

Bilingualism Tunes the Anterior Cingulate Cortex for Conflict Monitoring

Jubin Abutalebi^{1,2}, Pasquale Anthony Della Rosa¹, David W. Green³, Mireia Hernandez^{4,5}, Paola Scifo¹, Roland Keim¹, Stefano F. Cappa¹ and Albert Costa^{4,6}

¹Vita-Salute San Raffaele University and Division of Neuroscience, San Raffaele Scientific Institute, 20132 Milan, Italy, ²Division of Speech and Hearing Sciences, University of Hong Kong, Pokfulam, Hong Kong, ³Cognitive, Perceptual and Brain Sciences, University College London, WC1E 6BT London, UK, ⁴Deptmet of Technology, Universitat ePompeu Fabra, 08018 Barcelona, Spain, ⁵Center for Mind/Brain Sciences, University of Trento, 38122 Trento, Italy and ⁶Institucio Catalana de Recerca i Estudies Avancats (ICREA), Barcelona, Spain, 08018

Address correspondence to Dr Jubin Abutalebi, Faculty of Psychology, Vita-Salute San Raffaele University, Via Olgettina 58, 20132 Milano, Italy. Email: abutalebi.jubin@hsr.it.

Monitoring and controlling 2 language systems is fundamental to language use in bilinguals. Here, we reveal in a combined functional (event-related functional magnetic resonance imaging) and structural neuroimaging (voxel-based morphometry) study that dorsal anterior cingulate cortex (ACC), a structure tightly bound to domain-general executive control functions, is a common locus for language control and resolving nonverbal conflict. We also show an experience-dependent effect in the same region: Bilinguals use this structure more efficiently than monolinguals to monitor non-linguistic cognitive conflicts. They adapted better to conflicting situations showing less ACC activity while outperforming monolinguals. Importantly, for bilinguals, brain activity in the ACC, as well as behavioral measures, also correlated positively with local gray matter volume. These results suggest that early learning and lifelong practice of 2 languages exert a strong impact upon human neocortical development. The bilingual brain adapts better to resolve cognitive conflicts in domain-general cognitive tasks.

Keywords: anterior cingulate cortex (ACC), bilinguals, brain plasticity, cognitive control, event-related fMRI, VBM

Introduction

Everyday life requires us to monitor cognitive conflicts induced by distracting information from either perceptual sources (e.g., competing traffic signs when driving) or internal sources (e.g., thoughts about matters irrelevant to the current goal). The anterior cingulate cortex (ACC) is an important component in the neural circuit mediating cognitive control and one intimately tied to monitoring conflicting information (Carter et al. 1999; Botvinick et al. 2004). Language use also requires cognitive control and plausibly recruits a similar circuit (Abutalebi and Green 2007). The demand for such control is most evident in bilinguals, and such speakers provide an opportunity to test the generality of the neural mechanisms involved in cognitive control.

Bilinguals must monitor and select the relevant language for discourse. For example, when a speaker of just one of the languages in current use enters conversation, each bilingual must deliberately switch away from the language the new person does not know to the one that they do know. They must react to the change in circumstance and ensure that they continue speaking in that language even when addressing the other original participant who speaks both of their languages. Here, they can act proactively. In contrast to monolingual speakers, bilinguals have to avoid items from the nontarget language that expresses the same concept. When a Spanish-

English bilingual addresses a monolingual English speaker about neuroscience, she has to withhold the Spanish word “neurociencia” (Rodríguez-Fornells et al. 2002; Abutalebi and Green 2007). In most situations, bilinguals are successful in selecting the intended language, but sometimes, a word of the nontarget language intrudes and a cross-language speech error arises. This common observation indicates that in the bilingual brain, words from the different languages compete with each other. Such unwanted interference between languages can be characterized as “language conflict.”

How do bilinguals control their 2 language systems and avoid these language conflicts? Recent work (Crinion et al. 2006; Abutalebi et al. 2007, 2008; Wang et al. 2007, 2009; Guo et al. 2011; Garbin et al. forthcoming; Zou et al. forthcoming) suggests that bilinguals use neural regions similar to those responsible for nonverbal cognitive control including the dorsal ACC, the prefrontal cortex, and the caudate nuclei. A limited number of studies have examined the neural response to nonverbal conflict in bilinguals using either a nonverbal interference task (Bialystok et al. 2005; Luk et al. 2010) or a nonverbal switching task (Garbin et al. 2010). Activation associated with the control of interference typically included the ACC/pre-Supplementary Motor Area (SMA). However, these studies have not also included a language control task. It therefore remains to be determined whether the neural regions supporting language control are the same as those supporting cognitive control in nonverbal domains.

In order to directly examine the link between the regions involved in control of language conflict and those involved in cognitive control, more generally, we need to examine the regions involved within the same study. Accordingly, we asked bilinguals to perform a language control task (i.e., language switching) and a nonverbal conflict task (a flanker task) during the same event-related functional magnetic resonance imaging (er-fMRI) session

If bilinguals constantly use networks that support domain-general cognitive control, then the interesting question arises as to the neural consequences of this extra use of executive control. Our hypothesis was that early and lifelong bilingualism (i.e., practice in monitoring language conflicts) induces beneficial neural changes upon brain structures mediating cognitive control, specifically the ACC. Bilinguals we supposed might be better adapted to manage interference/conflict.

We investigated the neurofunctional and structural consequences of bilingualism by comparing our group of high-proficient bilinguals who acquired their second language relatively early in life with a group of monolinguals who

performed the same nonverbal task. In order to ensure comparability with the bilingual group, monolinguals also performed a language-switching task but within the one language they knew. We hypothesized that in bilinguals at least there would be a strong correlation in the ACC between the functional activation induced by resolving nonverbal conflict and gray matter (GM) density. Voxel-based morphometry (VBM) is commonly employed to detect regional group differences in GM (or white matter [WM]), tissue volume, density, or concentration (e.g., Maguire et al. 2000; Schneider et al. 2002; Mechelli et al. 2004; Bermudez et al. 2009). However, the technique can also be used to investigate correlations between regional GM measures and clinical, neuropsychological, or behavioral-functional variables (Ashburner and Friston 2000; Good et al. 2001). We implemented the latter approach and thus performed a hypothesis-driven VBM “functional-structural” correlation study in order to assess differences between bilinguals and monolinguals in the strength of the association between fMRI activity driven by conflict and GM density in the ACC.

If bilinguals are better adapted to manage conflict in a behavioral task, then they may also more readily adapt to the specific kind of conflict. We divided the nonverbal conflict task into 2 sessions in order to investigate adaptive changes in each group. Prior behavioral research has found a bilingual advantage in a range of nonverbal conflict tasks (Bialystok 2009), but functional changes over time have not been examined.

