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Anterior cingulate cortex sulcation and its differential effects on conflict monitoring in bilinguals and monolinguals

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ABSTRACT

The role of the anterior cingulate cortex (ACC) in modulating the effect of bilingual experience on cognitive control has been reported at both functional and structural neural levels. Individual differences in the ACC sulcal patterns have been recently correlated with cognitive control efficiency in monolinguals. We aimed to investigate whether differences of ACC sulcation mediate the effect of bilingualism on cognitive control efficiency. We contrasted the performance of bilinguals and monolinguals during a cognitive control task (*i.e.*, the Flanker Task) using a stratification based on the participants' ACC sulcal features. We found that performance of the two groups was differentially affected by ACC sulcation. Our findings provide the first evidence that early neurodevelopmental mechanisms may modulate the effect of different environmental backgrounds – here, bilingual vs monolingual experience – on cognitive efficiency.

1. Introduction

Monitoring cognitive conflicts induced by distracting information from either external or internal sources is a core executive function required by everyday life. The anterior cingulate cortex (ACC) has been indicated as a key structure in the neural circuit mediating domain-general cognitive control processes such as goal maintenance, conflict monitoring, error detection and response inhibition (Botvinick, Cohen, & Carter, 2004; Carter, Botvinick, & Cohen, 1999; Petersen & Posner, 2012).[1] The demand for monitoring conflicting information is also evident in bilingual individuals, who must select one language for communication avoiding interference from the language not in use (Abutalebi & Green, 2007). The study of bilingual language processing thus provided a chance to test whether the neural mechanisms mediating language control are shared with more general cognitive control functions. Functional neuroimaging investigations have shown that the ACC is recruited when bilinguals perform both linguistic and non-linguistic conflict tasks, indicating the ACC as a critical component of the neural network underpinning conflict monitoring, whether in verbal or non-verbal domains (Abutalebi et al., 2012; Branzi, Della Rosa, Canini, Costa, & Abutalebi, 2016; Crinion et al., 2006; Hernandez, 2009). It has been suggested that bilinguals may have a so-called "cognitive advantage" over monolinguals on tasks that require attention, memory and cognitive control in terms of differences in response times (RTs) (see Valian, 2015, for a review). For instance, faster RTs for bilingual speakers have been reported on the Attention Network Test (ANT) (Costa, Hernández, & Sebastián-Gallés, 2008; Luk, De Sa, & Bialystok, 2011), the Simon task (Bialystok, Craik, Klein, & Viswanathan, 2004; Linck, Hoshino, & Kroll, 2008), the Stroop (Bialystok, Craik, & Luk, 2008; Heidlmayr et al., 2014) and other conflict-related tasks (see Bialystok, Craik, & Luk, 2012, for a review). These effects tend to be more robust in children and seniors although

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[1] Cognitive control may be characterized as a multi-componential construct comprising a range of mechanisms that support flexible, goal-directed behavior by representing task-relevant information in order to guide thought and action (Yeung, 2013). Following common practice in the literature, we will use the terms "cognitive control", "executive control" and "executive function" interchangeably.

