composed by 451 vertices, was subdivided into the posterior, mid-posterior, middle, mid-anterior, and anterior parts, composed respectively by 101, 114, 126, 117, and 100 vertices, while the left transverse temporal sulcus, composed by only 13 vertices, was excluded from the analyses. This was done to alleviate the variability in number of vertices across the 148 original ROIs and reduce the number of ROIs included in the analysis while ensuring a homogeneous covering of the cortical surface. The modifications we made to the Destrieux atlas were indeed effective in reducing the size variability of the ROIs, measured as the *SD* of the number of vertices composing the ROIs, which was almost halved in the modified atlas (from 81 to 42; the average number of vertices was 98 and 91, respectively). Moreover, the source activity for each of the resulting ROIs was estimated by averaging the current strength time series of each elementary dipole source within each ROI (Hsiao et al., 2014) to reduce the computational load and to better calculate the asymmetry scores. Note that the results were virtually the same when computing the median instead of the mean.

We then exported the data in Matlab and estimated the source-based spectral power of each participant's cortical activity by using the EEGLAB (Delorme and Makeig, 2004) spectopo function to obtain a .25 Hz resolution (Welch's averaged, modified periodogram method, 256-points Hamming window, 2048-points discrete Fourier transform, 8× oversampling). For each epoch, the current strength time series of each ROI was converted into the power spectral density in the frequency range of 1–45 Hz. The obtained absolute power spectra were then averaged across epochs, transformed into relative power by calculating the proportion of each frequency with respect to the total absolute power, and again averaged across frequencies to compute the mean relative power for the alpha (7.5–12.5 Hz) and beta (12.5–24 Hz) frequency bands.

Next, for each ROI, we computed the ratio between relative power in beta and alpha bands (beta/alpha ratio: β/α) as a quantitative measure of brain dynamics at rest reflecting spontaneous fluctuations of attention and vigilance levels (Laufs et al., 2006). This measure was log-transformed to improve normality. In view of the peculiar pattern of EEG spectral profile during resting state, we chose to use the β/α measure, instead of the relative power in separate frequency bands, because it would represent a better quantitative measure of intrinsic (i.e., resting-state-related) brain activity (Kilner et al., 2005) reflecting increased attentional investment and cortical engagement in information processing (Laufs et al., 2006). Most of the existing rsEEG studies have focused mainly on the power in the alpha band, as it is considered the hallmark of the brain resting-state, with maximal amplitude during an eye-closed relaxed condition. When the power in the alpha band is high (and thus the β/α is low), the cortex is in a "idling" or unoccupied state

(Pfurtscheller et al., 1996), or even inhibited (Klimesch et al., 2007), and the attentional resources are not engaged (Laufs et al., 2003). However, the rsEEG relative alpha power cannot be interpreted as a marker of cortical engagement/activity on its own, but should be analyzed with respect to the power in other, specific frequency bands. Indeed, low rsEEG relative alpha power may indicate either low or high vigilance/attentional investment at rest (Ota et al., 1996) when it is respectively accompanied by high relative theta power or high relative beta power (and thus high β/α), which in turn can be conceived as an EEG marker of attention and active cognitive processing (Freeman, 2004). Moreover, the shift in the EEG spectral profile toward beta frequencies in a given cortical region (i.e., an enhancement in its β/α) has been shown to be associated with its blood oxygen level dependent (BOLD) activation (Kilner et al., 2005), indicating heightened attentional levels along with engagement in a variety of mental activities (Laufs et al., 2006). Take for example the case of two individuals with the same relative rsEEG alpha power of .5. What are their brain states and level of cortical activation (i.e., their intrinsic brain activity) during the resting state session? Based on the above mentioned findings, we cannot provide a reliable answer without considering the relative power in other frequencies and, in particular, the relative beta power. Indeed, these two individuals would have very different brain states and cortical activation levels according to the distribution of the remaining 50% or the total power across the different frequency bands: a relative power of .45 either in the delta/theta bands (i.e., a high theta/alpha ratio) or in the beta/gamma bands (i.e., a high β/α) would indicate, respectively, low-arousal/drowsiness, local cortical deactivation, and a "visual" occipital pattern of fMRI activations, or high arousal, local cortical activation, and an "attentional" parieto-frontal pattern of fMRI activations (Kilner et al., 2005; Laufs et al., 2006; Ota et al., 1996). Further supporting our choice, finally, the power in the beta and alpha bands has been shown to be oppositely correlated to behavioral measures of cognitive functioning (MacLean et al., 2012).

Finally, to quantify hemispheric asymmetries in intrinsic brain dynamics, we computed β/α hemispheric asymmetry scores (β/α_HAS) as the right-left difference for each pair of ROIs. Therefore, higher (i.e., more positive) β/α_HAS values represent a strongly right-lateralized brain activity at rest, whereas lower (i.e., more negative) β/α_HAS values represent a strongly left-lateralized brain activity at rest. Note that, since we computed the relative (instead of absolute) power in alpha and beta bands (see above), we already controlled for potential individual differences in skull thickness and volume conduction, which could produce differences in the spectral power.

Inferential statistics

Our aim was to investigate whether hemispheric asymmetries in rsEEG spectral activity in certain cortical regions – in particular, the PFC – are specifically related to behavioral indexes of paradigm- and domain-general phasic and sustained cognitive control abilities. To this end, we first performed a series of correlation analyses between, on the one side, the β/α_HAS for each ROI and, on the other side, either the general switching cost or the general mixing cost, respectively.

We computed the Pearson's correlation coefficients and conducted null hypothesis statistical significance testing by using the nonparametric percentile bootstrap test (2000 resamples; two-sided 95% confidence intervals, corresponding to an alpha level of .05), which is more robust against heteroscedasticity compared with the traditional t-test (Pernet et al., 2012). Nevertheless, GLM statistical procedures – especially the correlation/regression analyses – are known to be overly sensitive to deviant observations and characteristics of the dataset (Rousselet and Pernet, 2012). In particular, the results of such analyses can be flawed by the presence of bivariate outliers, which are hard to identify with classical methods. Therefore, to overcome this problem, we confirmed and refined the results of the standard correlation analysis by performing robust regression analyses using the Robust Correlation toolbox (Pernet et al., 2012). Specifically, we computed skipped

correlations (Wilcox, 2004), which provide a robust generalization of Pearson's correlation coefficient r by measuring the strength of the linear association between the pair of variables (i.e., the results are comparable across the [−1:1] range). Differently from the standard Pearson correlation, the skipped Pearson correlation takes the overall structure of the data into account in protecting against the detrimental effects of aberrant observations. Moreover, it can be more powerful than Pearson correlation when data contain outliers (especially the bivariate ones), and it allows maintaining the false positive rate below the nominal alpha level (Pernet et al., 2012). As for the regular Pearson correlation, null hypothesis statistical significance testing was conducted using the nonparametric percentile bootstrap test. Therefore, for both the paradigm- and domain-general phasic and sustained cognitive control abilities, we first reported the ROIs for which the regular and/or skipped Pearson's correlation coefficients were significant. We also report both regular and skipped Spearman's ρ values for these ROIs as a further caution, to control for the potential detrimental effect of deviant observations and characteristics of the samples.

