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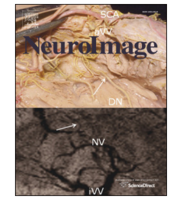

Asymmetry in prefrontal resting-state EEG spectral power underlies individual differences in phasic and sustained cognitive control

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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.

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 (see also Braver et al., 2003; Wang et al., 2009). However, despite accumulating evidence supporting the proposed function-based prefrontal hemispheric asymmetry (see also 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

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