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they are not exclusive to these groups (Zhou & Krott, 2016). One popular account of the putative bilingual advantage is that the simultaneous management of multiple languages provides bilinguals with enhanced executive control abilities, due to continuous monitoring for potential cross-linguistic interference (Kroll & Bialystok, 2013). However, it should be underlined that evidence on bilingual advantage has been challenged in recent years, as an increasing number of behavioral studies reported null or negative differences in executive control performance between bilingual and monolingual speakers (e.g. Antón et al., 2014; Duñabeitia et al., 2014; Gathercole et al., 2014; see, for a review, Hilchey & Klein, 2011). These inconsistent findings have led some to question the veracity of the bilingual advantage (Paap, Johnson, & Sawi, 2015), which is currently the basis of a lively debate in the field of bilingual studies (Bak, 2016; Bialystok, Kroll, Green, MacWhinney, & Craik, 2015; De Bruin, Treccani, & Della Sala, 2015). Mixed results across studies may be due to a range of different factors. For instance, Prior and Gollan (2011) claim that language background variability of bilingual speakers makes the bilingual advantage elusive, while Valian (2015) argues the bilingual advantage may depend on age and notes that it is more common in seniors (see also Bialystok et al., 2004; Zahodne, Schofield, Farrell, Stern, & Manly, 2014). On the other hand, one factor that has never been considered is the role of individual cortical fold patterns such as ACC sulcal patterns in modulating the effect of bilingualism on conflict monitoring. ACC sulcation is an indirect marker of early brain development determined in utero and not affected by neuroplastic processes like brain maturation (Cachia et al., 2016) or cognitive training (e.g. forced use of the right hand in left handers, see Sun et al., 2012). The effects of ACC sulcation on conflict monitoring in bilingual and monolingual speakers will be tested in the present study. In addition to functional activation during cognitive control tasks, the role of the ACC in conflict information processing has been suggested by the identified relationship between differences in adults' cognitive control efficiency and inter-individual variation in the ACC's quantitative morphology, as measured by structural brain imaging (cortical thickness: Westlye, Grydeland, Walhovd, & Fjell, 2011; cortical surface area (CS): Fjell et al., 2012; gray matter volume (GMV): Takeuchi et al., 2012). For instance, Abutalebi et al. (2012) combined functional and structural neuroimaging to examine whether bilingualism induces beneficial neuroplasticity both at a functional and structural level. When compared to monolinguals on a cognitive control task (*i.e.* the Flanker task), less activity in the dorsal ACC was detected for the bilingual group, suggesting that bilinguals used ACC more efficiently than their monolingual peers to monitor nonlinguistic cognitive conflicts. Interestingly, although bilinguals activated the ACC less than monolinguals already in the first session of the Flanker task, in the second session they showed a radical decrease in signal in the dorsal ACC, while the monolingual group did not. This activation pattern correlated with the conflict effect scores observed in behavioral data, indicating that bilinguals adapted better to conflicting situations than monolinguals. Moreover, a negative correlation was detected in bilinguals between ACC activity and local GMV, as increased gray matter in the dorsal ACC was significantly associated with lower ACC activation. These findings have been interpreted as a result of the beneficial neuroplastic effects induced by life-long bilingual experience. However, quantitative measures of cortex anatomy like thickness and GMV are known to be affected by brain maturation (Giedd & Rapoport, 2010) and learning (Draganski et al., 2004, 2006; Hyde et al., 2009) both during the course of development and later in life. Accordingly, these state markers cannot provide information on the potential role played by early neurodevelopmental characteristics in modulating the effect of bilingual experience on conflict monitoring. Such information, on the other hand, can be provided by the cortical sulcation, a qualitative anatomical feature which is stable from childhood to adulthood irrespective of brain maturation and experience-related factors (Cachia et al., 2016; Sun et al., 2012). Individual differences in the ACC sulcal pattern have been recently correlated with cognitive control efficiency both in monolingual children (Borst et al., 2014; Cachia et al., 2014) and adults (Huster et al., 2009). Interference scores from a Stroop task performed by participants with symmetrical vs asymmetrical ACC sulcal patterns showed a significant cognitive advantage for participants, either children or adults, with asymmetrical ACC sulcal patterns (*i.e.* lower RT scores in participants with asymmetrical ACC sulcation). If these results seem to underscore the critical role of neurodevelopmental factors assessed by qualitative features of brain anatomy on human executive abilities, the possible interaction with experience in terms of learning/training effects on cognitive control efficiency remains incompletely understood.

In this context, the present study uses high resolution magnetic structural imaging (MRI) to investigate whether the ACC sulcation modulates the effects of bilingual experience on conflict monitoring. The behavioral and structural MRI data used in this study are from Abutalebi et al. (2012). However, a different set of analyses was performed on existing data in order to assess new factors.

2. Material and methods

2.1. Participants

Thirty-one healthy right-handed participants from Abutalebi et al. (2012) were included in the study. Participants comprised 17 highly-proficient German–Italian bilinguals (all females; mean age: 23.35, standard deviation [SD] ± 4.59) and 14 Italian monolinguals (all females; mean age: 26.55, SD ± 4.15) with a comparable educational and socio-economical background. Individuals with a history of psychiatric care, neurological disease or head injury were excluded. Bilinguals came from South Tyrol, a bilingual region in Italy in which German and Italian are official languages. For all bilinguals German was the first and dominant language (*i.e.*, L1), whereas Italian was the second language (*i.e.*, L2) acquired at kindergarten age and regularly spoken in the bilingual environment of South Tyrol. Participants' language proficiency was assessed with translation tasks (see Abutalebi et al., 2012, for details and results). Monolingual participants were from mainland Italy.