Materials and Methods

Subjects

The participants comprised 17 healthy high-proficient German-Italian right-handed bilinguals (all females; mean age 23.35, standard deviation [SD] ± 4.59) and 14 healthy Italian right-handed monolinguals (all females; mean age = 26.55, SD ± 4.15) with a comparable educational (i.e., university students or graduates) and socioeconomic background. Individuals with a history of inpatient psychiatric care, neurological disease, or head injury were excluded. Bilingual participants came from South Tyrol, a bilingual region in Italy in which the first language (L1) is German. However, Italian (L2) is also acquired early in life (i.e., kindergarten age). We assessed their language proficiency using translation tasks (see Perani et al. 1998; Abutalebi et al. 2007). Monolingual participants were from mainland Italy.

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

Stimuli, Design, and Experimental Procedures for the fMRI Studies

Language Switching

Bilinguals. We investigated language switching using er-fMRI and a naming paradigm. The required language was indicated by the color of the image (green for German and blue for Italian). We contrasted switching trials, where the language of the specific trial differed from that of the preceding trial (i.e., naming a picture in L1 after naming one in L2 and vice versa), and non-switch trials, where the language of that specific trial did not differ from the preceding one (e.g., naming a picture in L1 after naming one in L1). This experimental paradigm has been successfully employed in behavioral studies (e.g., Costa and Santesteban, 2004).

For both languages, 32 different pictures were selected from the Snodgrass battery (Snodgrass and Vanderwart 1980). All pictures, 8.5 × 8.5 cm, were presented in both conditions (naming in L1 and in L2).

Each picture was repeated 3 times totaling 96 stimuli for each language. Two pr randomized lists were created to balance the alternation of switch trials and non-switch trials (with a maximum number of five non-switch trials before each switch trial). Across 2 experimental runs, there were 48 switch trials (for each language) and 48 non-switch trials (for each language). We also maximized the number of trials (16) between each picture occurring in the same language and between languages in order to limit priming effects and cross-linguistic interference. All stimuli were controlled for frequency based on the German (Genzel et al. 1995) and Italian norms (Laudanna et al. 1995). The experimental runs were randomized across participants.

Monolinguals. Monolingual participants completed a different naming task in order to reproduce an experimental setting as similar as possible to the bilingual setting. An artificial switching context consisted in the production of a noun or verb associated with the same set of 32 pictures selected for the bilingual experiment (for prior use of this procedure, see Abutalebi et al. 2008). Stimuli were also randomized and pictures separated by the maximum number of trials between first and second appearance as in the bilingual paradigm. Color again coded for the required task, in this case, red for nouns and green for verbs.

Practice and Procedure

Prior to scanning, participants practiced naming pictures according to the color cues using a set of pictures different from those in the scanning session. We supposed that such practice would mitigate any prior semantic associations between color and response (e.g., between green and “go” or between red and “no go”), though we stress that any such associations are not material because our interest lay in the difference between switch and non-switch trials and this difference is unconfounded by such associations. Participants were also trained to minimize head, jaw, and tongue movement while naming in order to reduce the amount of movement artifacts. During the experiment, participants viewed projected pictures (available for 2 s each) via a mirror system attached to the top of the head coil. In order to optimize statistical power (Dale 1999), the inter stimulus interval (ISI) was jittered with a blank screen of either 1880 or 3550 or 4950 ms appearing between each trial. Participants named each picture out loud but technical constraints precluded the recording of reaction times (RTs), but we were able to perform an error analysis.

The Flanker Task (i.e., Conflict Effect) in Monolinguals and Bilinguals

Participants indicated as quickly and as accurately as possible whether a central arrow (the target) pointed to the right or left by pressing 1 of 2 buttons on a response pad. Accuracy and RT were recorded. The target arrow was presented along with 4 flanker stimuli: Arrows pointing in the same direction as the target (congruent trials) or in the opposite direction (incongruent trials) or flanking lines without arrowheads (neutral trials). A fixation cross stayed on the center of the screen during the whole trial (Fig. 1).

As in Fan et al. (2005), the target stimulus could be preceded by different visual cues (no cue, center cue, double cue, and spatial cue) allowing for the calculation of the so-called alerting and orienting effects (Costa et al. 2008). However, given our purpose, we focused only on the conflict effect. Congruent, neutral and incongruent trials were distributed evenly across the different type of cues and presented in 2 experimental runs of 96 trials each under a different random order. Our key behavioral contrast between congruent and incongruent trials was therefore based on 64 trials for each type across the 2 runs. The event presentation is illustrated in Figure 1.

During the fMRI experiment, stimuli were presented to participants through the same system and software as in the language switching study (see above). The ISI was the same as in the language switching study. Before scanning, all participants underwent a training session consisting of 20 trials.

For both groups, the two language switching runs and two flanker runs were always presented in a consecutive manner, although the order of presentation of the language switching task and the flanker task was counterbalanced across subjects in each group.

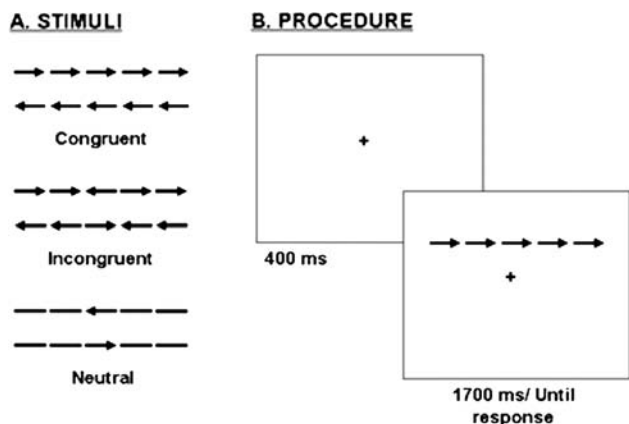


Figure 1. Schematic representation of the flanker task. The stimuli are illustrated in (A). In congruent trials, the direction of the central arrow was the same as that of the flanker arrows, while in the incongruent trials, the direction of the central arrow and the direction of the flanker ones was different. There were also some filler trials (i.e., neutral trials) in which the central arrow was flanked by lines without arrowheads. In (B), the events in a trial of the flanker task are reported. First, a fixation cross appeared at the center of a computer screen. After 400 ms, a row containing the 5 arrows appeared remaining for 1700 ms. Subjects were instructed to pay attention only to the arrow in the center of the row and to respond as fast as possible in what direction the middle arrow pointed to. If pointed to the left, they were asked to press a button of the response box and if pointed to the right, they were asked to press a different button of the response box. The conflict effect properly is calculated by subtracting responses of congruent trials from those of incongruent trial.

Imaging Procedures, Acquisition, Processing, and Statistical Analysis

MR images were acquired with a 3-T Achieva Philips MR scanner (Philips Medical Systems, Best, NL) equipped with an 8-channel sense head coil.

For functional scans, an echo planar imaging (EPI) fMRI event-related scan was used (time repetition [TR] = 2400 ms, time echo [TE] = 30 ms, Field of View = 240 × 240, matrix size = 128 × 128, 30 contiguous axial slices per volume, 210 volumes for each run of language switching and 222 volumes for each run of the flanker task, slice thickness = 4 mm, sense reduction factor = 2). Ten dummy scans preceded each run to optimize EPI image signal.