However, the analysis just outlined can only verify whether the participants' β/α_HAS at rest for a given ROI is associated with either their phasic or sustained cognitive control abilities, but it cannot verify whether the participants' β/α_HAS for the same ROI is selectively (or significantly differently) associated with one of the two general cognitive control abilities. In other words, with the analysis outlined above one cannot verify whether there is a differential power–behavior correlation effect, that is, a significant correlation between the β/α_HAS in an ROI and one of the two general cognitive control abilities that is also significantly different from the correlation with the other general cognitive control ability (see Nieuwenhuis et al., 2011). Therefore, since our main aim was to identify the cortical regions in which the hemispheric asymmetry in intrinsic brain dynamics has a stronger correlation with one of the two paradigm- and domain-general cognitive control abilities compared to the other one, we first compared these two correlations for each ROI by using a two-tailed z-test for correlations. It should be noted, however, that it is possible (in principle) to have an ROI for which there is significant result in the z-test comparing the mixing- and switching-related correlations (i.e., a significant differential correlation) even if neither of these correlations are significant on their own. In this case, that ROI would show a significantly greater power–behavior correlation for one of the two cognitive control processes as compared to the other, but this very same correlation would be non-significant in itself: the ROI would thus be relatively more involved in that control process, but this involvement cannot be deemed as reliable.

To overcome this potential issue, we finally performed an intersection analysis. With this analysis, we determined the ROIs for which: 1) both the standard and the skipped Pearson correlation between the β/α_HAS and the general switching cost (or, respectively, the general mixing cost) were significant in the nonparametric bootstrap test, as detailed above, and 2) they were also significantly different from those found for the general mixing cost (or, respectively, the general switching cost) in a two-tailed z-test comparison for correlations. This ensured that the obtained power–behavior significant correlations specifically and/or differentially involved either the phasic or the sustained general cognitive control ability (see Nieuwenhuis et al., 2011).

It should be noted that our procedure should have reduced the risk of Type I error rate inflation due to multiple comparisons, since we i) reported ROIs for which the statistical significance of the power–behavior correlation was stable across both standard and robust correlations, as tested with a nonparametric bootstrap test, ii) statistically compared both correlation measures to test for differential correlation effects, and iii) performed an intersection analysis between these two results. However, the precise determination of the actual Type I error rate in our results is a hard problem to solve, and thus we cannot be sure to have completely eliminated the risk of its inflation. Therefore, to overcome this potential drawback, we also applied a stricter control against the risks of multiple comparisons to the results of the z-test

(FDR correction at a .05 level; Benjamini and Hochberg, 1995), further protecting the results of primary theoretical interest against inflation of Type I error rate. We also performed the same set of analyses on the participants' β/α values for the 150 ROIs, but we do not report them here for the sake of brevity, as no ROIs survived the FDR correction for both the regular and skipped Pearson correlation. Inline Supplementary Table S1 shows the results of the differential correlation analysis on the β/α values that survived the FDR correction for the skipped Pearson correlation only.

Inline Supplementary Table S1 can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.09.035.

Results

Behavioral results

For the color–shape task-switching paradigm, the analysis revealed a characteristic pattern of results for the participants' RTs. Mean M-estimates of log-transformed RTs were 6.202 ($SE = .016$), 6.742 ($SE = .025$), and 6.959 ($SE = .028$) for the single-task, repeat, and switch trials, respectively. This resulted in significant switching ($M = .217$, $t_{(55)} = 13.661$, $p < 10^{-18}$, $d = 1.826$) and mixing ($M = .540$, $t_{(55)} = 29.061$, $p < 10^{-34}$, $d = 3.883$) costs that were exhibited by almost all of the participants (respectively, 55/56 and 56/56; see Fig. 2A and E) with substantial inter-individual variability (see inset in Fig. 2A and E, respectively). A similar pattern of results for the participants' RTs was found in the verbal task-switching paradigm. Mean M-estimates of log-transformed RTs were 6.577 ($SE = .019$), 6.879 ($SE = .019$), and 7.091 ($SE = .016$) for the single-task, repeat, and switch trials, respectively. The resulting switching and mixing costs were significant (respectively, $M = .211$ and .302, $t_{(55)} = 14.873$ and 18.632, $p < 10^{-20}$ and 10^{-24}, $d = 1.987$ and 2.490) and observed in almost all of the participants (respectively, 55/56 and 56/56) (Fig. 2B and F, respectively). Finally, as for the preceding analyses, the characteristic pattern of results for the participants' RTs emerged also for the spatial task-switching paradigm. Mean M-estimates of log-transformed RTs were 6.538 ($SE = .024$), 6.778 ($SE = .024$), and 7.021 ($SE = .024$) for the single-task, repeat, and switch trials, respectively. Again, the resulting switching and mixing costs were significant (respectively, $M = .243$ and .240, $t_{(55)} = 20.135$ and 13.561, $p < 10^{-26}$ and 10^{-18}, $d = 2.691$ and 1.812) and observed in most of the participants (respectively, 56/56 and 51/56) with substantial variability (Fig. 2C and G, respectively).

After having checked the reliability and the stability of the results across the task-switching paradigms (see General Switching and Mixing Costs), we computed the general switching and mixing cost measures as the average of the three paradigm-specific switching and mixing costs after z-standardization (Fig. 2D and H). It should be noted here that general switching and mixing costs were anti-correlated ($r = -.36$) across participants. However, this did not bias our result of main interest (see Differential correlations and Intersection analysis sections), as the statistical significance of the differential correlation (see the Inferential Statistics section) was assessed using a z-test that controls for the correlation between the switching and mixing costs (Meng et al., 1992).