The study was approved by the University Vita-Salute San Raffaele Research Ethics Committee and carried out in compliance with their guidelines. Written informed consent was obtained from all participants.

2.2. Behavioral assessment

All participants (bilinguals and monolinguals) performed a revised version of the Flanker Task (Fan, McCandliss, Fossella, Flombaum, & Posner, 2005) divided into two sessions to investigate adaptive changes in each group. Participants performed the task on a computer screen using an external mouse. A fixation point appearing at the center of the screen for 400 ms was followed by a target, *i.e.* a central arrow presented foveally on the screen for 1700 ms, pointing to left or right. Targets were presented in congruent, incongruent or neutral conditions, *i.e.* with additional arrows flanked to the same direction as the target (→→→→→), with additional arrows flanked to the opposite direction of the target (←←→←←) or with additional neutral lines (– – → – –). Participants were instructed to press the left or the right button of the mouse as quickly as possible depending on whether the target pointed to left or right, respectively. Accuracy and RTs were recorded. Whereas the neutral lines surrounding the target typically bias neither the correct nor the incorrect response, the incongruent flankers represent conflicting information with the correct response and are generally associated with decline in performance, *i.e.* lower accuracy and increasing RTs. By contrast, congruent flankers favor the correct response and are generally associated with better performance, *i.e.* higher accuracy and lower RTs. Target stimuli appeared either above or below a fixation cross that remained at the center of the screen during the whole trial and could be preceded or not by visual cues (no cue, center cue, double cue, spatial cue), with cue-to-target interval at 400 ms. In attention studies, visual cues are usually employed to investigate the alerting and orienting components of the attentional system (Fan et al., 2005). However, being selectively interested in cognitive control as indexed by RT performance on Flanker conditions (congruent, incongruent, neutral), effects related to the alerting and orienting components were not analyzed. Congruent, neutral and incongruent trials were distributed across the different type of cueing trials and presented in two experimental sessions of 96 trials each (Session 1 and Session 2) under a different random order. Our key behavioral contrast between congruent and incongruent trials (*i.e.* the ‘conflict effect’) was thus based on 64 trials for each trial type across the two sessions (see Abutalebi et al., 2012).

2.3. MRI acquisition

Structural MR images (MRI) were acquired with a 3-T Achieva Philips MR scanner (Philips Medical Systems, Best, NL) equipped with an 8-channel sense head coil. An axial high-resolution structural MRI was obtained for all participants (magnetization prepared rapid gradient echo, 150 slice T1-weighted image, TR = 8.03 ms, TE = 4.1 ms; flip angle = 8°, TA = 4.8 min, resolution = $1 \times 1 \times 1$ mm). These MRIs were adapted for sulcus segmentation required for the three dimensional reconstruction of the fine individual cortical folds.

2.4. MRI analysis

An automated pre-processing step skull-stripped T1 MRIs and segmented the brain tissues. Neither linear nor non-linear spatial normalization to a common space (e.g. MNI or Talairach space) was applied to MRIs to overcome the 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 with standard parameters (http://brainvisa.info).

2.5. ACC classification

The sulcal pattern of the dorsal part of the ACC was visually assessed using three-dimensional, mesh-based reconstruction of cortical folds (Cachia et al., 2014) in order to measure the occurrence and extent of the local sulci (see Fig. 1). This three-dimensional approach was used to overcome methodological issues inherent to the analysis of the three-dimensional sulcal pattern of the ACC from two-dimensional sagittal slices. All MRI data were anonymized and manual labelling of ACC in left and right hemispheres was carried out blind to the participants’ demographic characteristics (*i.e.*, age, group, gender). The ACC sulcal pattern was classified as ‘single’ or ‘double parallel’ type (Ono, Kubik, & Abernathey, 1990) based on the absence or presence of a variable secondary sulcus known as paracingulate sulcus (PCS). We used this binary classification of the ACC sulcal pattern based on a qualitative feature of the cortical anatomy (presence/absence of the PCS), since it has been found to be stable during development (Cachia et al., 2016). The length of the PCS was not included in the analysis because this quantitative feature of the sulcal anatomy varies with age (Cachia et al., 2016), which indicates that it is a plastic feature that may be modified by environmental factors (e.g. monolingual vs bilingual family).

