

# The Shape of the ACC Contributes to Cognitive Control Efficiency in Preschoolers

Arnaud Cachia<sup>1,2\*</sup>, Grégoire Borst<sup>1,2\*</sup>, Julie Vidal<sup>1,2</sup>, Clara Fischer<sup>3</sup>,  
Arlette Pineau<sup>4</sup>, Jean-François Mangin<sup>3</sup>, and Olivier Houde<sup>1,2,5</sup>

## Abstract

■ Cognitive success at school and later in life is supported by executive functions including cognitive control (CC). The pFC plays a major role in CC, particularly the dorsal part of ACC or midcingulate cortex. Genes, environment (including school curricula), and neuroplasticity affect CC. However, no study to date has investigated whether ACC sulcal pattern, a stable brain feature primarily determined in utero, influences CC efficiency in the early stages of cognitive and neural development. Using anatomical MRI and three-dimensional reconstruction of cortical folds, we investigated the effect that ACC sulcal pattern may have on the Stroop score, a classical behavioral index of CC efficiency, in 5-year-old preschoolers. We found higher CC efficiency, that is,

lower Stroop interference scores for both RTs and error rates, in children with asymmetrical ACC sulcal pattern (i.e., different pattern in each hemisphere) compared with children with symmetrical pattern (i.e., same pattern in both hemispheres). Critically, ACC sulcal pattern had no effect on performance in the forward and backward digit span tasks suggesting that ACC sulcal pattern contributes to the executive ability to resolve conflicts but not to the ability to maintain and manipulate information in working memory. This finding provides the first evidence that preschoolers' CC efficiency is likely associated with ACC sulcal pattern, thereby suggesting that the brain shape could result in early constraints on human executive ability. ■

## INTRODUCTION

Cognitive control (CC) including inhibitory control—that is, the ability to overcome conflicts and inhibit a dominant response—is one of the core executive functions that enable us to resist habits or automatisms, temptations, distractions, or interference and allow us to adapt to complex situations by means of mental flexibility, namely, dynamic inhibition/activation of competing cognitive strategies (Diamond, 2013). The Stroop Color–Word task (Stroop, 1935) is a seminal task designed to assess the ability to process conflicting information, drawing, in part, on CC. In the classical Stroop Color–Word task, participants are instructed to name the color of the ink of printed words that denote colors. In the no-conflict condition, the ink colors match the colors denoted by the words (e.g., “RED” appears in red ink), whereas in the conflict condition, the colors denoted by the words interfere with the ink colors to be named (e.g., “RED” appears in blue ink). The conflict condition, in contrast to the no-

conflict condition, typically results in increased RTs and error rates (ERs) because of the need to inhibit irrelevant stimulus feature (i.e., the color denoted by the word) to focus on an alternative feature of the stimulus (i.e., the ink color). The Stroop interference score reflect the ability of CC to overcome perceptual and cognitive conflicts through the inhibition of a dominant response, namely reading when verbal material is presented (MacLeod, 1991). However, the Stroop Color–Word task involves other cognitive processes, such as selective attention, conflict monitoring, perceptual, semantic interference, response interference, and working memory (MacLeod, Dodd, Sheard, Wilson, & Bibi, 2003). Functional brain-imaging studies (Roberts & Hall, 2008; Matthews, Paulus, Simmons, Nelesen, & Dimsdale, 2004; Bush, Luu, & Posner, 2000; Casey et al., 2000; Pardo, Pardo, Janer, & Raichle, 1990) have demonstrated that the medial pFC and more precisely the dorsal ACC, also referred to as the midcingulate cortex (Vogt, 2009), is consistently activated in Stroop tasks (Petersen & Posner, 2012) and other tasks that involve overriding prepotent responses, selecting responses in underdetermined contexts, or errors (Petersen & Posner, 2012). According to the conflict-monitoring hypothesis (Botvinick, 2007; Botvinick, Braver, Barch, Carter, & Cohen, 2001), one of the core functions of the dorsal ACC is to signal conflict in information processing to the CC system supported through dorsolateral prefrontal cortices. To resolve this conflict, the CC system increases

<sup>1</sup>CNRS U3521, Laboratory for the Psychology of Child Development and Education, Sorbonne, Paris, France, <sup>2</sup>Université Paris Descartes, Paris, France, <sup>3</sup>Computer-Assisted Neuroimaging Laboratory, Neurospin, I2BM, CEA, Gif/Yvette, France, <sup>4</sup>Université Caen Basse Normandie, Caen, France, <sup>5</sup>Institut Universitaire de France, Paris, France

\*These authors contributed equally to this work.

the activation of task-relevant information and inhibits task-irrelevant information (see Egner & Hirsch, 2005).

From a developmental psychology perspective, executive functions including CC are known to support qualities such as self-control, creativity, and reasoning that children require to be successful in school and later in life (Diamond, 2013). Executive function efficiency is a better predictor of school readiness and future academic success than intelligence quotient (Blair & Razza, 2007; Duckworth & Seligman, 2005). Given the critical role that executive functions play in academic achievement, numerous studies have focused on how to improve executive function efficiency. Diverse activities seem to increase executive function efficiency (Diamond & Lee, 2011), including school curricula (Diamond, Barnett, Thomas, & Munro, 2007), attention training (Rueda, Rothbart, McCandliss, Saccomanno, & Posner, 2005), computerized training (Holmes, Gathercole, & Dunning, 2009), noncomputerized games (Mackey, Hill, Stone, & Bunge, 2011), aerobics (Hillman, Erickson, & Kramer, 2008), martial arts (Lakes & Hoyt, 2004), yoga, and mindfulness (Flook et al., 2010). For instance, *Tools of the Mind*—a school curriculum for preschool kindergarten that emphasizes imaginary play—improves executive functions to a larger extent than high-quality school curricula based on literacy and thematic units (Diamond et al., 2007).

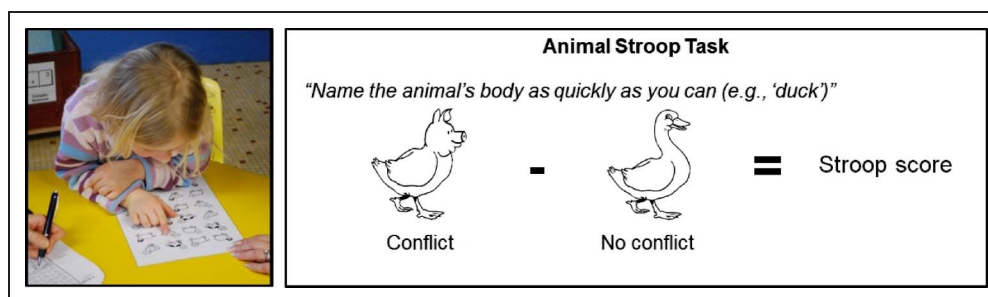
From a neuroscience perspective, studies have demonstrated that prolonged learning and specific trainings—leading to the improvement of cognitive efficiency—can modify the structure (e.g., gray matter volume, cortical thickness) of brain areas functionally related to the processes trained (Hyde et al., 2009; Draganski et al., 2004, 2006). For example, adults who learned to juggle over a 3-month period present an increase of the gray matter volume in the visual motion area. The increase of the gray matter volume reveals one of the neuroplasticity mechanisms mediating the improvement of cognitive ability following intense training (Draganski et al., 2004). This is not limited to the motor domain; studies have demonstrated variation of the structure of the brain in response to intense learning for medical examinations (Draganski et al., 2006) and in response to 15 months of musical training in early childhood—with a correlation between the structural brain changes induced by training and behavioral improvements (Hyde et al., 2009). Although there is no study to date that has investigated the structural change in ACC in response to CC training, previous studies have provided evidence that interindividual differences in adults' CC efficiency are associated with differences in the structure of ACC, that is, the local cortical thickness (Westlye, Grydeland, Walhovd, & Fjell, 2011) or the local gray matter volume (Takeuchi et al., 2012) of ACC.