Source-based spectral analysis

As detailed in the Source Analysis and Spectral Power Analysis sections, participants' rsEEG data were submitted to a distributed source reconstruction to estimate the current strength dynamics of the rsEEG cortical sources. We then carried out a spectral power analysis on the model-derived current strength time-series within 150 anatomically-defined ROIs and computed the relative power (% of the total power) for the alpha (7.5–12.5 Hz) and beta (12.5–24 Hz) frequency. Figs. 3 and 4 show the cortical maps of the source-based relative power of the alpha and beta bands, respectively. Next, for each ROI, we computed
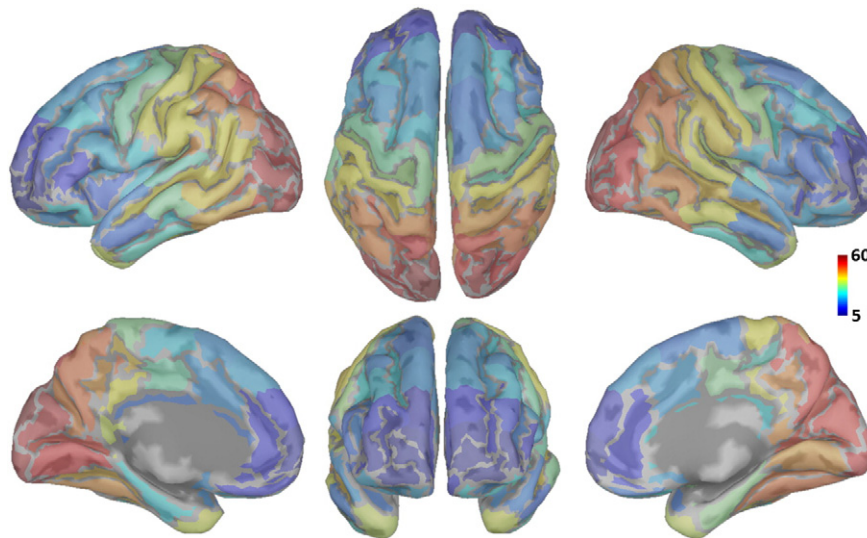
Fig. 3. Cortical map of the source-based relative power (%) of the alpha (7.5–12.5 Hz) frequency band within the 150 anatomically-defined ROIs.

the β/α ratio as a quantitative measure of brain dynamics at rest reflecting spontaneous fluctuations of attention and vigilance levels (Laufs et al., 2006) (see the Spectral Power Analysis and Discussion sections). Fig. 5 shows the cortical map of the natural log-transformed β/α ratio. Finally, to quantify hemispheric asymmetries in intrinsic brain dynamics, we computed the β/α_HAS, that is, the hemispheric asymmetry score for the β/α measure, as the right-left difference for each pair of ROIs. Therefore, higher (i.e., more positive) β/α_HAS values represent a strongly right-lateralized brain activity at rest, whereas lower (i.e., more negative) β/α_HAS values represent a strongly left-lateralized brain activity at rest. Inline Supplementary Fig. S1 shows the cortical map of the β/α_HAS values.

Inline Supplementary Fig. S1 can be found online at http://dx.doi. org/10.1016/j.neuroimage.2015.09.035.

We assessed the reliability of our spectral measures. To this aim, we split the model-derived current strength time-series into two halves (corresponding to the first and second half of the rsEEG session) and carried out a separate spectral power analysis on each half as detailed in the Spectral Power Analysis section. Then, for each participant and for each ROI, we computed the split-half reliability index between the power spectral densities in the 1–45 Hz range for the first and the second half of the rsEEG session. The reliability index was computed as

the Pearson's correlation coefficient corrected with the Spearman–Brown prophecy formula. This analysis revealed that the power spectral densities for the first and the second half of the rsEEG session were very similar, with a median reliability index of .998 across both participants and ROIs (interquartile range = .003). Moreover, we also computed the reliability indices for the β/α_HAS values. The analysis revealed that the asymmetry scores were stable both across participants (i.e., when correlating the β/α_HAS values in the 75 ROIs in the first vs. second half for each participant; median = .975, interquartile range = .028) and across ROIs (i.e., when correlating the β/α_HAS values of the 56 participants in the first vs. second half for each ROI; median = .961, interquartile range = .026).

Power–behavior correlations

Correlation analysis

Tables 1 and 2 shows the statistics for the results of the robust correlation analysis for both the behavioral measures of phasic and sustained general cognitive control ability, that is, the general switching and mixing costs, respectively (see General Switching and Mixing Costs). Inline Supplementary Figs. S2 and S3 show the cortical maps of the correlations for the switching and mixing costs, respectively.
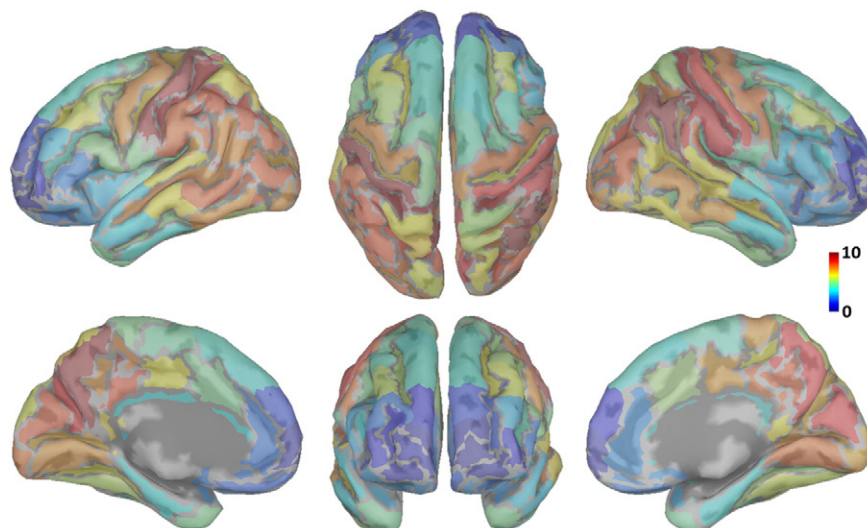

Fig. 4. Cortical map of the source-based relative power (%) of the beta (12.5–24 Hz) frequency band within the 150 anatomically-defined ROIs.
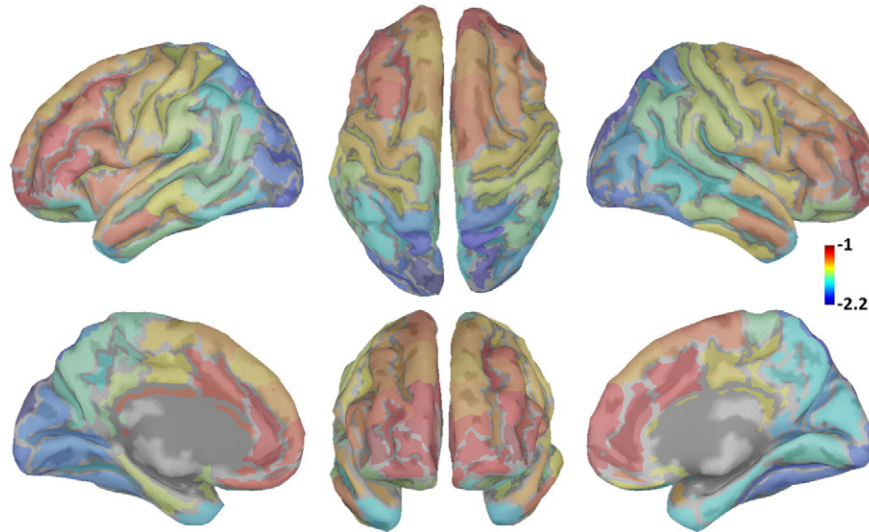
Fig. 5. Cortical map of the source-based relative power (%) of the natural log-transformed β/α ratio within the 150 anatomically-defined ROIs. Warmer and cooler colors indicate, respectively, higher and lower β/α values (dark red and dark blue correspond to a β/α ratio of ≈ .37 and .11, respectively).