The PCS was defined as the sulcus located dorsal to the cingulate sulcus with a course clearly parallel to the cingulate sulcus (Paus et al., 1996; Yücel et al., 2001). To reduce the ambiguity from the confluence of the PCS and the cingulate sulcus with the superior rostral sulcus, we determined the anterior limit of the PCS as the point at which the sulcus extends posteriorly from an imaginary vertical line running parallel to the anterior commissure and perpendicular to the line passing through the anterior and posterior commissures (AC–PC). The PCS was anteriorly limited by an imaginary vertical line passing through the anterior commissure (Yücel 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 were not taken into account for the length measure). To control for inter-individual differences in global brain size, the measurements of PCS length were performed in MNI space after linear spatial registration on MNI152 T1 template.

The classification of the sulcal patterns was performed after the testing sessions by experimenters that did not participate in the behavioral testing (AC & GB) using a dichotomous variable code for the absence (‘single type’) or presence (‘double parallel type’) of a PCS. Reliability was 100% (kappa = 1) among the two raters for the left and the right hemispheres. The experimenters that collected the behavioral data were blind to the classification of the sulcal patterns, and the experimenters that performed the classification of the sulcal patterns were blind to the behavioral data.

2.6. ACC asymmetry

An asymmetry index of ACC sulcal pattern was assigned to each individual (Cachia et al., 2014; Fornito et al., 2004; Huster et al., 2009; Whittle et al., 2009). A three-level asymmetry index was derived from the ACC sulcal pattern in the left and right hemispheres: ‘leftward asymmetry’ if there was a PCS (double parallel type) in the left hemisphere but not in the right hemisphere (simple type); ‘rightward asymmetry’ if there was a PCS in the right hemisphere but not in the left hemisphere; ‘symmetry’ if the ACC sulcal pattern was the same in the left and right hemispheres. Because of the sample size, we did not distinguish symmetric ACC due to the presence of a PCS in both hemispheres from symmetric ACC due to the absence of a PCS in both hemispheres.

2.7. Statistical analysis

Mixed-design analyses of variance (ANOVAs) were conducted on the Flanker RTs, with Flanker condition and test session as within-subject factors and ACC sulcal pattern and group as between-subject factors. When we compared two means, two-tailed *t*-tests were computed. All statistical analyses were performed using the R 3.1. Software (https://www.r-project.org/) along with ‘car’ and ‘effects’ libraries.

3. Results

3.1. Distribution of ACC sulcal pattern in monolinguals and bilinguals

Bilinguals and monolinguals were divided into subgroups based on the asymmetry of the ACC sulcal pattern (see Fig. 1 for the inter-individual variability of the ACC sulcal pattern in the left and right hemispheres). Among the 17 bilinguals, 9 participants (53%) had a left asymmetry, 7 participants (41%) displayed symmetrical patterns, and one participant (6%) had a right asymmetry. Among the 14 monolinguals, 6 participants (43%) had a leftward asymmetry, 7 participants (50%) displayed symmetrical patterns and one subject (7%) had a right asymmetry. The subgroup of right asymmetry was not included in the analysis because its size was too small (N = 2) and would raise statistical concerns. The proportion of participants with leftward asymmetry and symmetry in bilinguals and monolinguals was similar (Chisq = 1.1244, df = 1, $p = 0.72$).

Fig. 1. Morphological patterns of the anterior cingulate cortex (ACC). The three ACC sulcal patterns: 'absent', 'present' and 'prominent'. The ACC sulci (yellow) and the paracingulate sulci (blue) are represented on the cortical surface (gray/white interface).