Early determined anatomical features of ACC also contribute to interindividual differences in adults' CC efficiency. The sulcal pattern constitutes one of these early anatomical factors (Welker, 1988). This pattern is determined in utero by genetic and environmental factors (Barkovich,

Guerrini, Kuzniecky, Jackson, & Dobyns, 2012; Rakic, 2004; Molko et al., 2003; Dehay, Giroud, Berland, Killackey, & Kennedy, 1996). As opposed to quantitative measures of the cortex morphology, such as the Gyrfication Index (Zilles, Palomero-Gallagher, & Amunts, 2013; White, Su, Schmidt, Kao, & Sapiro, 2010; Armstrong, Schleicher, Omran, Curtis, & Zilles, 1995) or cortex structure, such as the thickness, surface, and volume (Giedd et al., 2009; Gogtay et al., 2004), that vary from childhood through early adulthood, the sulcal pattern, a qualitative measure of the cortex morphology, is a stable feature of the brain anatomy apparently less affected by brain maturation, training, and learning occurring after birth (Sun et al., 2012). Two types of ACC sulcal pattern (Ono, Kubik, & Abarnathey, 1990) are defined between 10 and 15 weeks of fetal life (White et al., 2010): the “single” type, with only the cingulate sulcus, and the “double parallel” type, with an additional paracingulate sulcus (PCS; Paus et al., 1996). Recent functional data indicate that participants without a PCS do not lack a particular cortical area, that is, “single” and “double parallel” ACC types are homologous cortical regions (Amiez et al., 2013). The “double parallel” is observed in 30–60% of individuals, and this ACC type is more frequent in the left hemisphere (Yucel et al., 2001). In adults, asymmetry in the sulcal pattern of ACC (i.e., the “single” type in the left hemisphere and the “double parallel” type in the right hemisphere or vice versa) is associated with increased CC efficiency (Huster, Westerhausen, & Herrmann, 2011; Fornito et al., 2004) and the increased efficiency to manage cognitive conflicts and inhibit dominant responses as measured by the performance in a Stroop Color–Word task at the behavioral and electrophysiological level (Huster, Enriquez-Geppert, Pantev, & Bruchmann, 2012; Huster et al., 2009). However, no study to date has investigated whether the sulcal pattern of ACC already affects CC efficiency in the early stages of cognitive and neural development.

In our study, using anatomical MRI, we investigated whether an early neurodevelopmental constraint—that is, the sulcal pattern of ACC—contributes to preschoolers' CC efficiency as measured by their performance on the “Animal Stroop task” (Wright, Waterman, Prescott, & Murdoch-Eaton, 2003)—an adaptation of the Stroop Color–Word task for young nonreading children. In the “Animal Stroop task” (Figure 1), children are required to name an animal's body in a no-conflict condition—that is, the head and the animal's body are matched (e.g., a duck's head on a duck's body)—and in a conflict condition—that is, the head of the animal is replaced by the head of a different animal (e.g., a pig's head on a duck's body). As in the classical Stroop Color–Word task, CC efficiency is reflected by the difference in RTs (or ERs) between the conflict and the no-conflict conditions. If the sulcal pattern of ACC contributes to preschoolers' CC efficiency, we expect lower Stroop interference scores (i.e., better CC efficiency) for children with asymmetric (i.e., the “single” type in the left hemisphere and

**Figure 1.** Assessment of CC efficiency using the “Animal Stroop task.” (Left) A child performing the “Animal Stroop task” in the classroom. (Right) Example of “conflict” and “no-conflict” stimuli used in the “Animal Stroop task” to assess the CC efficiency of preschoolers.



the “double parallel” type in the right hemisphere or vice versa) rather than symmetric (i.e., the “single” type or “double parallel” type in both hemispheres) sulcal pattern of ACC (Figure 2).

In addition, to assess the specificity of the effect of ACC sulcal pattern on the CC efficiency of preschoolers, the same group of children performed both forward and backward digit span tasks from the Wechsler Intelligence Scale for Children (WISC-IV; see Wechsler, 2003). We reasoned that if ACC sulcal pattern contributes specifically to the CC efficiency and not to the efficiency of other executive functions, such as verbal working memory, then ACC sulcal pattern should have no effect on the performance in the two-digit span tasks, even on the backward digit span task, which requires more executive

load (Gathercole, Pickering, Ambridge, & Wearing, 2004; Baddeley, 2003).

## METHODS

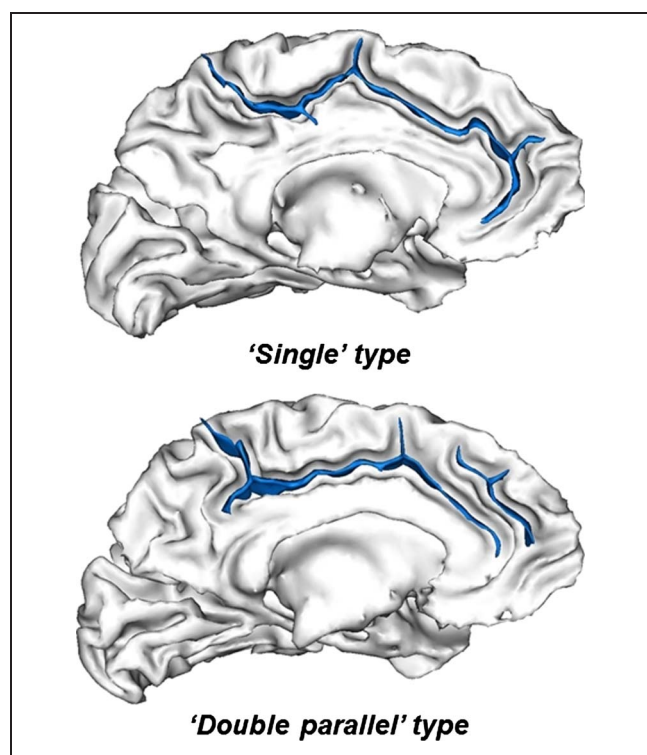
### Participants

Nineteen 5-year-old right-handed preschoolers (mean  $\pm$  standard deviation age:  $5.47 \pm 0.18$  years; 11 girls) were recruited from a public preschool in Caen (France). They had no history of neurological disease and no cerebral abnormalities. The children were tested in accordance with national and international norms that govern the use of human research participants. We obtained written informed consent from the children’s parents that allowed us to enroll their children in the study. The ethics committee approved our study (CPP Nord-Ouest III, France).

### Behavioral Assessment

The preschoolers’ CC efficiency was assessed using the “Animal Stroop task,” an adaptation of the Stroop Color–Word task for preschoolers (Wright et al., 2003). Each preschooler performed two experimental conditions—each comprised 24 Animal Stroop stimuli printed on a sheet of paper. The stimuli were designed and based on four images of animals: a cow, a duck, a pig, and a sheep. In both conditions, the children were asked to name the animal’s body. In the conflict condition, the head of the animal was substituted with the head of another animal. In the no-conflict condition, the head and the animal’s body were matched (Figure 1). All preschoolers named each of the 24 animal bodies under the no-conflict condition before naming the 24 animal bodies under the conflict condition. RTs and ERs were recorded separately for the conflict and the no-conflict conditions. The Stroop interference score was defined as the differences in RTs or ERs between the two experimental conditions. The higher Stroop interference scores reflected lower CC efficiency in these children.

The verbal working memory efficiency was assessed using the forward and backward digit span tasks from the WISC-IV (Wechsler, 2003). In these two working memory tasks, the children listened to a series of discrete digits and subsequently recalled the series of digits in the same



**Figure 2.** Morphological patterns of ACC. The two ACC sulcal patterns: “single” type, with only the cingulate sulcus, and “double parallel” type, with an additional PCS. ACC sulci (blue) are represented on the cortical surface (gray/white interface).