Inline Supplementary Figs. S2 and S3 can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.09.035.

The robust and regular correlation analyses detected three ROIs for which the participants' general sustained cognitive control ability was significantly associated with their hemispheric asymmetry in intrinsic rsEEG spectral activity (Table 1). In particular, significant skipped and regular Pearson correlations between participants' general mixing costs and β/α_HAS were found in the ROI including the four orbital gyri (OG), in an ROI in the dorsolateral PFC, namely the middle part of the middle frontal gyrus (mMFG), and in the mid-posterior superior frontal gyrus (mpSFG) ROI, which included the pre-supplementary motor area (pre-SMA). For all of these ROIs, participants who showed higher β/α power in the right than left hemisphere (i.e., with higher β/α_HAS in these ROIs) also had significantly smaller general mixing costs. In other words, participants who showed a more strongly right-lateralized brain activity at rest in these cortical regions also showed smaller mixing costs when subsequently performing the task-switching paradigms. Moreover, significant skipped correlations were found in four additional ROIs, namely the inferior frontal gyrus, pars opercularis (IFGop), the superior segment of the circular sulcus of the insula (sCirInS), the superior precentral sulcus (supPrCS), and the anterior inferior temporal gyrus (aITG) (Table 1). The results for these ROIs were consistent with those described above for the OG, mMFG, and mpSFG ROIs, as they also reflected negative skipped correlations between the participants' β/α_HAS and their general mixing costs. However, these latter results were presumably influenced by the presence of outliers, since the nonparametric percentile bootstrap test failed to find the statistical significance of the regular Pearson correlation indexes for these ROIs (Table 1). Therefore, we suggest caution in their interpretation.

The analysis also revealed that the participants' general phasic cognitive control ability was significantly associated with their hemispheric asymmetry in intrinsic rsEEG spectral activity in two of the ROIs for which a significant correlation between mixing costs and β/α_HAS was found, namely the mpSFG/pre-SMA and mMFG (Table 2). In particular, for these two PFC ROIs, a significant positive association was found between the participants' β/α_HAS and their general switching costs, meaning that participants who showed higher β/α power in the left than right hemisphere, that is, with a more strongly left-lateralized brain activity at rest in these PFC regions, also showed a greater ability to phasically exert cognitive control to rapidly switch between different tasks when subsequently asked to perform the task-switching paradigms. The analysis also revealed three ROIs for which contrasting results were found between the skipped and regular correlation

analyses. Indeed, two additional ROIs exhibited significant skipped Pearson correlations but non-significant regular Pearson correlations, that is, the posterior inferior temporal gyrus (pITG) and the adjacent anterior occipital sulcus (aOS) (Table 2). Moreover, a further temporal region (the anterior transverse temporal gyrus, aTransTG) showed a significant regular Pearson correlation but a non-significant skipped correlation (Table2). For all these temporal ROIs, there was an inverse relationship between the participants' β/α_HAS and their general switching costs. Also in this case, however, the lack of consistency in the results of both correlation analyses calls for caution in their interpretation.

Note that the reported results did not depend on the size of the ROIs or the differences in size between left and right hemisphere, both when using the strength of both the regular and the skipped Pearson's correlation reported above (all $|r|s ≤ .187$, all $ps ≥ .109$) and when using the corresponding r^2 values (all $|r|s ≤ .127$, all $ps ≥ .276$). Similarly, we can exclude potential confounding effects on our results due to the β/α_HAS variability (SD) across participants (all $|r|s ≤ .115$, all $ps ≥ .326$) or the split-half reliability computed across participants (see the Spectral Power Analysis section; all $|r|s ≤ .141$, all $ps ≥ .229$).

Finally, we assessed whether the significant correlations revealed by the correlational analyses detailed above can be specifically attributed to the β/α_HAS values in those ROIs or, rather, could be biased by the β/α_HAS values in nearby regions. We first carried out two stepwise regression analyses with either the switching or the mixing costs as the dependent variable and the β/α_HAS values in all of the 75 ROIs as regressors. The analysis on the switching costs revealed that the β/α_HAS for the mMFG ROI was the only significant regressor to enter the model ($β = .309$, $t_{(54)} = 2.384$, $p = .021$), which explained the 9.53% of the variance. The β/α_HAS for the mMFG ROI was also one of the two significant regressors to enter the model for the mixing costs ($β = −.304$, $t_{(54)} = −2.482$, $p = .016$) along with the β/α_HAS for OG ROI, the first regressor to enter the model ($β = −.327$, $t_{(54)} = −2.677$, $p = .010$). In this case, the model explained the 20.96% of the variance ($F_{(2,53)} = 7.027$, $p = .002$). Therefore, the results of the stepwise regression analyses suggested that the β/α_HAS for the mMFG ROI was a specific and reliable predictor of the participants' task switching performance. Next, we further verified the potential confounding effect of the β/α_HAS values in the ROIs surrounding the mMFG region. We thus carried out two separate multiple regressions for the switching and mixing costs by forcing the β/α_HAS values for all of the ROIs surrounding the mMFG to enter the model. These ROIs were the posterior and anterior part of the MFG, the superior and

Table 1
Results of the power–behavior correlation analyses for the general mixing costs.

| ROI | #Out | Pearson's correlation | | | | | | Spearman's correlation | | | | | |
| | | Skipped | | | Regular | | | Skipped | | | Regular | | |
		r	$_{LB}CI_{95\%}$	$_{UB}CI_{95\%}$	r	$_{LB}CI_{95\%}$	$_{UB}CI_{95\%}$	ρ	$_{LB}CI_{95\%}$	$_{UB}CI_{95\%}$	ρ	$_{LB}CI_{95\%}$	$_{UB}CI_{95\%}$
mMFG	0	−.321	−.545	−.068*	−.321	−.551	−.067*	−.229	−.464	−.001*	−.239	−.475	−.001*
OG	0	−.343	−.579	−.097*	−.343	−.575	−.033*	−.312	−.556	−.019*	−.312	−.556	−.023*
mpSFG	1	−.235	−.428	−.040*	−.215	−.399	−.037*	−.229	−.442	−.003*	−.218	−.433	.015
supPrCS	3	−.290	−.507	−.046*	−.167	−.444	.161	−.285	−.493	−.031*	−.244	−.479	−.161*
aITG	4	−.275	−.439	−.097*	−.030	−.303	.232	−.312	−.517	−.081*	−.151	−.397	.109
IFGop	2	−.239	−.438	−.024*	−.181	−.466	.129	−.237	−.464	.031	−.203	−.460	.079
sCirInS	1	−.305	−.545	−.025*	−.223	−.514	.058	−.273	−.520	.022	−.237	−.500	.060

#Out, number of data points identified as outliers; $_{LB}CI_{95\%}$ and $_{UB}CI_{95\%}$, lower and upper bound of the 95% bootstrap confidence interval, respectively; mMFG, middle part of the middle frontal gyrus; OG, orbital gyri; mpSFG, mid-posterior superior frontal gyrus; supPrCS, superior precentral sulcus; aITG, anterior inferior temporal gyrus; IFGop, inferior frontal gyrus, pars opercularis; sCirInS, superior segment of the circular sulcus of the insula.