For the structural imaging, an axial high-resolution structural MRI was obtained for all subjects (magnetization prepared rapid gradient echo, 150 slice T_1 -weighted image, TR = 8.03 ms, TE = 4.1 ms; flip angle = 8°, TA = 4.8 min, resolution = 1 × 1 × 1 mm).

fMRI Studies

Data were preprocessed and analyzed using SPM5 (Statistical Parametric Mapping; Wellcome Department of Cognitive Neurology, London, UK). Slice-timing correction to correct for the different sampling times of the slices was performed by interpolating the voxel time series using sinc interpolation and resampling with the middle (15th) slice in time as a reference point. All functional volumes were realigned to the first one in the time series to correct for between-scan motion and subsequently realigned to the mean of all images. The structural T_1 -weighted volume was first segmented to create a bias-corrected image and correct for intensity inhomogeneities. This bias-corrected structural image was in turn segmented using the “unified segmentation” function in SPM5. This algorithm is based on a probabilistic framework that enables image registration, tissue classification, and bias correction to generate a normalization transformation.

The derived spatial transformations for each participant were applied to the original structural and realigned functional volumes, in order to place them into standardized Montreal Neurological Institute (MNI) space. After normalization, all volumes were resampled in 2 × 2 × 4 mm voxels. Finally, the functional T_2^* -weighted volumes were smoothed using a Gaussian kernel with 8 mm full-width at half-maximum (FWHM), in order to account for any residual between-

subject variation and allow application of Gaussian random field theory to provide for corrected statistical inference.

Functional data were analyzed using SPM5 employing a random effects model implemented into a two-level procedure. At the first level, in a subject-specific analysis, we specified a general linear model including 16 effects of interest: 4 events corresponding to the switching context (switches into L1 and L2, non-switch trials in L1 and in L2 for the bilingual group; switches to nouns and verbs, non-switch trials for nouns and verbs for the monolingual group) and 12 events corresponding to the flanker task. These latter events resulted from crossing the values of our primary factor, flanker type (neutral, congruent, and incongruent) with type of visual cue (no cue, center cue, double cue, and spatial cue).

All effects were modeled by convolving a delta function of each event type with the hemodynamic response function to create regressors for each effect. Movement parameter estimates produced by the realignment procedure were entered as covariates of no interest in the first-level single-subject design matrices, in order to correct for potential movement artifacts. Temporal autocorrelation was treated with an AR(1) regression algorithm setting a high-pass filter of 128 s. We used the global scaling option to adjust for global differences over the 4 separate runs (2 for each task).

Task Effects (Language Switching and Conflict Monitoring)

One-sample *t*-test. In order to assess the effects of conflict monitoring, namely “the conflict effect,” we first focused on 2 comparisons of interest in each group separately: switch versus non-switch trials in the naming task and incongruent versus congruent trials in the flanker task. For the switching contrast, we compared all switching trials versus all non-switching trials (independently of the language in use in the bilingual group) since this comparison may reveal areas engaged during language control (Abutalebi et al. 2007). For the conflict effect in the flanker task, the comparison between incongruent and congruent trials was computed collapsing across cue type for both groups of subjects. For each of the four comparisons of interest (2 contrasts × 2 groups), a contrast of parameter estimates was calculated in a voxelwise manner to produce a “contrast image” for each participant. For each contrast of interest, a one-sample *t*-test was performed for every voxel in the brain to obtain population inferences for each group. The resulting set of voxel values for each contrast constituted the SPM{t}. The threshold for SPM{t} maps was set to $P < 0.001$ uncorrected for multiple comparisons at the voxel level. The statistical threshold for the spatial extent test on the clusters was set at $P < 0.05$ cluster family-wise error (FWE) correction over the search volume for each contrast.

Conjunction analysis. Subsequently, in order to test the hypothesis that language-switching and the conflict effect contrasts activate common areas, we conducted a conjunction analysis for each of the 2 groups over the switching contrast and the conflict effect, using a second level two sample *t*-test and testing against conjunction null (Nichols et al. 2005; see also Friston et al. 2005). For the conjunction analysis, individual voxels were significantly activated only if each subject activated the identical voxel at or above a height threshold of $P < 0.05$ (uncorrected) in each of the 2 contrasts of interest. Thus, results were assessed at a conjunction threshold of $P < 0.0025$ (0.05×0.05).

As we hypothesized that activation produced by language switching should overlap with that produced by conflict in brain areas that subtend domain-general cognitive control, and specifically ACC, we used a reduced search volume with a radius of 10 mm centered on the maxima of the 2 main contrasts (language-switching and conflict effect) as proposed by Friston et al. (2005). Activations in the ACC were small volume corrected for FWE at voxel level ($P < 0.05$) around cluster peak coordinates.

Conflict Monitoring

Search volume for the ACC cluster. Given that we had an a priori hypothesis that the conflict effect of the Flanker task would activate the ACC (Botvinick et al. 1999; Fan et al. 2003, 2005) and since we identified the ACC as the region of activation common to both tasks

(i.e., language-switching and conflict effect) for all further analysis, we limited our search to the ACC region defined by the 2 clusters of activation elicited by the conflict effect contrast in each group of participants. Specifically, MarsBar (Brett et al. 2002) was used to define 2 binarized masks of the ACC cluster of activation based on the “functional” conflict effect contrast (incongruent trials vs. congruent trials of the Flanker task) specified at the random effects level for each group (bilinguals and monolinguals). The contrast images at the group level were thresholded at a voxelwise intensity threshold of $P < 0.001$ and $P < 0.05$ corrected for spatial comparisons across the whole brain. Mask 1 corresponded to the ACC cluster highlighted in the bilingual group SPM(t)-statistic map resulting from the one-sample t -test for the conflict effect (see previous section). Mask 2 corresponded to the ACC cluster highlighted in the monolingual group SPM(t)-statistic map resulting from the one-sample t -test for the conflict effect (see previous section). A single ACC conflict effect region resulting from the “union” of Mask 1 and Mask 2 was then created. This ACC region was generated using the ImCalc tool in SPM5. The union was computed as the sum of all voxels included in each group for the conflict effect contrast (a value of 1 was assigned to any activated voxel in the ACC cluster between the 2 groups and 0 to all the voxels outside the ACC activations). The search volume for this region was $73\,840\text{ mm}^3$ corresponding to 4615 voxels.

Two-sample t -test (magnitude of conflict effect). To test for differences in the magnitude of the conflict effect between the 2 groups (monolinguals vs. bilinguals and vice versa), a second level analysis was performed using a two-sample t -test. SPM(t) maps were thresholded at $P < 0.001$ uncorrected for multiple comparisons at the voxel level and $P < 0.005$ cluster FWE correction over the search volume.