(i.e., forward digit span task) or reverse (i.e., backward digit span task) order of presentation. In each task, the children first performed two series of two digits. The series of digits were subsequently increased by one digit every two trials. The task was terminated when a child failed to recall two consecutive series with the same number of digits. The working memory span (or score) was defined as the number of correctly recalled digits in the last series. The forward and backward digit span tasks were used to assess the ability to maintain (i.e., forward digit span task) or maintain and manipulate information (i.e., backward digit span task), respectively, in verbal working memory.

In addition, children performed a battery of nonexecutive tasks: three Piagetian logic/mathematical tasks (i.e., the number conservation task, the substance conservation task, and the class inclusion task), a numerical task (i.e., the number estimation line task), and a visual task (i.e., Navon's local-global task). Therefore, children's performance on these tasks were not analyzed in this study.

### MRI Acquisition

We acquired anatomical MRI from the Cyceron biomedical imaging platform (Caen, France, [www.cyceron.fr](http://www.cyceron.fr)) on a 3T MRI scanner (Achieva, Philips Medical System, The Netherlands), using 3-D T1-weighted spoiled gradient images (field of view = 256 mm, slice thickness = 1.33 mm, 128 slices, matrix size = 192 × 192 voxels). To reduce motion, provide a positive experience, and decrease wait times, we obtained MRIs as the children passively watched a cartoon on an MRI-compatible screen (Lemaire, Moran, & Swan, 2009).

### MRI Analysis

An automated preprocessing step skull-stripped T1 MRIs and segmented the brain tissues. No spatial normalization was applied to MRIs to overcome potential bias that may result from the sulcus shape deformations induced by the warping process. The cortical folds were automatically segmented throughout the cortex from the skeleton of the gray matter/cerebrospinal fluid mask, with the cortical folds corresponding to the crevasse bottoms of the "landscape," the altitude of which is defined by its intensity on the MRIs. This definition provides a stable and robust sulcal surface definition that is not affected by variations in cortical thickness or gray matter/white matter contrast (Mangin et al., 2004). For each participant, images at each processing step were visually checked. No segmentation error was detected. Image analysis was performed with the Morphologist toolbox using BrainVISA 4.2 software ([brainvisa.info](http://brainvisa.info)).

### ACC Classification

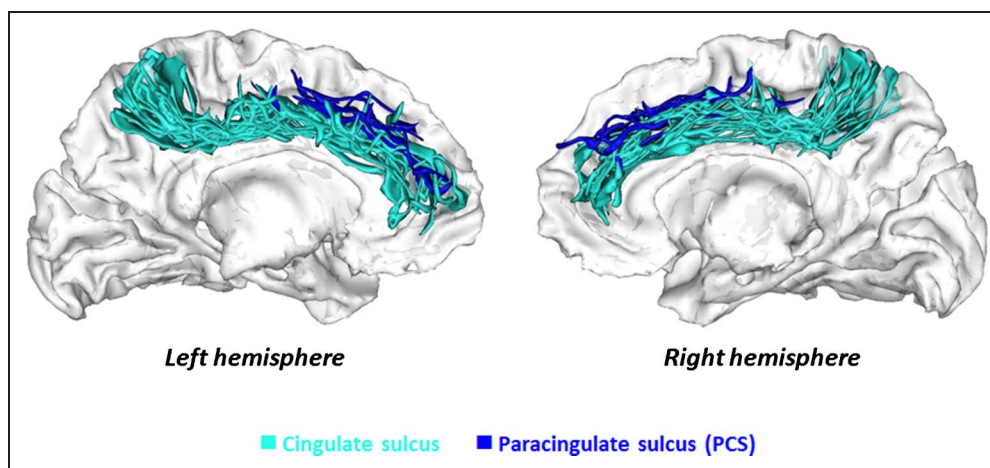
The sulcal pattern of ACC was visually assessed using 3-D, mesh-based reconstruction of cortical folds to measure

the occurrence and extent of local sulci (e.g., Leonard, Towler, Welcome, & Chiarello, 2009; Huster, Westerhausen, Kreuder, Schweiger, & Wittling, 2007; Fornito et al., 2004; Yucel et al., 2001). ACC sulcal pattern was classified as "single" or "double parallel" type (Ono et al., 1990) based on the presence or absence of a PCS (Figure 2). This 3-D approach was used to overcome methodological issues inherent to the analysis of the sulcal pattern of ACC from the two-dimensional sagittal slices. The PCS was defined as the sulcus located dorsal to the cingulate sulcus with a course clearly parallel to the cingulate sulcus (Yucel et al., 2001; Paus et al., 1996). To reduce the ambiguity from the confluence of the PCS and the cingulate sulcus with the superior rostral sulcus (Paus et al., 1996), we determined the anterior limit of the PCS as the point at which the sulcus extends posteriorly from an imaginary vertical line running perpendicular to the line passing through the anterior and posterior commissures (AC-PC) and parallel to the anterior commissure (Huster et al., 2007; Yucel et al., 2001). The PCS was considered absent if there were no clearly developed horizontal sulcus elements parallel to the cingulate sulcus and extending at least 20 mm (interruptions or gaps in the PCS course was not taken into account for the length measure). The finer distinction between "present" and "prominent" PCS (Yucel et al., 2001; Paus et al., 1996), leading to three ACC sulcal pattern types, was not used here because this distinction is based on the PCS length of adult brains—that is, greater than 20 mm according to Paus's classification (Paus et al., 1996) or greater than 40 mm according to Yucel's classification (Yucel et al., 2001) for a prominent PCS (Leonard et al., 2009). Furthermore, the classification of ACC morphology into five categories by grouping the individual measurements of PCS in 15-mm steps was also proposed (Huster et al., 2007). However, the present/prominent or five categories of ACC sulcal pattern cannot be applied to characterize ACC sulcal pattern of developing brains, as brain size and PCS length increase with age. Notably, the binary classification of ACC sulcal pattern ("single"/"double parallel" type) used in our study was previously used in a study on schizophrenia (Fornito, Yucel, et al., 2006).

### Statistical Analysis

We conducted separately 2 (ACC Sulcal Pattern, i.e., "symmetric" vs. "asymmetric") × 2 (Stroop Condition, i.e., "conflict" vs. "no-conflict") mixed-design ANOVAs on the RTs and ERs of the Stroop task. In addition, we ran a 2 (ACC Sulcal Pattern, i.e., "symmetric" vs. "asymmetric") × 2 (Working Memory Task, i.e., "forward" vs. "backward") mixed-design ANOVA on the scores in the forward and backward digit span tasks. When we compared two means, we computed two-tailed *t* tests or Welch's *t* tests in cases of unequal variances. For each analysis, we reported the effect size either in the ANOVA

**Figure 3.** Interindividual variability of ACC sulcal pattern. Superimposition of the 3-D mesh-based reconstructions of the cingulate sulcus (turquoise) and PCS (blue) for all children included in the study. Sulci were represented on the cortical surface (gray/white interface). The reconstructions of the sulci of each child were linearly aligned in a common referential (MNI space) for visualization purpose.



(partial  $\eta^2$ ) or in terms of the difference of the means (Cohen's  $d$ ).

## RESULTS

Participants were divided into two groups based on the asymmetry of the sulcal pattern of ACC: 11 children with symmetrical ACC sulcal pattern—"single" ( $n = 9$ ) or "double parallel" ( $n = 2$ ) type in both hemispheres—and 8 children with asymmetrical ACC sulcal pattern—"single" type in the left hemisphere and "double parallel" type in the right hemisphere ( $n = 4$ ) or vice versa ( $n = 4$ ; see Figure 3 for the interindividual variability of ACC sulcal pattern). These groups were matched for age, sex, household income as a proxy indicator for socioeconomic status, scores on the Edinburgh Handedness Inventory (Oldfield, 1971), and raw scores on the colored progressive matrices of Raven as a proxy indicator for general intelligence (Raven, Raven, & Court, 1976; see Table 1).