* $p < .05$ at the nonparametric percentile bootstrap test (see the Inferential Statistics section).

inferior frontal sulci, the mid-posterior, middle, and mid-anterior parts of the SFG, and the opercular and triangular parts of the IFG. The results revealed that none of the regressors were significant predictors of either the switching or mixing costs. However, a closer inspection of the results revealed that in both the analyses there was a risk of overfitting and high multicollinearity that was likely due to the inclusion of the regressors for the inferior and superior frontal sulcus ROIs, which both had low tolerance values (.14 and .16, respectively). Therefore, we re-ran the two multiple regression analyses excluding these two regressors. The results showed that the β/α_HAS for the mMFG ROI was the only significant predictor of the participants' mixing costs ($\beta = −.380$, $t_{(47)} = −2.346$, $p = .023$) and the only marginally significant predictor of the participants' switching costs ($\beta = .300$, $t_{(47)} = 1.800$, $p = .078$), thus suggesting that the β/α_HAS in the mMFG ROI predicted the participants' task switching performance over and above the potential confounding contribution of the nearby PFC ROIs.

Differential correlations

Table 3 shows the results of the z-test comparing both the standard Pearson and the skipped Pearson correlation between the β/α_HAS for each ROI and either the general switching cost or the general mixing cost (see Inline Supplementary Fig. S4 for the corresponding cortical map). This analysis revealed five ROIs showing a differential correlation effect for both correlation indexes, namely the three PFC ROIs which already emerged in the previous analyses (i.e., the mMFG, mpSFG/pre-SMA, and OG ROIs), as well as the contiguous temporal ROIs pITG and aOS (Table 3). The analysis also revealed three ROIs for which contrasting results were found between the z-tests for the skipped and regular correlations. Indeed, the analysis revealed a differential correlation effect for the regular Pearson correlation, but not the skipped Pearson correlation, in the aTransTG ROI, as well as in the posterior inferior temporal sulcus (ITS) and the inferior frontal sulcus (IFS). As for the other results showing a discrepancy between the skipped and regular correlation analyses, we suggest caution in the interpretation of these results.

Inline Supplementary Fig. S4 can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.09.035.

Again, these results (in terms of the absolute value of the z for both the regular and skipped Pearson's correlation) did not depend on the size of the ROIs or on the differences in size between the left and right hemisphere (all $|r|s ≤ .130$, all $ps ≥ .265$). Similarly, we can exclude potential confounding effects on our results due to the β/α_HAS variability (SD) across participants (both $|r|s ≤ .080$, all $ps ≥ .497$) or the split-half reliability computed across participants (see the Spectral Power Analysis section; both $|r|s ≤ .163$, all $ps ≥ .162$).

Intersection analysis

We then refined our results by performing an intersection analysis. The specific purpose was to determine for which of the ROIs emerging from the correlation analyses the significant correlation between the β/α_HAS and one of the two general cognitive control abilities was also significantly different from the correlation with the other general cognitive control ability (see the Inferential Statistics section).

Among the above reported ROIs showing a significant power–behavior correlation, a first PFC ROI emerged from the intersection analysis as the one for which participants' β/α_HAS was significantly more strongly and selectively associated with their general mixing costs, namely the OG ROI (Fig. 6). Specifically, participants who showed higher β/α power in the right than left OG (i.e., with a more strongly right-lateralized β/α_HAS in this ROI) also had significantly smaller general mixing costs (Table 1), and this association was significantly stronger than the correlation revealed for the general switching costs (Table 3), which were not significantly associated with individual differences in β/α_HAS in these ROIs (Table 2). Moreover, a further frontal ROI, the mpSFG/pre-SMA, showed a significantly bivalent differential power–behavior correlation effect (Table 3, Fig. 6). In fact, the analysis revealed that a higher β/α power in the right than left mpSFG/pre-SMA was associated with smaller general mixing costs (Table 1), while a higher β/α power in the left than right mpSFG/pre-SMA was

Table 2
Results of the power–behavior correlation analyses for the general switching costs.

| ROI | #Out | Pearson's correlation | | | | | | Spearman's correlation | | | | | |
| | | Skipped | | | Regular | | | Skipped | | | Regular | | |
		r	$_{LB}CI_{95\%}$	$_{UB}CI_{95\%}$	r	$_{LB}CI_{95\%}$	$_{UB}CI_{95\%}$	r	$_{LB}CI_{95\%}$	$_{UB}CI_{95\%}$	r	$_{LB}CI_{95\%}$	$_{UB}CI_{95\%}$
mMFG	1	.341	.114	.544*	.309	.094	.520*	.349	.107	.565*	.341	.099	.558*
mpSFG	1	.246	.006	.459*	.232	.017	.421*	.244	.004	.461*	.244	.006	.450*
pITG	2	−.461	−.634	−.269*	−.251	−.542	.055	−.443	−.638	−.197*	−.313	−.558	−.024*
aOS	3	−.345	−.551	−.128*	−.189	−.523	.120	−.364	−.579	−.093*	−.280	−.538	.014
aTransTG	1	−.208	−.429	.032	−.259	−.463	−.026*	−.224	−.477	.047	−.262	−.488	.016

#Out, number of data points identified as outliers; $_{LB}CI_{95\%}$ and $_{UB}CI_{95\%}$, lower and upper bound of the 95% bootstrap confidence interval, respectively; mMFG, middle part of the middle frontal gyrus; mpSFG, mid-posterior superior frontal gyrus; pITG, posterior inferior temporal gyrus; aOS, anterior occipital sulcus; aTransTG, anterior transverse temporal gyrus.

* $p < .05$ at the nonparametric percentile bootstrap test (see the Inferential Statistics section).

Table 3
Results of the differential correlation and intersection analyses.