Session effects (bilinguals vs. monolinguals). Since we observed a significant reduction of the conflict effect in the bilingual group, we further specified the neural response in bilingual and monolingual participants. In a second-level analysis, contrast images for each subject were entered in a 2×2 mixed design analysis of variance (ANOVA), with the conflict effect for each session (Session 1 and Session 2) as a within-subject factor and group (bilinguals and monolinguals) as a between-subjects factor. Within this ANOVA, we isolated brain activations in the ACC as a function of group by contrasting 1) incongruent trials versus congruent trials in Session 1 for bilinguals, 2) incongruent trials versus congruent trials in Session 2 for bilinguals, 3) incongruent trials versus congruent trials in Session 1 for monolinguals, and 4) incongruent trials versus congruent trials in Session 2 for monolinguals. The cluster of activation in ACC was revealed by the main effect.

All statistical maps were thresholded at a voxelwise threshold of $P < 0.005$ (uncorrected). We subsequently limited our search to the ACC conflict effect region ($73\,840\text{ mm}^3$) when we evaluated the contrasts for the main effect of the conflict effect broken down by session and group. As in the previous analysis (two-sample t -test), for the definition of activation extent, we applied a correction for multiple spatial comparisons within the ACC conflict effect region as a more stringent test of our a priori hypothesis.

To increase the power of this more fine-grained analysis, we examined conflict effect differences in the ACC computing SPM(t) maps contrasting monolinguals versus bilinguals for each of the 2 sessions. Results were small volume corrected at the voxel level using a sphere with 10 mm radius around the ACC cluster peak coordinates of the contrast between monolinguals versus bilinguals assessing differences in the magnitude of the conflict effect (two-sample t -test).

VBM-Behavioural/fMRI Correlational Analysis

Customized VBM8-DARTEL Preprocessing

Data preprocessing were performed using SPM8 (Statistical Parametric Mapping software; <http://www.fil.ion.ucl.ac.uk/spm>) implemented in Matlab 7.4 (R2007a) (MathWorks, Natick, MA). For morphometric analysis of the data, we used VBM. A customized VBM approach was implemented following the combination of the VBM8 toolbox ([\[dbm.neuro.uni-jena.de/vbm.html\]\(http://dbm.neuro.uni-jena.de/vbm.html\)\) and the Diffeomorphic Anatomical Registration through Exponentiated Lie algebra toolbox \(DARTEL\) \(Ashburner 2007\). The VBM8 toolbox was used to minimize the noise level of the segmentation. The DARTEL toolbox provided instead a high-dimensional normalization protocol expected to increase registration accuracy, thereby increasing sensitivity and improving localization in our comparisons of bilingual and monolingual subjects.](http://</p>
</div>
<div data-bbox=)

Preprocessing included the following steps: 1) automatic reorientation of the all structural images to the anterior commissure; 2) segmentation of the anatomical images using the VBM8 toolbox; and 3) applying the DARTEL approach for registration, normalization, and modulation.

As a first processing step, to provide better initial estimates for the segmentation algorithm, a customized Matlab script was used to manually set the image space origin to the anterior commissure and align each image with the plane of the anterior and posterior commissures of the IXI-template included in the VBM8 toolbox.

At a second step, images were corrected for bias field inhomogeneities, registered using linear (12-parameter affine) transformations, and tissue-classified into GM, WM, and cerebrospinal fluid (CSF). The VBM8 toolbox improves tissue classification as additional tissue probability maps are included to better model CSF and other non-brain voxels. The segmentation procedure was further refined by applying 2 denoising methods. The first method is a spatially adaptive nonlocal means denoising filter (Manjon et al. 2010). This filter removed noise while preserving edges. The second method is a classical Markov random field approach, which incorporates spatial prior information of adjacent voxels into the segmentation estimation (Rajapakse et al. 1997). This filter removed isolated voxels, which were unlikely to be a member of a certain tissue class and also closed holes in clusters of connected voxels of a certain class, resulting in a higher signal-to-noise ratio of the final tissue probability maps. The segmentation procedure from the VBM8 toolbox produced registered rigid-body aligned tissue segments for each image in the MNI template space.

At a third step, the GM and WM segments were input into DARTEL in order to create a customized DARTEL template, which reflected a high-dimensional normalization of the average (local) anatomy of all subjects (both bilingual and monolingual group). DARTEL then registered the individual tissue segments to the template in order to obtain the individual deformation fields. These individual tissue deformations were then used to warp and modulate each participant’s GM tissue maps for nonlinear effects in order to account for brain sizes. In the resulting images, each voxel represents an absolute amount of brain volume, equivalent to the brain volume per unit prior to normalization and because we applied a nonlinear spatial registration the same voxel location in each image can be assumed to correspond to the same brain structure.

To summarize, in this approach, a DARTEL template is created based on the registered tissue segments (GM and WM) in MNI space that are produced by the VBM8 segmentation procedure. Next, all individual deformation fields obtained via the DARTEL toolbox are used to warp and modulate the GM tissue segments to match this template.

Finally, the modulated GM and segments were written with an isotropic voxel resolution of 1.5 mm and smoothed with a 4 mm FWHM Gaussian kernel to increase signal to noise ratio. The considerably improved anatomical overlap of individual tissue maps obtained through the VBM8-DARTEL approach allowed the use of a small kernel width and thus facilitated a high spatial resolution of the voxel-level inference. After this preprocessing, we obtained smoothed modulated normalized data that we used for the statistical analysis.

Behavioral/Functional and Structural Data (Statistical Analysis)

To better interpret the significant fMRI findings and to test the association between regional GM volume in the ACC and the “behavioral” and “functional” conflict effect (Flanker incongruent-congruent), we performed 2 different analysis aimed at 1) establishing a “behavioral-structural correlation” between the ACC conflict effect region volumes and behavioral conflict effect values for all the participants and 2) to test if the association between GM density in the partial ACC volumes and the functional conflict effect is significantly stronger for the bilingual group relative to the monolingual group.

Behavioral Structural Correlation

The purpose of this analysis was to assess the relation between GM volumes extracted from the ACC conflict effect region and the behavioral conflict effect measured for all subjects. Nonsmoothed and modulated partial GM volumes in liters were extracted with the Easy Volume toolbox (http://www.sbir.ced.ac.uk/cyril/cp_download.html) (Pernet et al. 2009) from the ACC conflict effect region for each subject in both groups. The effect of GM volumes on behavioral measures was examined through a simple linear regression analysis. Assumptions of linear regression were confirmed. The predictor variable (GM volumes) was normally distributed ($D(31) = 0.14$). Residuals of the predictor variable were consistent across values, showing homoscedasticity (Breusch-Pagan test: $BP(1) = 2.56$, $P = 0.10$; Koenker Test: $K(1) = 1.46$, $P = 0.22$) and were not autocorrelated (Durbin-Watson test: $DW = 1.68$).