The two-way mixed-design ANOVA in the RTs demonstrated that, irrespective of ACC sulcal pattern, children needed more time to name the animals' bodies in the conflict ( $65.1 \pm 28.3$  sec) than in the no-conflict ( $37.5 \pm 10.5$  sec) conditions,  $F(1, 17) = 32.57, p < .0001, \eta_p^2 = .66$ , revealing a classical Stroop-like interference effect on the RTs. Furthermore, we found no main effect of ACC Sulcal Pattern—that is, RTs averaged over the Stroop conditions did not differ between children with symmetric ACC and children with asymmetric ACC,  $F(1, 17) = 1.67,$

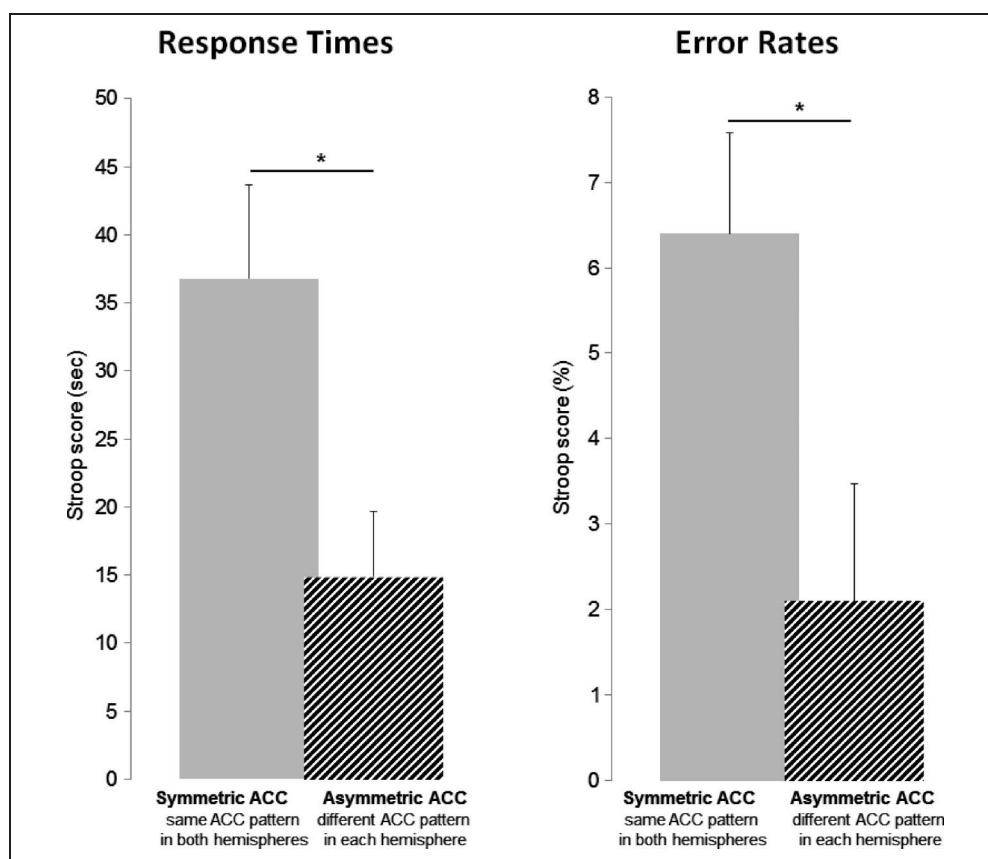
$p = .26$ . Finally, the difference in RTs between the conflict and the no-conflict conditions was greater for children with symmetric ACC sulcal pattern ( $74.2 \pm 31.8$  sec vs.  $37.3 \pm 10.8$  sec) than for children with asymmetric ACC sulcal pattern ( $52.5 \pm 17.6$  sec vs.  $37.7 \pm 10.8$  sec) as witnessed by a significant two-way interaction,  $F(1, 17) = 5.87, p < .025, \eta_p^2 = .26$ . Critically, the Stroop interference scores (i.e., RT difference between the conflict and no-conflict conditions) were lower; thus, CC efficiency was higher in children with asymmetrical ACC ( $14.9 \pm 13.2$  sec) than in children with symmetrical ACC ( $36.8 \pm 22.9$  sec), Welch- $t(16.32) = 2.64, p < .025, d = 1.17$  (Figure 4). ACC asymmetry explained 21% of Stroop interference score variability based on RTs. Finally, we note that children in the two groups required the same amount of time to name the animal body in the no-conflict condition ( $37.3$  sec vs.  $37.7$  sec),  $t(17) = .06, p = .95$  (see Table 2).

A two-way mixed-design ANOVA on the ERs demonstrated a similar pattern of results. Children had more errors in the conflict ( $8.1 \pm 4.7\%$ ) than in the no-conflict conditions ( $3.5 \pm 3.7\%$ ),  $F(1, 17) = 22.37, p < .0001, \eta_p^2 = .57$ ; the sulcal pattern of ACC had no main effect on the ERs,  $F < 1$ . Finally, similar to the findings for the RTs, the difference in ERs between the conflict and the no-conflict conditions was greater for children with symmetric ACC sulcal pattern ( $8.7 \pm 4.4\%$  vs.  $2.3 \pm 3.9\%$ ) than for children with asymmetric ACC sulcal pattern ( $7.3 \pm 5.3\%$  vs.  $5.2 \pm 2.9\%$ ), as demonstrated by a significant two-way interaction,  $F(1, 17) = 5.84, p < .025, \eta_p^2 = .26$ .

**Table 1.** Demographic Characteristics of the Sample of Preschoolers ( $n = 19$ )

|                             | Sym. $n = 11$ | Asym. $n = 8$ | Welch- $t/\chi^2$ | $p$ |
|-----------------------------|---------------|---------------|-------------------|-----|
| Age (years)                 | 5.48 (0.2)    | 5.47 (0.15)   | $t = 0.10$        | .91 |
| Sex (female/male)           | 5/6           | 5/3           | $\chi^2 = 0.12$   | .73 |
| Household (low/high income) | 5/6           | 6/2           | $\chi^2 = 1.66$   | .19 |
| Handedness (Oldfield score) | 91.9 (26.8)   | 94.4 (15.7)   | $t = .025$        | .80 |
| Raven (raw score)           | 27.9 (3.2)    | 29.3 (1.1)    | $t = .087$        | .40 |

**Figure 4.** Asymmetry of ACC and cognitive control efficiency in preschoolers ( $n = 19$ ). Average Stroop interference scores (RTs and ERs) in preschoolers with symmetrical ACC (“single” type or “double parallel” type in both hemispheres; light gray;  $n = 11$ ) or asymmetrical ACC (“single” type in the left hemisphere and “double parallel” type in the right hemisphere or vice versa; hashed;  $n = 8$ ). Error bars denote *SEM*.



Consistent with the results reported on the RTs, the Stroop interference scores computed on the ERs were lower in children with asymmetrical ACC sulcal pattern ( $2.1 \pm 3.9\%$ ) than in children with symmetrical ACC sulcal pattern ( $6.4 \pm 3.9\%$ ), Welch- $t(15.32) = 2.42, p < .05, d = 1.1$ . As for the RTs, 21% of the variance of the Stroop interference score computed on the ERs is explained by the sulcal pat-

**Table 2.** Mean (*M*) and Standard Deviation (*SD*) of the RTs and ERs in the Stroop Color Word Task for Children with Symmetrical (Sym.) and Asymmetrical (Asym.) Sulcal Pattern of ACC

|                  | Sym.     |           | Asym.    |           |
|------------------|----------|-----------|----------|-----------|
|                  | <i>M</i> | <i>SD</i> | <i>M</i> | <i>SD</i> |
| <i>RTs (sec)</i> |          |           |          |           |
| No conflict      | 37.3     | 10.8      | 37.6     | 10.7      |
| Conflict         | 74.2     | 31.8      | 52.5     | 17.6      |
| Stroop score     | 36.8     | 22.9      | 14.9     | 13.4      |
| <i>ERs (%)</i>   |          |           |          |           |
| No conflict      | 2.3      | 3.9       | 5.2      | 2.9       |
| Conflict         | 8.7      | 4.4       | 7.3      | 5.3       |
| Stroop score     | 6.4      | 3.9       | 2.1      | 3.9       |

tern of ACC. As for the RTs, children with asymmetrical ( $5.2 \pm 2.9\%$ ) and symmetrical ( $2.3 \pm 3.9\%$ ) sulcal pattern of ACC committed approximately the same number of errors in the no-conflict condition,  $t(17) = 1.79, p = .09$ .