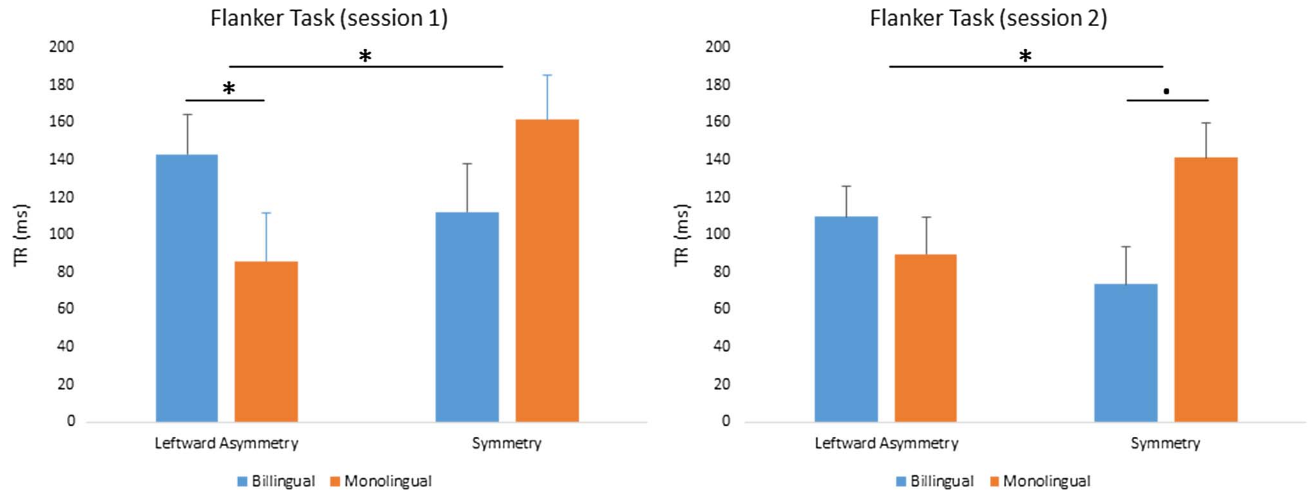

Fig. 2. Asymmetry of the anterior cingulate cortex (ACC) and cognitive control efficiency in bilinguals and monolinguals in Sessions 1 and 2. Conflict effect scores (differential RTs: Incongruent minus Congruent trials) in bilinguals and monolinguals with different ACC morphology. Error bars denote the standard error of the mean. *: $p < 0.05$; .: $p < 0.1$.

3.2. *Flanker task response times (RTs)*

The 2 (ACC sulcal pattern, *i.e.*, 'Leftward Asymmetry' vs 'Symmetry') × 2 (Flanker condition, *i.e.*, 'congruent' vs 'incongruent') × 2 (test session, *i.e.* 'first session' vs 'second session') × 2 (Group, *i.e.* 'Bilingual' vs 'Monolingual') mixed-design ANOVA revealed significant main effects of Flanker Condition [$F\ (1,24) = 143.55$, $p = 1.29\text{e-}11$], Test session [$F\ (1,24) = 13.97$, $p = 0.001$] and ACC pattern [$F\ (1,24) = 10.35$, $p = 0.003$] as well as a Condition-by-Session interaction [$F\ (1,24) = 7.52$, $p = 0.01$] and a ACC pattern-by-Group-by-Condition interaction [$F\ (1,24) = 5.98$, $p = 0.02$]. There was also a trend toward a Group-by-Session interaction [$F\ (1,24) = 2.52$, $p = 0.12$] and a Group-by-Session-by-Condition interaction [$F\ (1,24) = 2.71$, $p = 0.11$].

The main effect of Condition is related to the conflict effect induced by the Flanker task, namely that the RT is slower in the incongruent condition than in the congruent condition. The interaction Condition-by-Session further indicates that the conflict varies between the two sessions (see Fig. 2). The triple interaction ACC pattern-by-Group-by-Condition on Flanker's RT indicates that the difference in conflict effect between bilinguals and monolinguals is modulated by the ACC asymmetry. In participants with leftward asymmetry, RTs are slower in bilinguals than in monolinguals and, conversely, in participants with symmetrical patterns RTs are faster in bilinguals than in monolinguals (see Table 1 and Fig. 2). The quadruple interaction ACC pattern-by-Group-by-Condition-by-Session is not significant [$F\ (1,24) = 0.67$, $p = 0.42$], meaning that this modulatory effect of ACC pattern on the Flanker score difference between monolinguals and bilinguals is the same in Sessions 1 and 2 (see Fig. 2). Noteworthy, explorative analyses in leftward asymmetry subgroup indicated a trend toward a Group-by-Session-by-Condition interaction [$F\ (1,13) = 3.66$, $p = 0.07$], suggesting a less significant session effect in bilinguals vs monolinguals with leftward asymmetry.