VBM-Based Group Comparison of Associations between Conflict Effect Activity and ACC Structure in Bilinguals and Monolinguals

In order to test for group differences in terms of association strength between GM density in the ACC conflict effect region and the functional conflict effect between the bilingual and the monolingual group, we used the ACC conflict effect region as an exclusive mask in a VBM-based pairwise group comparison of associations. MarsBar (Brett et al. 2002) was employed to extract the mean blood oxygen level-dependent (BOLD) signal time series in the ACC for the functional conflict effect contrast (incongruent trials vs. congruent trials parameters of the Flanker task) for each individual in the bilingual group from Mask 1 (see search volume for conflict effect section) and for each individual in the monolingual group from Mask 2 (see search volume for conflict effect section). Specifically, a time series was extracted from the mean BOLD signal of all voxels within the mask defining the ACC for each single-subject contrast. This procedure resulted in one average fMRI contrast value for the conflict effect for each ACC region specific to each subject.

Groupwise comparison of the association between structural data (smoothed and modulated GM tissue segment for each subject) and functional data (functional conflict effect) for each subject was performed using a general linear model implemented in SPM5 (Statistical Parametric Mapping) with the conflict effect functional values defined as a covariate and the ACC conflict effect region as the explicit mask. This type of analysis is equivalent to an interaction model testing for different regression slopes in bilinguals and monolinguals between GM density in the ACC (defined by the between-group ACC conflict effect region mask) and conflict effect activity in each voxel (conflict effect activity by group interaction). Because we expected variance to differ between samples, we applied a nonsphericity correction. We restricted the statistical analysis to areas with a minimum probability value of 0.1 to avoid possible edge effects around tissue borders. Within the ACC mask, we set significance at a threshold of uncorrected $P < 0.005$.

Results

Behavioral Results

Proficiency Assessment

A quite similar pattern of performance was observed on the word lists to be translated from L1 to L2 and vice versa indicating that our participants may be classified as high-

proficient bilinguals (for details, see Supplementary Table S1). The means for percentages of errors for naming in the 2 languages for the bilingual group were, respectively, 1.96% (SD ± 1.32) for L1 and 2.76% (SD ± 1.6) for L2. Within this group, there was no difference for error rates between L1 and L2 ($P = 0.17$). These data underline the high L2 proficiency of our subjects. The mean error percentage of the monolingual group on the nouns was 2.46% (SD 1.13) and was comparable to the L1 naming of the bilingual group

Conflict Effect

We analyzed error rates and RTs in order to address differences in the adaptation to conflict between bilinguals and monolinguals. In both analysis, type of trial (congruent/incongruent) and session were within-subjects factors, and participant group (monolingual/bilingual) was a between-subjects factor (for details, see Table 1). We describe the results of the error analysis first and then focus on the interaction between trial type, session, and participant group in the RT analysis.

In the error analysis, incongruent trials induced fewer correct responses, $F_{1,29} = 10.14$, $P = 0.003$, $\eta_p^2 = 0.259$, though there were more correct responses for these trials in the second session, $F_{1,29} = 6.87$, $P = 0.014$, $\eta_p^2 = 0.192$.

In the RT analysis, there was no overall difference between the groups in mean RT, $F < 1$. There was a significant conflict effect ($F_{1,29} = 145.37$, $P < 0.0001$, $\eta_p^2 = 0.834$) with slower responses to incongruent (Mean: 693 ms, 95% confidence interval [CI] from 651 to 736 ms) compared with congruent trials (576 ms, 95% CI 543–613 ms). RTs were faster in the second compared with the first session, $F_{1,29} = 11.39$, $P = 0.002$, $\eta_p^2 = 0.282$, largely because of faster responses to incongruent trials ($F_{1,29} = 9.41$, $P = 0.005$), $\eta_p^2 = 0.245$. In the bilingual group, as expected, the conflict effect significantly reduced (by 36 ms, 95% CI, 21–53 ms) in the second session ($F_{1,16} = 23.38$, $P < 0.001$, $\eta_p^2 = 0.594$). By contrast, the 11 ms (95% CI, –20–41 ms) reduction for the monolingual group was not significant ($F < 1$, $\eta_p^2 = 0.040$). This result indicates a marked adaptive change in response to conflict for the bilingual group (Fig. 2).

er-fMRI Results

Task Effects (Language Switching and Conflict Monitoring)

Bilinguals: language switching. Between language switching, as calculated by the direct comparison between language switch trials and language non-switch trials, yielded significant clusters of activity bilaterally in the ACC (Brodmann's area [BA] 32) and the left precentral gyrus (BA 6) (see Fig. 3 and Supplementary Table S2).

Monolinguals: language switching. Within-language switching in monolinguals, as calculated by the direct comparison

Table 1

Mean correct RT (milliseconds, ms) and proportion correct (%) as a function of group, session, and trial type (standard error in brackets) for the flanker task.

Group	Session 1				Session 2			
	Congruent		Incongruent		Congruent		Incongruent	
	RT (ms)	%	RT (ms)	%	RT (ms)	%	RT (ms)	%
Monolingual	564 (28.3)	99 (0.01)	693 (34.9)	92 (0.03)	552 (25.7)	99 (0.00)	670 (29.5)	94 (0.02)
Bilingual	604 (25.7)	99 (0.01)	733 (31.6)	96 (0.02)	583 (21.5)	99 (0.01)	676 (26.8)	98 (0.02)