ROI	Skipped correlation		Regular correlation	
	z	p	z	p
mMFG[a]	−3.538	.0004*	−3.352	.0008*
mpSFG[b]	−2.526	.0115*	−2.344	.0191*
OG[b]	−2.273	.0230*	−2.273	.0230*
pITG	3.658	.0003*	2.403	.0163*
aOS	2.859	.0043*	1.994	.0461*
IFS	1.311	.1898	2.312	.0208*
ITS	1.845	.0651	2.177	.0294*
aTransTG	.930	.3522	2.140	.0324*

mMFG, middle part of the middle frontal gyrus; mpSFG, mid-posterior superior frontal gyrus; OG, orbital gyri; pITG, posterior inferior temporal gyrus; aOS, anterior occipital sulcus; IFS, inferior frontal sulcus; ITS, inferior temporal sulcus; aTransTG, anterior transverse temporal gyrus.

[a] Significant at the intersection analysis, FDR-corrected.
[b] Significant at the intersection analysis, uncorrected.
* $p < .05$.

associated with smaller general switching costs (Table 2). In other words, participants with a strongly right-lateralized brain activity at rest in the mpSFG/pre-SMA were more able to exert a sustained cognitive control and had a better management of competition between different task sets, whereas participants with a strongly left-lateralized brain activity at rest in the same PFC region were more able to phasically exert cognitive control to rapidly switch between different tasks when subsequently asked to perform the task-switching paradigms.

However, the results for these two PFC ROIs were not strictly controlled for multiple comparisons (see the Inferential Statistics section) and they did not survive the FDR correction for both the skipped and regular correlation analysis, so we cannot absolutely exclude a potential inflation of the Type I error rate for these results. The only result that remained significant when performing the same intersection analysis while controlling for the inflation of Type I error risk due to multiple comparisons concerned, again, a PFC ROI. In fact, the FDR-corrected intersection analysis revealed that the mMFG showed a significant bivalent differential power–behavior correlation effect (Table 3, Fig. 6)

similar to that observed for the mpSFG/pre-SMA ROI, as the participants' β/α_HAS values were negatively correlated with the mixing costs (Table 1) and positively correlated with the switching costs (Table 2). This result was further confirmed by a quartile split analysis showing that participants' with a more strongly right-lateralized β/α power in the mMFG showed significantly smaller general mixing costs (−.125, $SD = .562$) as compared to participants' with a more strongly left-lateralized β/α power in the same PFC ROI (.411, $SD = .759$; $t_{(26)} = 2.123$, $p = .043$, $d = .833$) while, conversely, participants' with a more strongly left-lateralized β/α power in the mMFG showed significantly smaller general switching costs (−.373, $SD = .535$) as compared to participants' with a more strongly right-lateralized β/α power in the same PFC ROI (.461, $SD = .781$; $t_{(26)} = 3.298$, $p = .003$, $d = 1.294$). To sum up, participants with a strongly right-lateralized brain activity at rest in the mMFG had a better sustained cognitive control to resolve the competition between different task sets, whereas participants with a strongly left-lateralized brain activity at rest in the same PFC region were more able to phasically exert cognitive control to rapidly switch between different tasks.

Finally, to further assess the exclusivity of the β/α_HAS effects and, thus, provide stronger evidence for the functional specificity of the chosen rsEEG measure and the relevance of the observed effects, we also performed the same set of analyses on two other rsEEG asymmetry scores for which we did not predict a functional relevance to the phasic/sustained cognitive control processes, that is, the β/θ_HAS and γ/α_HAS. These measures were computed in the same way as for the β/α_HAS (see the Spectral Power Analysis section) as, respectively, the right-left difference in the ratio between relative power in beta and theta (θ, 4–7.5 Hz) bands, and that between relative power in gamma (γ, 24–45 Hz) and alpha frequency bands. Inline Supplementary Tables S2 and S3 show the results of the differential correlation analysis on the β/θ_HAS and γ/α_HAS measures, respectively. No single ROI survived the FDR correction for both the regular and skipped Pearson correlation for either the β/θ_HAS and γ/α_HAS measures. In the differential correlation analysis on the β/θ_HAS values, two frontal ROIs survived the FDR correction for the skipped Pearson correlation only, namely, the
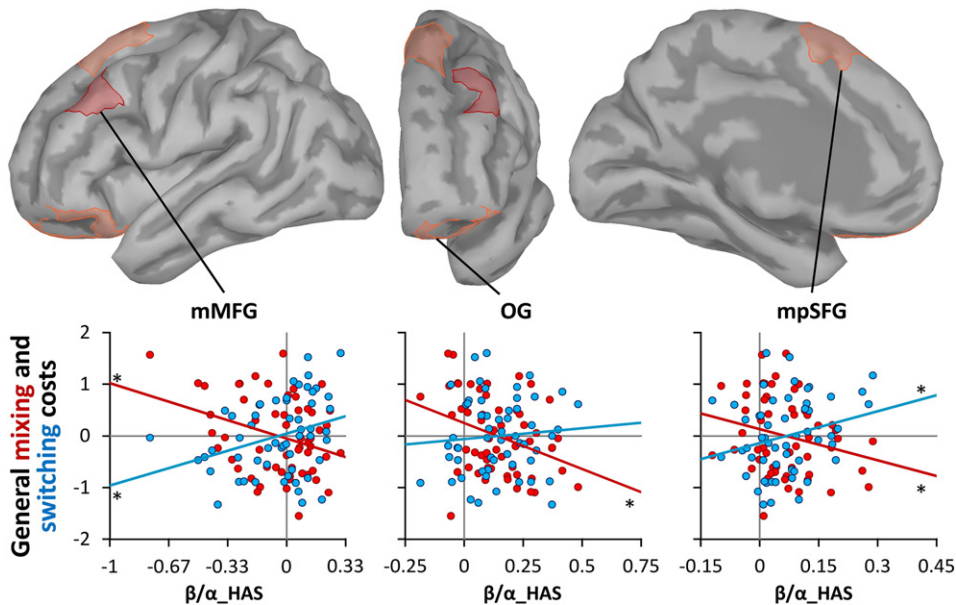

Fig. 6. Results of the intersection analysis. Upper row, partially inflated cortical surface of the left hemisphere showing the ROIs detected by the intersection analysis. ROIs that were significant at the uncorrected and FDR-corrected intersection analysis are presented in orange and red, respectively. The scatterplots in the lower row show the corresponding correlations between the participants' hemispheric asymmetry of rsEEG spectral activity (β/α_HAS, x-axis) and their general mixing and switching costs (y-axis) in red and light blue points, respectively. General mixing and switching costs are measured as the difference in the natural log-transformed RTs (see General Switching and Mixing Costs section and Figs. 2D and 2H). Positive values of β/α_HAS indicate a stronger right-lateralized brain activity at rest (see Spectral Power Analysis section). The red and light blue regression lines reflect the skipped Pearson correlation for the general mixing and switching costs, respectively. *Indicates significant correlations (see Tables 1 and 2 for the general mixing and switching costs, respectively).

inferior frontal gyrus, pars opercularis, and the short insular gyrus (Inline Supplementary Table S2). These results provide some further support for the functional specificity of the β/α_HAS effects we found but, again, we suggest caution in their interpretation as they show a discrepancy between the skipped and regular correlation analyses.