A 2 (ACC Sulcal Pattern, i.e., symmetric vs. asymmetric)  $\times$  2 (Working Memory Task, i.e., forward vs. backward) mixed-design ANOVA revealed that irrespective of ACC sulcal pattern, the scores in the backward digit span tasks were smaller ( $M = 2.32 \pm .58$ ) than those obtained in the forward ( $M = 3.79 \pm .92$ ) digit span tasks,  $F(1, 17) = 30.85, p < .0001, \eta_p^2 = .65$ . There was no main effect of ACC Sulcal Pattern on the scores averaged over the two conditions,  $F < 1$ . Critically, the differences between the forward and backward scores were similar for children with symmetric ( $4.09 \pm 1.04$  vs.  $2.18 \pm .41$ ) and asymmetric ( $3.38 \pm .52$  vs.  $2.5 \pm .76$ ) ACC patterns, as the lack of significant two-way interactions suggests,  $F(1, 17) = 4.26, p = .06$ . Moreover, planned comparisons revealed that the scores did not differ between the children with symmetric and asymmetric ACC sulcal patterns in the forward,  $t(17) = 1.77, p = .09$ , and backward,  $t(17) = 1.19, p = .25$ , digit span tasks.

## DISCUSSION

As expected, children with an asymmetrical sulcal pattern of ACC are less sensitive to the interference in a

Stroop-like task than children with a symmetrical sulcal pattern of ACC. Thus, preschoolers' CC efficiency including inhibitory control—that is, the ability to overcome a cognitive conflict and inhibit a dominant response—is directly related to their ACC sulcal pattern. Critically, the effect of the sulcal pattern of ACC on the Stroop interference score unlikely results from a difference in the ability to name the animals, given that we found no difference in the no-conflict condition between the two groups. Furthermore, we note that analyses of the RTs and ERs revealed a similar pattern of results, with strong effect sizes providing evidence (a) of the robustness of the behavioral effects of ACC sulcal pattern, despite the sample size, and (b) the lack of speed accuracy trade-off. Moreover, ACC sulcal pattern had no effect on performances in the forward and backward digit span tasks. Taken together, the results suggest that ACC sulcal pattern contributes to the ability to resolve conflicts (i.e., as in the Animal Stroop task) but did not contribute to the ability to maintain and manipulate information in verbal working memory (i.e., as in the forward and the backward digit span tasks) or manage the increasing difficulty of a task (i.e., the difference between the scores in the backward and the forward digit span tasks). A potential limitation of this study is the small sample size, reflecting the difficulty to conduct brain imaging studies in young children.

This study focuses on the general construct of executive functions and the inhibition of prepotent responses; therefore, our findings do not provide information on the specific cognitive processes affected by ACC sulcal pattern. Indeed, although ACC is consistently activated in the Stroop task (Roberts & Hall, 2008; Nee, Wager, & Jonides, 2007), the precise role of this region remains elusive (Botvinick, Cohen, & Carter, 2004; MacLeod & MacDonald, 2000). ACC is critical for monitoring conflicts (Kerns et al., 2004; Botvinick et al., 2001; Carter et al., 2000), selecting responses in underdetermined contexts (Palmer et al., 2001), detecting errors (Braver, Barch, Gray, Molfese, & Snyder, 2001; Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Carter et al., 1998), making reward-based decisions (Nieuwenhuis, Yeung, Holroyd, Schurger, & Cohen, 2004; Bush et al., 2002), and encoding cognitive efforts (Rushworth, Walton, Kennerley, & Bannerman, 2004; Botvinick et al., 2001). Additional studies are needed to determine the precise cognitive process affected by the morphology of ACC, which in turn might shed light on the cognitive processes critical to perform the Animal Stroop task and the role of ACC in supporting these processes. For instance, future researches should study the effect of ACC sulcal pattern on the performance in different executive tasks tackling different types of executive processes.

Thus, our results support the hypothesis that CC efficiency in preschoolers is rooted in early neurodevelopmental processes. The cortical folding patterns are primarily determined in utero (Welker, 1988) and are

robust to changes induced by maturation after birth and experience-dependent factors (Sun et al., 2012). The sulcal pattern results from early neurodevelopmental processes, starting as early as 10 weeks of fetal life, that shape the cortex anatomy from a smooth lissencephalic structure to a highly convoluted surface (Welker, 1988). In particular, the development of ACC sulcal pattern occurs between 10 and 15 weeks of fetal life (Feess-Higgins & Larroche, 1987; Chi, Dooling, & Gilles, 1977). Such long-term effect of early neurodevelopmental constraints on the subsequent development of cognitive capacities is in line with previous studies in adults showing that variations in ACC sulcal patterns are related to individual differences in CC efficiency (Huster et al., 2009; Fornito et al., 2004) as well as in four core temperament dimensions, that is, effortful control, negative affectivity, surgency, and affiliation (Whittle et al., 2009). An important contribution of our findings is that such long-term effect was observed for the first time in preschoolers, namely in the early stages of cognitive and neural development. However, because of the sample size, we could not statistically determine whether children with a leftward asymmetry of the sulcal pattern of ACC (i.e., PCS in the left but not in the right hemispheres) have greater CC efficiency than children with a rightward asymmetry (i.e., PCS in the right but not in the left hemispheres) as in adults (Huster et al., 2009; Whittle et al., 2009; Fornito et al., 2004).<sup>1</sup>

Several factors contribute to the neurodevelopmental processes that influence the shape of the folded cerebral cortex (Mangin, Jouvent, & Cachia, 2010), including structural connectivity through axonal tension forces (Hilgetag & Barbas, 2006; Van Essen, 1997). These mechanical constraints lead to a compact layout that optimizes the transmission of neuronal signals between brain regions (Klyachko & Stevens, 2003) and thus brain network functioning. In this context, we speculate that the differences in CC efficiency observed in preschoolers with symmetrical or asymmetrical ACC might reflect differences in brain network efficiency because of differences in long-range (i.e., interhemispheric) and short-range (i.e., intrahemispheric) brain connectivity. Increased cognitive efficiency in asymmetric brains might be associated with hemispheric specialization, as it is more efficient to transfer information between close areas within the same hemisphere rather than between distant areas distributed in the two hemispheres (Deary, Penke, & Johnson, 2010; Toga & Thompson, 2003). The association between hemispheric specialization and the asymmetry of the brain morphology is supported by studies of the corpus callosum, a large bundle of interhemispheric fibers, showing that asymmetrical brains have fewer and/or thinner fibers connecting the two hemispheres relative to more symmetrical brain, as evidenced by a reduced midsagittal area (Witelson, 1985) and microstructural integrity measured using diffusion MRI (Putnam, Wig, Grafton, Kelley, & Gazzaniga, 2008). Individuals with no corpus callosum (i.e., complete

agenesis) exhibit an intact Stroop interference effect (Brown, Thrasher, & Paul, 2001), suggesting that the processes involved in performing the Stroop task are highly lateralized in the brain. If these processes are lateralized, then it is reasonable to expect that morphological asymmetry in the regions involved in performing the Stroop task, such as ACC, would produce better efficiency by reinforcing hemispheric specialization. This hypothesis is supported by multimodal brain imaging of the cortex morphology and the white matter connectivity in the same individuals, revealing that participants with different sulcal patterns have distinct short-range white matter connectivity (Leonard, Eckert, & Kuldau, 2006). Therefore, the increased CC efficiency observed in children with asymmetric ACC in our study might reflect the asymmetry of the underlying white matter connectivity of ACC.