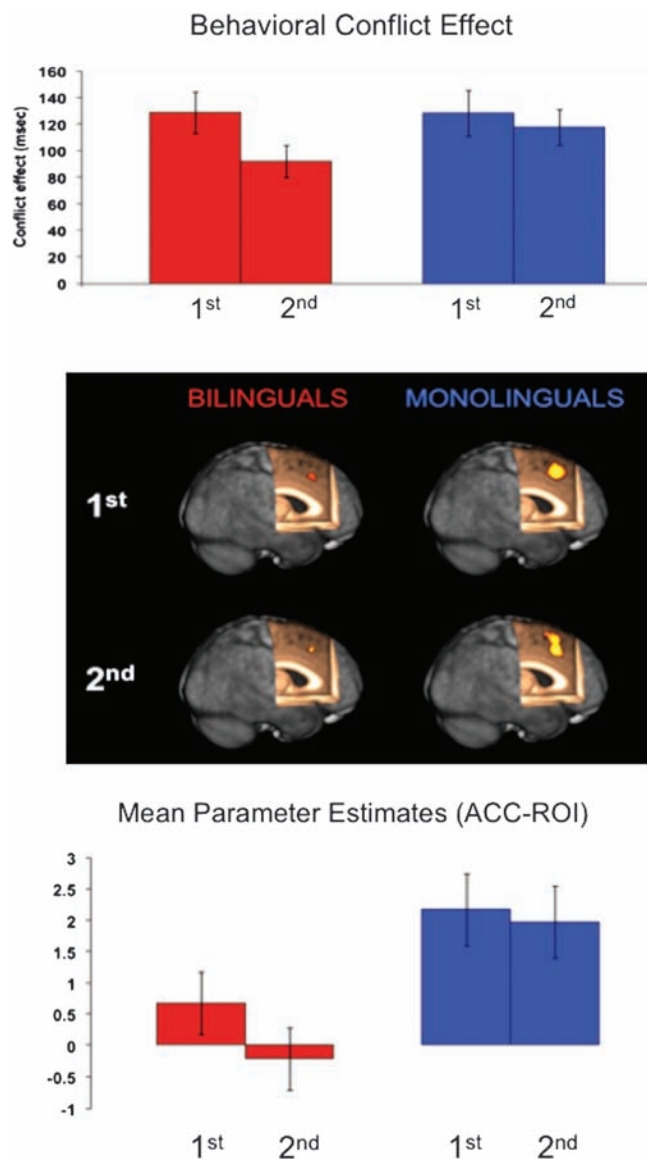


Figure 2. Session effects of the Flanker task. The behavioral conflict effect (red = bilinguals; blue = monolinguals) is displayed on the graph on the top panel. The conflict effect was significantly reduced only for bilinguals during the second session as compared with the first (see Results). The session effects as measured with *erfMRI* are represented in the middle panel. Only bilinguals reported reduced activity in the ACC during the second session. Finally, in the bottom panel, the mean parameter estimates of the BOLD effect in the ACC-region of interest (peak coordinate: $x = 4$, $y = 16$, $z = 44$).

between the noun-verb switch trials and their respective non-switch trials, elicited no significant activity (see Fig. 3 and Supplementary Table S2). However, in order to verify whether or not monolinguals activated similar areas in switching given our a priori hypothesis (see Abutalebi and Green 2008), we used an uncorrected threshold, ($P < 0.001$) with a spatial extent threshold of >15 contiguous voxels. At this lower threshold, the ACC was also activated. (see Fig. 3 and Supplementary Table S2).

Bilinguals: conflict effect. The conflict effect in bilinguals, as calculated by the direct comparison between the incongruent and congruent trials of the flanker task, activated the following

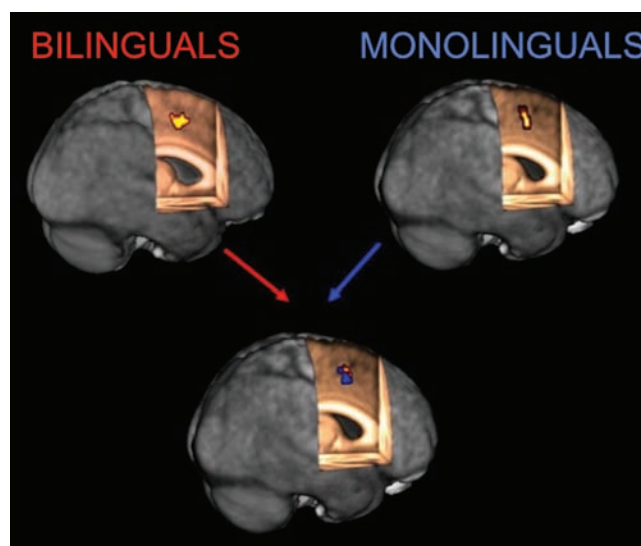


Figure 3. Language conflict and cognitive conflict monitoring in bilinguals and monolinguals. Brain activity elicited when bilinguals (top, left) have to switch between languages and, hence, to control their languages. A large cluster of activity is observed in the ACC (see Supplementary Table S2 for coordinates). Likewise, monolinguals (top, right) activate the ACC (see Supplementary Table S2), although this task is almost artificial in monolinguals. Finally, activity elicited by the conjunction analysis of language switching and conflict monitoring on an executive task (i.e., flanker task) in both groups (bottom). Activity related to bilinguals is depicted in red and in blue for monolinguals. As may be observed, the ACC is commonly engaged by these 2 different tasks. The second level T-maps are rendered on the mean structural image of the study sample (31 subjects) with MRIcron (<http://www.sph.sc.edu/comd/rorden/mricron/>).

brain areas: bilaterally the ACC (BA 32), the left pre-SMA (BA 6), the left fusiform gyrus (BA 19/37) and the left middle occipital gyrus (BA 19), the right Precuneus (BA7), the right fusiform gyrus (BA 37), and the right inferior and superior occipital gyri (BA 18 and 19) (see Fig. 4 and Supplementary Table S2).

Monolinguals: conflict effect. The conflict effect in monolinguals elicited brain activity in the left hemisphere in the following brain areas: ACC (BA 32), the middle frontal gyrus (BA 6), the inferior and superior parietal lobule (BA 7 and 40), the precuneus (BA 7/19), the superior and middle occipital gyrus (BA 19 and 19/37), and in the head of the caudate. In the right hemisphere, brain activity was observed in the ACC (BA 24 and 32), the pre-SMA (BA 6), the inferior parietal lobule (BA 40), the angular gyrus (BA 39), the fusiform gyrus (BA 37), and the middle occipital gyrus (BA 19 and 19/37) (see Fig. 4 and Supplementary Table S2).

Conjunction analysis of language-switching and the conflict effect (i.e., flanker task) for bilinguals. The conjunction analysis, reporting what is commonly engaged by both experimental conditions, revealed bilateral brain activity along the mesial surface of the frontal lobes comprising the ACC (BA 32) and the pre-SMA (BA 6) (see Fig. 3 and Supplementary Table S2).

Conjunction analysis of within-language switching and conflict effect (i.e., flanker task) for monolinguals. Brain activity for the conjunction analysis was observed bilaterally in the ACC (BA 32).

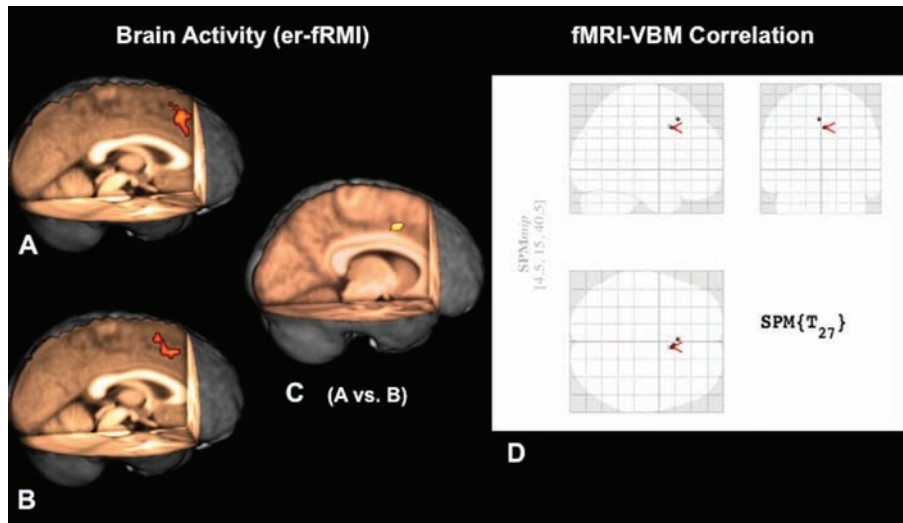


Figure 4. Neurofunctional and structural differences between bilinguals and monolinguals. The neurofunctional differences are reported on the left side of the figure. In (A), the conflict effect for monolinguals who activated more extensively neural structures related to conflict monitoring (i.e., bilaterally the ACC) than bilinguals (B). This was confirmed also by the direct comparison for the conflict effect between monolinguals and bilinguals (C). The reverse contrasts (bilinguals vs. monolinguals) did not yield in significant clusters of brain activity. The right side of the figure reports the structural differences between the 2 groups. In (D), the VBM based correlational group comparison for the conflict effect and ACC GM density. A positive correlation was evident only for bilinguals in the dorsal ACC region. The second level T-maps for the fMRI contrasts (Panels A, B, and C) are rendered on the mean structural image of the study sample (31 subjects) with MRICron (<http://www.sph.sc.edu/comd/rorden/mricron/>).