Inline Supplementary Tables S2 and S3 can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.09.035.

Discussion

In the present study, we aimed to test the hypothesis of a left–right prefrontal hemispheric specialization for executive functions mediating switching and mixing costs, respectively (Vallesi, 2012), as implied by the ROBBIA model of executive functions (Stuss, 2011; Stuss et al., 2005). Specifically, we investigated whether participants' hemispheric asymmetry in rsEEG spectral activity can reflect differences in their phasic and/or sustained cognitive control abilities regardless of the particular task specifics, and would therefore be predictive of their general switching and mixing costs. To this end, we recorded participants' resting-state electroencephalographic activity and performed a source-based spectral analysis to obtain a quantitative ROI-based measure of hemispheric asymmetries in intrinsic brain dynamics, that is, the difference in β/α power between the right and left hemispheres (β/α_HAS). Moreover, we asked participants to perform three different task-switching paradigms involving different cognitive domains and processing streams in order to obtain paradigm- and domain-general measures of their phasic and sustained cognitive control abilities in task-switching contexts.

Our principal finding was a significant bivalent association between the β/α_HAS at rest in a PFC ROI (mMFG) and both the switching and mixing costs, as revealed by the intersection analysis: Participants with stronger left-lateralized intrinsic brain activity in the mMFG were more able to phasically exert cognitive control to rapidly switch between different tasks, whereas participants with stronger right-lateralized intrinsic brain activity in the same PFC region were more able to exert sustained cognitive control to resolve the competition between different task sets.

This result suggests that the differential neurophysiological activity of the left/right PFC at rest may complexly mediate the dynamic interplay between phasic and sustained cognitive control abilities, which in turn regulate our behavior in response to changing task demands. This is in line with the recently proposed hypothesis (Stuss and Alexander, 2007; Vallesi, 2012), which posits that switching and mixing costs would depend on complementary executive functions dissociable both temporally and along the left–right axis in the PFC, that is, respectively, the phasic left-lateralized criterion-setting processes and the sustained right-lateralized monitoring processes.

The putative PFC area we found to show a bivalent power–behavior correlation is consistent with previous fMRI literature showing differential lateral PFC activation patterns induced by phasic and sustained cognitive control processes. Indeed, task-related activity in the left PFC has been associated with phasic cognitive control processes (Badre and Wagner, 2006; Braver et al., 2003; Wang et al., 2009) and a better ability to rapidly switch between different tasks (Kim et al., 2011; Ravizza and Carter, 2008), whereas task-related activity in the right/bilateral PFC has been associated with sustained cognitive control processes (Dreher et al., 2002; Wang et al., 2009) and a better ability to resolve the competition between different task sets (Braver et al., 2003).

But what is the relevance of prefrontal β/α_HAS at rest to the phasic/sustained cognitive control processes? Building on previous EEG-fMRI studies (Kilner et al., 2005; Laufs et al., 2003, 2006), we measured participants' rsEEG β/α_HAS to operationalize their brain dynamics at rest reflecting increased brain activity and attentional investment (see the Spectral Power Analysis section). Indeed, Laufs and colleagues showed that the spectral power in the alpha band recorded from prefrontal electrodes is negatively correlated with the BOLD signal in bilateral parieto-prefrontal circuits (Laufs et al., 2003) and that rsEEG sessions characterized by alpha desynchronization and greater relative beta power (i.e., with higher β/α) were related to BOLD signal increases in the same bilateral parietal and prefrontal cortices (Laufs et al., 2006). Therefore, high relative rsEEG β/α power in PFC would indicate a particular brain state characterized by the engagement of bilateral parieto-prefrontal cortical circuits in unspecific attention-demanding cognitive processes. Albeit these studies did not investigate potential hemispheric asymmetries, left and right parieto-frontal networks may be considered as distinct resting-state networks (Damoiseaux et al., 2006; Meyer et al., 2013) reflecting distinct lateralized, task-related networks (Smith et al., 2009). Moreover, recent resting-state fMRI studies showed that individual differences in fluctuation amplitude of the BOLD signal during rest are related to differences in both evoked BOLD activity in task-related cortical regions and behavioral performance in executive function tasks (Mennes et al., 2011; Xu et al., 2014; Zou et al., 2013).

Building on this corpus of evidence, our results of a significantly bivalent power–behavior correlation in mMFG suggest that the variability in participants' prefrontal rsEEG β/α_HAS would reflect stable individual differences in preferentially engaging either the left-lateralized, phasic or the right-lateralized, sustained cognitive control processes to regulate their behavior in response to changing task demands, regardless of the particular task specifics. Specifically, smaller general switching (mixing) costs observed in individuals with stronger left-lateralized (right-lateralized) PFC β/α at rest would be the consequence of displaying a specific brain state at rest characterized by greater activity in the left (right) parieto-prefrontal circuit supposedly involved in the phasic criterion-setting (sustained monitoring) processes (Vallesi, 2012), which would in turn facilitate the activation of the same cortical circuit during the execution of task-switching operations, leading to a better performance in exerting phasic (sustained) cognitive control.

Our proposal of a stable individual disposition toward a specific executive function mediated by intrinsic brain dynamics finds support in a recent study investigating the relationship between cognitive functions and individual differences in the rsEEG spectral profile (MacLean et al., 2012). In this study, participants with a better performance in an attention task showed more beta than alpha power (i.e., higher β/α) in two rsEEG sessions recorded two hours before/after the attention task, leading the authors to propose that individual differences in the rsEEG spectral profile could represent a stable, trait-like measure. Further support comes from studies showing that personality traits can modulate behavioral performance (Genet and Siemer, 2011) and even brain responsiveness (Avila et al., 2012) in switching tasks. Furthermore, it should be noted that in the Laufs and colleagues' study (2006) no systematic within- or between-sessions difference was found in the participants' characteristic rsEEG-fMRI pattern, especially for the parieto-prefrontal "attentional" pattern, showing the stability over time of this brain state.