Faulty executive functions including CC can account for learning difficulties in children, such as errors, reasoning biases, and maladjustment, both in cognitive (Borst, Poirel, Pineau, Cassotti, & Houdé, 2013; Poirel et al., 2012; Houdé, 2000) and social (Steinberg, 2005) domains. Children's executive function efficiency actually predicts, for instance, health and professional success later in life (Moffitt et al., 2011). The predictive nature of children's executive functions including CC efficiency on cognitive and social development may be partly related to the early neurodevelopmental constraints induced by the sulcal pattern of ACC (Dubois et al., 2008).

However, brain-behavior associations are not fixed in all cases. For instance, previous studies reported that CC efficiency, assessed either in a visual discrimination task (Casey et al., 1997) or in a Flanker task (Fjell et al., 2012), is related to the cortical surface area of ACC (Fjell et al., 2012; Casey et al., 1997). Critically, the relationship is stronger for younger children (under 12 years old) and decreases linearly with age (Fjell et al., 2012). Because the cortical surface area of ACC is determined in part by ACC sulcal pattern (Fornito et al., 2008; Fornito, Whittle, et al., 2006), the relationship between ACC sulcal pattern and the CC efficiency reported in our study might vary with age. Hence, early neuroanatomical constraints might be overcome during cognitive development by training CC. Indeed, CC continues to mature from childhood to adolescence (Luna, 2009; Luna, Garver, Urban, Lazar, & Sweeney, 2004) and can be modified by training and practice (Diamond, 2013).

Longitudinal studies in large-scale samples should investigate the possible interactions between the sulcal pattern of ACC and intense preschool interventions that have shown to improve executive functions including CC efficiency (Diamond et al., 2007). An early objective assessment of CC in children is critical, given that (a) executive function training is more beneficial for children with faulty executive function efficiency (Diamond et al., 2007) and (b) executive functions can demonstrate improved results in children as early as 4 or 5 years (Moffitt et al., 2011). Hence, our brain-imaging findings may

ultimately contribute to shape specific educational interventions designed to help children overcome their CC deficits, particularly those with symmetrical sulcal pattern of ACC who are at increased risk of developing faulty CC efficiency.

In conclusion, this study provides the first evidence that preschoolers' CC efficiency is likely associated with ACC sulcal pattern, thereby suggesting that the brain shape could result in early constraints on human executive ability.

## Acknowledgments

We thank the CNRS for financial support and the French Board of Education for their collaboration.

Reprint requests should be sent to Arnaud Cachia, Laboratory for the Psychology of Child Development and Education, CNRS U3521, Paris-Descartes University, Alliance for Higher Education and Research Sorbonne Paris Cité, Sorbonne, 46 rue Saint-Jacques, 75005 Paris, France, or via e-mail: [arnaud.cachia@parisdescartes.fr](mailto:arnaud.cachia@parisdescartes.fr).

## Note

1. That said, the pattern of Stroop interference scores suggests that children with leftward asymmetry ( $13.1 \pm 17.4$ ;  $n = 4$ ) could have greater CC efficiency than children with rightward asymmetry ( $16.7 \pm 9.7$ ;  $n = 4$ ), children with PCS in both hemispheres ( $24.9 \pm 11.5$ ;  $n = 2$ ), and children with no PCS ( $39.5 \pm 24.4$ ;  $n = 9$ ).

## REFERENCES

- Amiez, C., Neveu, R., Warrot, D., Petrides, M., Knoblach, K., & Procyk, E. (2013). The location of feedback-related activity in the midcingulate cortex is predicted by local morphology. *Journal of Neuroscience*, *33*, 2217–2228.
- Armstrong, E., Schleicher, A., Omran, H., Curtis, M., & Zilles, K. (1995). The ontogeny of human gyrification. *Cerebral Cortex*, *5*, 56–63.
- Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience*, *4*, 829–839.
- Barkovich, A. J., Guerrini, R., Kuzniecky, R. I., Jackson, G. D., & Dobyns, W. B. (2012). A developmental and genetic classification for malformations of cortical development: Update 2012. *Brain*, *135*, 1348–1369.
- Blair, C., & Razza, R. P. (2007). Relating effortful control, executive function, and false belief understanding to emerging math and literacy ability in kindergarten. *Child Development*, *78*, 647–663.
- Borst, G., Poirel, N., Pineau, A., Cassotti, M., & Houdé, O. (2013). Inhibitory control efficiency in a Piaget-like class-inclusion task in school-age children and adults: A developmental negative priming study. *Developmental Psychology*, *49*, 1366–1374.
- Botvinick, M. M. (2007). Conflict monitoring and decision making: Reconciling two perspectives on anterior cingulate function. *Cognitive, Affective, & Behavioral Neuroscience*, *7*, 356–366.
- Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, *108*, 624–652.



- Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences*, 8, 539–546.
- Braver, T. S., Barch, D. M., Gray, J. R., Molfese, D. L., & Snyder, A. (2001). Anterior cingulate cortex and response conflict: Effects of frequency, inhibition and errors. *Cerebral Cortex*, 11, 825–836.
- Brown, W. S., Thrasher, E. D., & Paul, L. K. (2001). Interhemispheric Stroop effects in partial and complete agenesis of the corpus callosum. *Journal of the International Neuropsychological Society*, 7, 302–311.
- Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, 4, 215–222.
- Bush, G., Vogt, B. A., Holmes, J., Dale, A. M., Greve, D., Jenike, M. A., et al. (2002). Dorsal anterior cingulate cortex: A role in reward-based decision making. *Proceedings of the National Academy of Sciences, U.S.A.*, 99, 523–528.
- Carter, C. S., Braver, T. S., Barch, D. M., Botvinick, M. M., Noll, D., & Cohen, J. D. (1998). Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science*, 280, 747–749.
- Carter, C. S., Macdonald, A. M., Botvinick, M., Ross, L. L., Stenger, V. A., Noll, D., et al. (2000). Parsing executive processes: Strategic vs. evaluative functions of the anterior cingulate cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, 97, 1944–1948.
- Casey, B. J., Thomas, K. M., Welsh, T. F., Badgaiyan, R. D., Eccard, C. H., Jennings, J. R., et al. (2000). Dissociation of response conflict, attentional selection, and expectancy with functional magnetic resonance imaging. *Proceedings of the National Academy of Sciences, U.S.A.*, 97, 8728–8733.
- Casey, B. J., Trainor, R., Giedd, J., Vauss, Y., Vaituzis, C. K., Hamburger, S., et al. (1997). The role of the anterior cingulate in automatic and controlled processes: A developmental neuroanatomical study. *Developmental Psychobiology*, 30, 61–69.
- Chi, J. G., Dooling, E. C., & Gilles, F. H. (1977). Gyral development of the human brain. *Annals of Neurology*, 1, 86–93.
- Deary, I. J., Penke, L., & Johnson, W. (2010). The neuroscience of human intelligence differences. *Nature Reviews Neuroscience*, 11, 201–211.
- Dehay, C., Giroud, P., Berland, M., Killackey, H., & Kennedy, H. (1996). Contribution of thalamic input to the specification of cytoarchitectonic cortical fields in the primate: Effects of bilateral enucleation in the fetal monkey on the boundaries, dimensions, and gyrification of striate and extrastriate cortex. *Journal of Comparative Neurology*, 367, 70–89.
- Diamond, A. (2013). Executive functions. *Annual Review of Psychology*, 64, 135–168.
- Diamond, A., Barnett, W. S., Thomas, J., & Munro, S. (2007). Preschool program improves cognitive control. *Science*, 318, 1387–1388.
- Diamond, A., & Lee, K. (2011). Interventions shown to aid executive function development in children 4 to 12 years old. *Science*, 333, 959–964.
- Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U., & May, A. (2004). Neuroplasticity: Changes in grey matter induced by training. *Nature*, 427, 311–312.
- Draganski, B., Gaser, C., Kempermann, G., Kuhn, H. G., Winkler, J., Buchel, C., et al. (2006). Temporal and spatial dynamics of brain structure changes during extensive learning. *Journal of Neuroscience*, 26, 6314–6317.
- Dubois, J., Benders, M., Borradori-Tolsa, C., Cachia, A., Lazeyras, F., Ha-Vinh Leuchter, R., et al. (2008). Primary cortical folding in the human newborn: An early marker of later functional development. *Brain*, 131, 2028–2041.
- Duckworth, A. L., & Seligman, M. E. (2005). Self-discipline outdoes IQ in predicting academic performance of adolescents. *Psychological Science*, 16, 939–944.
- Egner, T., & Hirsch, J. (2005). Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nature Neuroscience*, 8, 1784–1790.
- Falkenstein, M., Hoormann, J., Christ, S., & Hohnsbein, J. (2000). ERP components on reaction errors and their functional significance: A tutorial. *Biological Psychology*, 51, 87–107.
- Feess-Higgins, A., & Larroche, J. (1987). *Development of the human foetal brain. An anatomical atlas*. Paris: Masson.
- Fjell, A. M., Walhovd, K. B., Brown, T. T., Kuperman, J. M., Chung, Y., Hagler, D. J., Jr., et al. (2012). Multimodal imaging of the self-regulating developing brain. *Proceedings of the National Academy of Sciences, U.S.A.*, 109, 19620–19625.
- Flook, L., Smalley, S. L., Kitil, M. J., Galla, B. M., Kaiser-Greenland, S., Locke, J., et al. (2010). Effects of mindful awareness practices on executive functions in elementary school children. *Journal of Applied School Psychology*, 26, 70–95.
- Fornito, A., Whittle, S., Wood, S. J., Velakoulis, D., Pantelis, C., & Yucel, M. (2006). The influence of sulcal variability on morphometry of the human anterior cingulate and paracingulate cortex. *Neuroimage*, 33, 843–854.
- Fornito, A., Wood, S. J., Whittle, S., Fuller, J., Adamson, C., Saling, M. M., et al. (2008). Variability of the paracingulate sulcus and morphometry of the medial frontal cortex: Associations with cortical thickness, surface area, volume, and sulcal depth. *Human Brain Mapping*, 29, 222–236.
- Fornito, A., Yucel, M., Wood, S. J., Proffitt, T., McGorry, P. D., Velakoulis, D., et al. (2006). Morphology of the paracingulate sulcus and executive cognition in schizophrenia. *Schizophrenia Research*, 88, 192–197.
- Fornito, A., Yucel, M., Wood, S., Stuart, G. W., Buchanan, J. A., Proffitt, T., et al. (2004). Individual differences in anterior cingulate/paracingulate morphology are related to executive functions in healthy males. *Cerebral Cortex*, 14, 424–431.
- Gathercole, S. E., Pickering, S. J., Ambridge, B., & Wearing, H. (2004). The structure of working memory from 4 to 15 years of age. *Developmental Psychology*, 40, 177–190.
- Giedd, J. N., Lalonde, F. M., Celano, M. J., White, S. L., Wallace, G. L., Lee, N. R., et al. (2009). Anatomical brain magnetic resonance imaging of typically developing children and adolescents. *Journal of the American Academy of Child & Adolescent Psychiatry*, 48, 465–470.
- Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., et al. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences, U.S.A.*, 101, 8174–8179.
- Hilgetag, C. C., & Barbas, H. (2006). Role of mechanical factors in the morphology of the primate cerebral cortex. *PLOS Computational Biology*, 2, e22.
- Hillman, C. H., Erickson, K. I., & Kramer, A. F. (2008). Be smart, exercise your heart: Exercise effects on brain and cognition. *Nature Reviews Neuroscience*, 9, 58–65.
- Holmes, J., Gathercole, S. E., & Dunning, D. L. (2009). Adaptive training leads to sustained enhancement of poor working memory in children. *Developmental Science*, 12, F9–F15.
- Houdé, O. (2000). Inhibition and cognitive development: Object, number, categorization, and reasoning. *Cognitive Development*, 15, 63–73.
- Huster, R. J., Enriquez-Geppert, S., Pantev, C., & Bruchmann, M. (2012). Variations in midcingulate morphology are related to ERP indices of cognitive control. *Brain Structure & Function*. Epub ahead of print.