4. Discussion

The aim of the present study was to determine whether the ACC sulcation pattern, a marker of early neurodevelopment, modulates the effect of bilingual experience on conflict monitoring. To answer this question, we contrasted the behavioral performance of German-Italian bilinguals and Italian monolinguals during an executive control task (*i.e.*, the Flanker task) using a stratification based on the participants' ACC sulcation pattern.

We found higher cognitive control efficiency (*i.e.* faster RTs) for monolinguals with leftward ACC asymmetry vs monolinguals with ACC symmetrical patterns. These results replicate previous findings in monolingual children and adults (Borst et al., 2014; Cachia et al., 2014; Huster et al., 2009). Using the same brain morphometry method as in the current study, lower Stroop interference scores (*i.e.*, faster RTs and lower error rates) were found for children at age 5 (Cachia et al., 2014) and age 9 (Borst et al., 2014) with asymmetric ACC. Our study confirms a correlation between ACC sulcal pattern and cognitive control efficiency, and provides further evidence that inter-individual differences in monolinguals' executive abilities partly arise from the fetal stages of brain development, when the ACC sulcal patterns are determined (Chi, Dooling, & Gilles, 1977; Feess-Higgins & Larroche, 1987) under the effects of genetic and environmental factors (Fernández, Llinares-Benadero, & Borrell, 2016; Ronan & Fletcher, 2015; Zilles, Palomero-Gallagher, & Amunts, 2013). The precise mechanism underlying cortical folding is still unknown. However, several factors likely contribute to the prenatal processes that influence the shape of the folded cerebral cortex, including cortical growth (Chenn & Walsh, 2002; Haydar, Kuan, Flavell, & Rakic, 1999; Kuida, Zheng, Na, & Kuan, 1996; Toro & Burnod, 2005), apoptosis (*i.e.*, programmed cell death) (Haydar et al., 1999), differential expansion of superior and inferior cortical layers (Kriegstein, Noctor, & Martínez-Cerdeño, 2006; Richman, Stewart, Hutchinson, & Caviness, 1975), differential tangential expansion

Table 1
Mean (M) and Standard Deviation (SD) of the Conflict effect scores (differential RTs: Incongruent minus Congruent trials) in Session 1 and Session 2 of the Flanker task for bilinguals and monolinguals with different ACC sulcal patterns. Differences between bilinguals and monolinguals were obtained with mixed-design ANOVA and post hoc Tests.

	Session 1						Session 2					
	Billingual		Monolingual		Differences		Billingual		Monolingual		Differences	
	M	SD	M	SD	F	*p*	M	SD	M	SD	F	*p*
Left Asymmetry	145.09	13.15	85.88	10.72	8.21	0.01	111.95	7.48	89.68	18.87	1.23	0.28
Symmetry	101.96	18.87	161.43	40.34	1.10	0.31	62.07	11.06	141.24	28.27	4.04	0.07

(Ronan et al., 2014) and/or structural connectivity through axonal tension forces (Dehay, Giroud, Berland, Killackey, & Kennedy, 1996; Hilgetag & Barbas, 2006; Van Essen, 1997). The ACC sulcal pattern has been found to be stable from childhood to adulthood in a large longitudinal study of 75 typically developing individuals spanning 7–32 years (Cachia et al., 2016). Available data also suggest that cortical shape within the anterior cingulate region is most-likely stable during the first years after birth, as evidenced by recent longitudinal studies reporting absent or minimal change in both cortical surface curvature (Li et al., 2014) and cortical surface expansion (Li et al., 2013) between 0 and 2 years as well as a continuous gyrification in this region after age of 6 (Mutlu et al., 2013).

Our analyses showed that the behavioral performance of the bilingual group was significantly affected by morphological differences among participants, indicating sulcal variability as a potential predictor of cognitive control efficiency in adulthood. Remarkably, however, an opposite pattern of correlation between ACC sulcal pattern and Flanker RTs was found for bilinguals and monolinguals, bilinguals with leftward ACC asymmetry showing poorer cognitive control efficiency (*i.e.* slower RTs) than bilinguals with ACC symmetrical patterns. This structural-behavioral pattern of correlation remained stable for both groups across testing sessions.