In light of our proposed explanation, the long-term temporal stability of the β/α_HAS at rest is particularly crucial, especially because rsEEG and behavioral measure were collected in different days. Despite the fact that, to the best of our knowledge, the test–retest reliability of the specific rsEEG asymmetry measure we used has not yet been investigated (see the Limitations and Considerations section), substantial converging evidence suggests that this index could have good temporal stability. Indeed, previous research has shown that resting-state EEG spectral measures have a good long-term stability (i.e., for test–retest intervals ranging from one week to several months) (e.g., McEvoy et al., 2000; Salinsky et al., 1991; see also Van Albada et al., 2007). Moreover, most of the variance in the EEG spectral profile appears to be genetically determined (e.g., Christian et al., 1988; Lykken et al., 1974; see van Beijsterveldt and van Baal, 2002, for a review and meta-analysis). These findings, however, provide only indirect evidence for the temporal stability of more complex or derived rsEEG spectral measures such as the β/α_HAS at rest we used. One could thus argue that

they cannot provide support for the long-term temporal stability of our β/α_HAS measure. Nonetheless, good test–retest reliability has also been shown for more derived rsEEG measures such as the (delta and theta)/(alpha and beta) ratio (Salinsky et al., 1991) and the asymmetry in alpha and beta bands (Tomarken et al., 1992). Even more relevant for our claims, high test–retest reliability at 1–2 weeks has been shown for a complex and highly-derived rsEEG measure reflecting the actual compositions of brain oscillations and their percent ratio (Fingelkurts et al., 2006), which was claimed by the authors to "possess distinct trait-like qualities". A high test–retest reliability has also been shown for rsEEG measures for test–retest intervals of more than a year, with the best results obtained by taking the shape of the entire power spectra into account (Napflin et al., 2007). Moreover, a recent study (La Rocca et al., 2014) showed that a very high degree of intra-individual repeatability of rsEEG biometrics over 1–3 weeks can be achieved by considering rsEEG spectral measures combining different frequency bands in the .5–30 Hz. Taken together, these findings strongly suggest that complex, highly-derived rsEEG spectral measures may be treated as an intra-individually "stable trait" (Gasser et al., 1985) or even as a "statistical signature of a person" (Napflin et al., 2007) and they may even be used for automatic biometric-based individual recognition (Campisi and La Rocca, 2014), thus providing indirect support for the proposed role of prefrontal rsEEG β/α_HAS in reflecting stable individual disposition toward specific cognitive control processes.

Furthermore, the hypothesis of an intrinsic (electro)physiological basis mediating individual differences in executive functioning is consistent with diffusion tensor imaging studies showing that switching costs depend on the integrity of a parieto-frontal network of white matter regions (Kennedy and Raz, 2009; Seghete et al., 2013). Of particular interest for the present study, Gold et al. (2010) showed an association between task-switching performance and microstructural properties of the left superior longitudinal fasciculus ensuring the transmission of information between left parietal and prefrontal cortices, including the mMFG. Moreover, the gray matter volume in subcortical regions connected with the PFC has been shown to mediate both switching and mixing costs (Leunissen et al., 2014). These findings suggest that the functional power–behavior association we found could be mediated by underlying individual differences in brain structural organization.

The intersection analysis also revealed other results that are consistent with our main finding and hypothesis. Indeed, we found a significant selective association between the participants' general mixing costs and their β/α_HAS at rest in the OG, a PFC region involved in cognitive processes important to cognitive control over simultaneous task sets, such as learning and retaining visuomotor associations to guide conditional choices (Rushworth et al., 2005) and implementing behavioral strategies to optimize task performance (Bussey et al., 2001). Moreover, a bivalent differential power–behavior correlation (similar to that found for the mMFG) was found for the mpSFG/pre-SMA, an area known to be implicated in both phasic (Chiu and Yantis, 2009; Cole and Schneider, 2007; Dove et al., 2000; Rushworth et al., 2002) and sustained (Wang et al., 2009) cognitive control. However, these results did not survive the FDR correction. Thus, they do not allow us drawing firm conclusions about our main question and should be taken with caution.

Limitations and considerations

A first limitation of the present study is that the estimation of the rsEEG cortical sources was performed by using a source model derived from a standard brain template (the MNI Colin27) that, as for the other brain templates available in Brainstorm, was not bilaterally symmetrical. Control analyses suggested that our results were not influenced by either the size of the ROIs in the left or right hemisphere or by the difference in size between the left and right hemisphere (see the Correlation Analysis and Differential Correlations sections). However, we cannot rule out the possibility that lateral asymmetries in the

anatomy of the participants, which cannot be modeled in the brain template, could have influenced in some way our results. Therefore, future studies should address this issue by either using a symmetrical brain template or, better, by using individual structural MR images in the source reconstruction to fully account for individual differences in anatomical hemispheric asymmetries.

Our proposal that a participant's lateralized prefrontal rsEEG spectral profile would bias which of the two cognitive control processes he/she would preferentially employ during task-switching – thus modulating his/her task-switching performance – has a logical implication, that is, lateralized β/α power at rest should be related to the BOLD activity in the corresponding lateralized parieto-prefrontal circuit during task-switching execution. However, we only recorded participants' electrophysiological activity at rest and, to the best of our knowledge, no study has yet investigated the relationship between resting-state EEG-fMRI correlation, EEG-fMRI measures of task-related brain activity, and behavioral performance in task-switching paradigms. Therefore, our account may be deemed as somewhat speculative, albeit it represents a testable hypothesis. It would thus be interesting to conduct further studies to directly verify this hypothesis by simultaneously recording EEG and fMRI at rest and fMRI during the execution of task-switching paradigms.

It should also be noted that, despite some promising findings supporting our use of the β/α power as a measure of cortical activity at rest in a given brain region (e.g., Kilner et al., 2005; Laufs et al., 2006), to fully establish what this measure means in terms of neural activity requires further investigation. Moreover, the β/α_HAS measure we used to assess hemispheric asymmetries in intrinsic brain dynamics is a highly derived measure, being the difference (right–left hemisphere) of a ratio (β/α) of relative spectral power estimated by a source space analysis, and the relationship between this measure and underlying cognitive processes is complex, even if we accept the β/α ratio as a reliable measure of cortical activity. Finally, even if there are reasons to believe that the rsEEG β/α_HAS we used may be considered a stable measure over time (see Discussion), as we noted above, no previous study has investigated the long-term temporal stability of this specific rsEEG measure.

These considerations add to the degree of novelty of our results and analytical approach in highlighting the need of further investigations to directly assess the long-term stability of our rsEEG spectral measure and to replicate the present results to further unravel how individual differences in executive control are influenced by hemispheric asymmetries in intrinsic brain dynamics.

Conclusions

The present study provides support for the hypothesis of a left–right prefrontal hemispheric specialization for executive functions mediating switching and mixing costs, respectively (Vallesi, 2012), above and beyond the specific task requirements. We propose that the variability in participants' prefrontal hemispheric asymmetry in the intrinsic EEG spectral profile at rest would reflect individual differences in preferentially engaging either the left-lateralized, phasic criterion-setting processes or the right-lateralized, sustained monitoring processes to regulate their behavior in response to changing task demands, regardless of both the cognitive domain involved and the particular task specifics.

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