Conflict Monitoring

Magnitude of conflict effect: direct comparison between monolinguals and bilinguals. Significant effects were observed in terms of magnitude (peak coordinates: $x = 12, y = 8, z = 44, k = 37$ voxels, $P = 0.018$; corrected for search volume) with stronger activity for monolinguals than bilinguals in the “conflict effect region.”

Magnitude of conflict effect: direct comparison between bilinguals and monolinguals. The reverse direct comparison, that is, bilinguals versus monolinguals, yielded no significant brain activity.

Conflict and session effects. Given that the behavioral data indicated a reduced conflict effect in the second session for bilinguals, we investigated the extent to which the 2 groups of participants activated the ACC through the 2 sessions of the flanker task (see Fig. 2).

- First session bilinguals: the conflict effect in the first session exhibited bilateral brain activity in the conflict effect region (BA 32; $x = -4, y = 16, z = 40$, cluster extent = 77 voxels, $P = 0.049$ (corrected)).
- Second session bilinguals: no brain activity related to the conflict effect for the second session was found in the conflict effect region at a FWE-corrected extent threshold. Although when lowering the spatial extent threshold, brain activity related to the conflict effect for the second session was found with a much reduced cluster extent (BA 32; $x = 2, y = 22, z = 44$, cluster extent = 10 voxels).
- First session monolinguals: brain activity was found in the conflict effect region (BA 32; $x = 4, y = 22, z = 44; x = -2, y = 20, z = 44$, cluster extent = 289 voxels, $P < 0.0001$ (corrected)).
- Second session monolinguals: the conflict effect activated the conflict effect region with a larger cluster extent in

the second session than in the first (BA 32; $x = 4, y = 22, z = 40; x = 10, y = 12, z = 44; x = -2, y = 20, z = 40$, cluster extent = 397 voxels, $P < 0.0001$ (corrected)).

- First session monolinguals versus bilinguals: conflict evoked no consistent group increases in activity within the conflict effect region ($x = 8, y = 6, z = 40, Z = 2.86, P = 0.12$, small volume correction (SVC) on the basis of a 10 mm sphere).
- Second session monolinguals versus bilinguals: brain activity related to the conflict effect was significantly increased in the second session for the monolingual group ($x = 12, y = 8, z = 44, Z = 3.57, P = 0.02$, SVC on the basis of a 10 mm sphere).

VBM-Behavioral/fMRI Correlational Analysis Results

Behavioral-Structural Correlation

GM volumes and the behavioral conflict effect over both sessions were correlated in the present sample (Pearson correlation: $r = -0.39, N = 31, P = 0.015$). Furthermore, GM volumes significantly predicted the behavioral conflict effect ($r^2 = 0.15, F_{1,29} = 5.16, P = 0.031$). Namely, there was a significantly negative effect of GM volumes on the behavioral conflict effect. Higher values of GM volume in the ACC conflict effect region were significantly associated with a reduced conflict effect over both sessions ($b = -0.39, t = -2.23, P = 0.031$) (see Fig. 5).

VBM-Based Group Comparison of Associations between Conflict Effect Activity and ACC

Comparing the conflict effect-ACC GM correlations maps in bilinguals with those for monolinguals, we found significant effects in areas included in the ACC conflict effect region. This comparison assesses the difference in the association of the conflict effect activity and ACC GM between the 2 groups. There is an interaction effect with a significantly steeper gradient of the regression in bilinguals as compared with

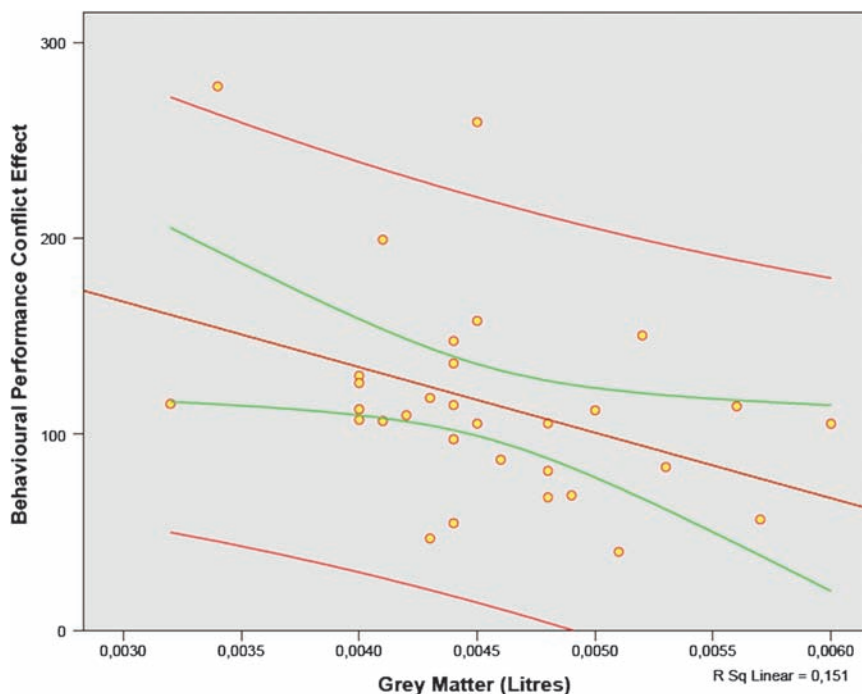


Figure 5. Scatter plot (with mean and individual CIs) of the relationship between GM volumes (in liters) in the ACC “conflict effect” region and the behavioral conflict effect (in ms) (measured as the difference between incongruent and congruent trials) for all subjects irrespective of group membership.

monolinguals. We found 2 clusters ($x = 5, y = 15, z = 40, 15$ voxels, $T = 3.46, P = 0.001$; $x = -2, y = 21, z = 48, 8$ voxels, $T = 3.27, P = 0.001$) showing significant group differences in the positive correlation of conflict effect activity and ACC GM density (see Fig. 4). The resultant SPM-T map was then converted to a correlation coefficient SPM R -map and the R -value for the cluster with peak maxima at $x = 5, y = 15, z = 40$ was 0.364. The reverse comparison revealed no significant differences.