Previous morphometric studies showed that individual differences in brain structure might predict later language skills in monolinguals (Deniz Can, Richards, & Kuhl, 2013) and affect language outcomes in bilinguals (Qi, Han, Garel, San Chen, & Gabrieli, 2015; Yamamoto & Sakai, 2017). If our results confirm previous literature in stressing the long-term impact of early neuroanatomical factors on human executive abilities beyond childhood, a higher cognitive control efficiency (*i.e.*, faster RTs) in the second session of the Flanker for bilinguals suggests an advantage for that group in processing conflict information, possibly due to a life-long experience of linguistic conflict. In Abutalebi et al. (2012), based on the same participants' sample, faster RTs for the bilingual group in the second session of the Flanker correlated with a decreased activation in the dorsal ACC exclusive to bilinguals. These findings were interpreted as suggesting a marked adaptive change in response to conflict for the bilingual group, *i.e.* a more efficient use of the ACC in monitoring nonlinguistic cognitive conflicts. However, adding a critical piece of information to previous literature, our study points to a compensatory effect of bilingualism to early neurodevelopmental factors, an effect not detectable in monolingual controls. It is thus possible that long-term exposure to a second language may overcome the known correlation between leftward asymmetry and better cognitive conflict resolution, at least in terms of better adaptation to conflicts. One possibility is that the effects found here are due to the early exposure to a second language. Our bilingual participants were all early bilinguals who acquired L2 at the age of kindergarten. It remains to be tested if such compensatory effects to early neurodevelopmental factors may be found in subjects who acquire an L2 later in life (e.g. during adulthood).

It is important to note that our study only involved females. Our findings may therefore not generalize to males. A previous study in patients with psychosis reports that the effect of the ACC sulcal pattern asymmetry on semantic fluency differs in males and females (Clark et al., 2010). Such differential effect may be related to the gender-related differences in the distribution of the ACC sulcal pattern asymmetry (Leonard, Towler, Welcome, & Chiarello, 2009; Yücel et al., 2001). Besides the classical issues related to sample size and composition, a potential limitation of this study may consist in the lack of mechanistic explanations for the opposite structural-behavioral pattern of correlation for bilinguals and monolinguals. Indeed, at best we are able to provide only a tentative explanation of our results, *i.e.*, a possible compensatory effect of bilingualism to early neurodevelopmental factors, in terms of better adaptation to conflict resolution. Beyond the merit of such explanations, what the present study highlights is that behavioral experiences may affect cognitive performance in different ways depending on the anatomical substrata of the brain that predates these experiences. Why is this so? This has to be further investigated, but we believe that our first evidence may open an avenue to a different field, *i.e.*, the interaction between behavioral differences, brain structure and early neurodevelopment. Not all behavioral experiences are going to affect people in the same way. One reason for this may indeed be differences in brain structure.

More data from different populations acquired through multimodal brain-imaging approaches are thus needed to formulate fine-grained explanations for the findings reported in this study. For instance, at present we have no precise explanation on why bilinguals with left asymmetry performed worse than their monolingual peers in Session 1. As a comparison, the analysis of the behavioral data from Session 1 in Abutalebi et al.'s (2012) original study did not reveal significant difference between the two groups. In the current study, we report that in Session 1 monolinguals with left asymmetry significantly outperformed bilinguals. In other words, we do not observe any bilingual advantage for participants with leftward asymmetry specifically in Session 1. However, we hope that the present first investigation of the interaction of early neurodevelopmental and later environmental factors may open up new opportunities for exploring neural and cognitive differences between different populations (such as bilinguals and monolinguals). These types of studies may add further insight into the hotly debated issue of bilingual cognitive benefits. As the neuroscience of bilingualism has predominantly focused on the impact of bilingual experience on brain structure and function (e.g. Pliatsikas, DeLuca, Moschopoulou, & Saddy, 2017), this type of evidence may add further grounds for discussion: besides the aforementioned methodological differences between behavioral studies that do or do not report cognitive benefits for bilinguals (see Zhou & Krott, 2016; and Valian, 2015, for review), one critical explanation might be found in the inter-individual variability of ACC sulcal patterns.

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