- Huster, R. J., Westerhausen, R., & Herrmann, C. S. (2011). Sex differences in cognitive control are associated with midcingulate and callosal morphology. *Brain Structure & Function*, *215*, 225–235.
- Huster, R. J., Westerhausen, R., Kreuder, F., Schweiger, E., & Wittling, W. (2007). Morphologic asymmetry of the human anterior cingulate cortex. *Neuroimage*, *34*, 888–895.
- Huster, R. J., Wolters, C., Wollbrink, A., Schweiger, E., Wittling, W., Pantev, C., et al. (2009). Effects of anterior cingulate fissuration on cognitive control during Stroop interference. *Human Brain Mapping*, *30*, 1279–1289.
- Hyde, K. L., Lerch, J., Norton, A., Forgeard, M., Winner, E., Evans, A. C., et al. (2009). Musical training shapes structural brain development. *Journal of Neuroscience*, *29*, 3019–3025.
- Kerns, J. G., Cohen, J. D., MacDonald, A. W., III, Cho, R. Y., Stenger, V. A., & Carter, C. S. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Science*, *303*, 1023–1026.
- Klyachko, V. A., & Stevens, C. F. (2003). Connectivity optimization and the positioning of cortical areas. *Proceedings of the National Academy of Sciences, U.S.A.*, *100*, 7937–7941.
- Lakes, K. D., & Hoyt, W. I. (2004). Promoting self-regulation through school-based martial arts training. *Journal of Applied Developmental Psychology*, *25*, 283–302.
- Lemaire, C., Moran, G. R., & Swan, H. (2009). Impact of audio/visual systems on pediatric sedation in magnetic resonance imaging. *Journal of Magnetic Resonance Imaging*, *30*, 649–655.
- Leonard, C. M., Eckert, M. A., & Kuldau, J. M. (2006). Exploiting human anatomical variability as a link between genome and cognome. *Genes, Brain and Behavior*, *5(Suppl. 1)*, 64–77.
- Leonard, C. M., Towler, S., Welcome, S., & Chiarello, C. (2009). Paracingulate asymmetry in anterior and midcingulate cortex: Sex differences and the effect of measurement technique. *Brain Structure & Function*, *213*, 553–569.
- Luna, B. (2009). Developmental changes in cognitive control through adolescence. *Advances in Child Development and Behavior*, *37*, 233–278.
- Luna, B., Garver, K. E., Urban, T. A., Lazar, N. A., & Sweeney, J. A. (2004). Maturation of cognitive processes from late childhood to adulthood. *Child Development*, *75*, 1357–1372.
- Mackey, A. P., Hill, S. S., Stone, S. I., & Bunge, S. A. (2011). Differential effects of reasoning and speed training in children. *Developmental Science*, *14*, 582–590.
- MacLeod, C. M. (1991). Half a century of research on the Stroop effect: An integrative review. *Psychological Bulletin*, *109*, 163–203.
- MacLeod, C. M., Dodd, M. D., Sheard, E. D., Wilson, D. E., & Bibi, U. (2003). In opposition to inhibition. In B. H. Ross (Ed.), *The psychology of learning and motivation* (Vol. 43, pp. 163–214). San Diego, CA: Academic Press.
- MacLeod, C. M., & MacDonald, P. A. (2000). Interdimensional interference in the Stroop effect: Uncovering the cognitive and neural anatomy of attention. *Trends in Cognitive Sciences*, *4*, 383–391.
- Mangin, J. F., Jouvent, E., & Cachia, A. (2010). In-vivo measurement of cortical morphology: Means and meanings. *Current Opinion in Neurology*, *23*, 359–367.
- Mangin, J. F., Riviere, D., Cachia, A., Duchesnay, E., Cointepas, Y., Papadopoulos-Orfanos, D., et al. (2004). A framework to study the cortical folding patterns. *Neuroimage*, *23(Suppl. 1)*, S129–S138.
- Matthews, S. C., Paulus, M. P., Simmons, A. N., Nelesen, R. A., & Dimsdale, J. E. (2004). Functional subdivisions within anterior cingulate cortex and their relationship to autonomic nervous system function. *Neuroimage*, *22*, 1151–1156.
- Moffitt, T. E., Arseneault, L., Belsky, D., Dickson, N., Hancox, R. J., Harrington, H., et al. (2011). A gradient of childhood self-control predicts health, wealth, and public safety. *Proceedings of the National Academy of Sciences, U.S.A.*, *108*, 2693–2698.
- Molko, N., Cachia, A., Riviere, D., Mangin, J. F., Bruandet, M., Le Bihan, D., et al. (2003). Functional and structural alterations of the intraparietal sulcus in a developmental dyscalculia of genetic origin. *Neuron*, *40*, 847–858.
- Nee, D. E., Wager, T. D., & Jonides, J. (2007). Interference resolution: Insights from a meta-analysis of neuroimaging tasks. *Cognitive, Affective, & Behavioral Neuroscience*, *7*, 1–17.
- Nieuwenhuis, S., Yeung, N., Holroyd, C. B., Schurger, A., & Cohen, J. D. (2004). Sensitivity of electrophysiological activity from medial frontal cortex to utilitarian and performance feedback. *Cerebral Cortex*, *14*, 741–747.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.
- Ono, M., Kubik, S., & Abarnathey, C. D. (1990). *Atlas of the cerebral sulci*. New York: Thieme.
- Palmer, E. D., Rosen, H. J., Ojemann, J. G., Buckner, R. L., Kelley, W. M., & Petersen, S. E. (2001). An event-related fMRI study of overt and covert word stem completion. *Neuroimage*, *14*, 182–193.
- Pardo, J. V., Pardo, P. J., Janer, K. W., & Raichle, M. E. (1990). The anterior cingulate cortex mediates processing selection in the Stroop attentional conflict paradigm. *Proceedings of the National Academy of Sciences, U.S.A.*, *87*, 256–259.
- Paus, T., Tomaiuolo, F., Otaky, N., MacDonald, D., Petrides, M., Atlas, J., et al. (1996). Human cingulate and paracingulate sulci: Pattern, variability, asymmetry, and probabilistic map. *Cerebral Cortex*, *6*, 207–214.
- Petersen, S. E., & Posner, M. I. (2012). The attention system of the human brain: 20 Years after. *Annual Review of Neuroscience*. doi: 10.1146/annurev-neuro062111-150525.
- Poirel, N., Borst, G., Simon, G., Rossi, S., Cassotti, M., Pineau, A., et al. (2012). Number conservation is related to children's prefrontal inhibitory control: An fMRI study of a Piagetian task. *PLoS One*, *7*:e40802.
- Putnam, M. C., Wig, G. S., Grafton, S. T., Kelley, W. M., & Gazzaniga, M. S. (2008). Structural organization of the corpus callosum predicts the extent and impact of cortical activity in the nondominant hemisphere. *Journal of Neuroscience*, *28*, 2912–2918.
- Rakic, P. (2004). Neuroscience. Genetic control of cortical convolutions. *Science*, *303*, 1983–1984.
- Raven, J., Raven, J. C., & Court, J. H. (1998). Manual for Raven's progressive matrices and vocabulary scales. *Section 2: The coloured progressive matrices*. San Antonio, Texas: Harcourt Assessment.
- Roberts, K. L., & Hall, D. A. (2008). Examining a supramodal network for conflict processing: A systematic review and novel functional magnetic resonance imaging data for related visual and auditory Stroop tasks. *Journal of Cognitive Neuroscience*, *20*, 1063–1078.
- Rueda, M. R., Rothbart, M. K., McCandliss, B. D., Saccomanno, L., & Posner, M. I. (2005). Training, maturation, and genetic influences on the development of executive attention. *Proceedings of the National Academy of Sciences, U.S.A.*, *102*, 14931–14936.
- Rushworth, M. F., Walton, M. E., Kennerley, S. W., & Bannerman, D. M. (2004). Action sets and decisions in the medial frontal cortex. *Trends in Cognitive Sciences*, *8*, 410–417.
- Steinberg, L. (2005). Cognitive and affective development in adolescence. *Trends in Cognitive Sciences*, *9*, 69–74.

- Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, *18*, 643–662.
- Sun, Z. Y., Kloppel, S., Riviere, D., Perrot, M., Frackowiak, R., Siebner, H., et al. (2012). The effect of handedness on the shape of the central sulcus. *Neuroimage*, *60*, 332–339.
- Takeuchi, H., Taki, Y., Sassa, Y., Hashizume, H., Sekiguchi, A., Nagase, T., et al. (2012). Regional gray and white matter volume associated with Stroop interference: Evidence from voxel-based morphometry. *Neuroimage*, *59*, 2899–2907.
- Toga, A. W., & Thompson, P. M. (2003). Mapping brain asymmetry. *Nature Reviews Neuroscience*, *4*, 37–48.
- Van Essen, D. C. (1997). A tension-based theory of morphogenesis and compact wiring in the central nervous system. *Nature*, *385*, 313–318.
- Vogt, B. (2009). *Cingulate neurobiology and disease*. Oxford: Oxford University Press.
- Wechsler, D. (2003). *Wechsler Intelligence Scale for Children-Fourth Edition. Administration and scoring manual*. San Antonio, TX: Harcourt Assessment, Inc.
- Welker, W. (1988). Why does cerebral cortex fissure and fold? *Cerebral Cortex*, *8B*, 3–135.
- Westlye, L. T., Grydeland, H., Walhovd, K. B., & Fjell, A. M. (2011). Associations between regional cortical thickness and attentional networks as measured by the attention network test. *Cerebral Cortex*, *21*, 345–356.
- White, T., Su, S., Schmidt, M., Kao, C. Y., & Sapiro, G. (2010). The development of gyrification in childhood and adolescence. *Brain and Cognition*, *72*, 36–45.
- Whittle, S., Allen, N. B., Fornito, A., Lubman, D. I., Simmons, J. G., Pantelis, C., et al. (2009). Variations in cortical folding patterns are related to individual differences in temperament. *Psychiatry Research*, *172*, 68–74.
- Witelson, S. F. (1985). The brain connection: The corpus callosum is larger in left-handers. *Science*, *229*, 665–668.
- Wright, I., Waterman, M., Prescott, H., & Murdoch-Eaton, D. (2003). A new Stroop-like measure of inhibitory function development: Typical developmental trends. *Journal of Child Psychology and Psychiatry*, *44*, 561–575.
- Yucel, M., Stuart, G. W., Maruff, P., Velakoulis, D., Crowe, S. F., Savage, G., et al. (2001). Hemispheric and gender-related differences in the gross morphology of the anterior cingulate/paracingulate cortex in normal volunteers: An MRI morphometric study. *Cerebral Cortex*, *11*, 17–25.
- Zilles, K., Palomero-Gallagher, N., & Amunts, K. (2013). Development of cortical folding during evolution and ontogeny. *Trends in Neurosciences*, *36*, 275–284.