GM/fMRI: Regression Coefficient Group Comparison

In order to provide more robustness to the VBM-based correlational analysis, we tested if the size of the regression coefficient of GM values extracted from the cluster with peak coordinates ($x = 5, y = 15, z = 40, N = 15$ voxels) predicting functional conflict effect values was significantly different between the bilingual and the monolingual groups. Non-smoothed and modulated partial GM volumes in liters were extracted with the Easy Volume toolbox (http://www.sbirc.ed.ac.uk/cyril/cp_download.html) from the ACC cluster of interest for each subject in both groups.

Residuals of the regression model explaining variation in functional conflict effect values were normally distributed (Skewness = 0.48, standard error [SE] = 0.42; Kurtosis = 0.58, SE = 0.82), homoscedastic (Breusch-Pagan test: $BP(1) = 0.013, P = 0.91$, Koenker Test: $K = 0.011, P = 0.91$), and not autocorrelated (Durbin-Watson test: $DW = 2.06$).

Levene’s test for equality of variances was performed for both the predictor (GM values) and the dependent variable (conflict effect activity values) prior to statistically testing the difference between the size of the regression coefficients between the 2 groups. The Levene test showed that the variances between the groups of the data set were homogeneous for both GM values ($P = 0.478$) and conflict effect activity

values ($P = 0.1$). Boxplots of GM partial volumes are presented in the Supplementary Figure S1 for the bilingual and monolingual group, which exclude the presence of outliers.

Correlation and regression analysis were subsequently performed separately for the bilingual and monolingual groups. Among bilinguals, GM values extracted from the ACC cluster of interest correlated positively with functional conflict effect values (Pearson correlation: $r = 0.453, N = 17, P = 0.034$). For the monolingual group, GM values were not significantly associated to functional conflict effect values (Pearson correlation: $r = -0.39, N = 14, P = 0.084$) (see Fig. 6).

Given our interest in differences between bilinguals and monolinguals, we carried out an exploratory post hoc analysis on the difference between slopes of regression lines for GM values for bilinguals and monolinguals. This analysis showed that GM values predict functional conflict effect values significantly more for bilinguals than monolinguals ($b = 1.309, t = 2.350, P = 0.026$). The slope for GM-related increments in functional conflict effect values indicated that these values increased for bilinguals ($b = 0.453, t = 1.967, P = 0.068$), though decreased for monolinguals ($b = -0.390, t = -1.469, P = 0.17$).

Discussion

The aim of the present study was 2-fold. First, to determine whether language control in bilinguals relies on a neural system shared with more general cognitive control processes. On the basis of our functional neuroimaging results, we can conclude that the neural structure commonly engaged by both cognitive processes is the dorsal ACC. Our second aim was to determine whether bilingualism induces beneficial structural and functional neuroplasticity. Our findings are affirmative. Remarkably, at the structural level in the dorsal ACC, bilinguals compared with monolinguals show first a positive correlation of

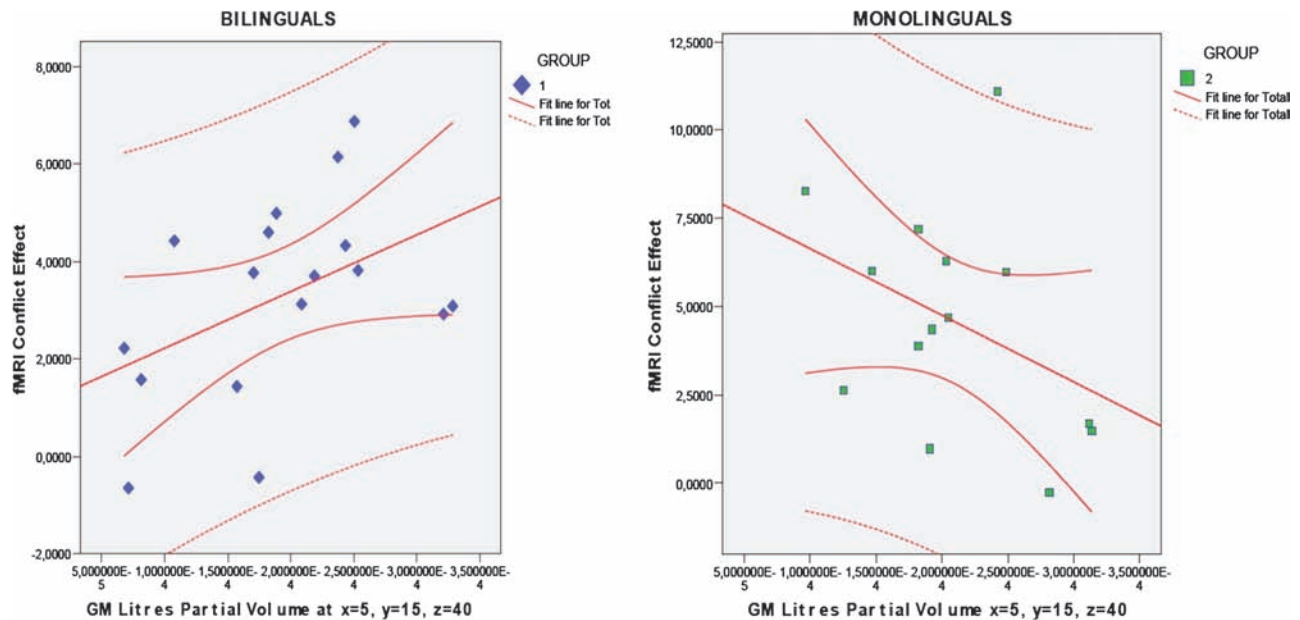


Figure 6. Scatter plots split by group (with mean and individual confidence intervals) of the relationship between partial GM volumes (in liters) (measured as the difference between incongruent and congruent trials) in the ACC cluster (at $x = 5$, $y = 15$, $z = 40$, 15 voxels) located in the ACC “conflict effect” region and mean values for BOLD signal measuring fMRI activity for the conflict effect contrast (incongruent–congruent). Green = Bilinguals; Blue = Monolinguals.

behavioral measures and local GM volume and, second, a positive correlation of conflict effect related brain activity and local GM volume. At the functional level, bilinguals also use the ACC more efficiently to monitor cognitive conflicts beyond the linguistic domain. They adapted better to the conflicting situations. Indeed, they seem to require less ACC activity to outperform monolinguals. These aspects will be discussed in detail.

Is Language Control Part of the Domain-General Cognitive Control Network?

In line with previous neuroimaging studies (Abutalebi et al. 2007, 2008; Wang et al. 2007, 2009), switching between languages elicited increased activity bilaterally in the ACC (BA 32) and the left precentral gyrus (BA 6) (Fig. 3 and Supplementary Table S2).

We also investigated what happens in monolinguals when they switch between 2 linguistic tasks within a single language. We asked them to either name a picture or generate a verb in response to it. This is an artificial task that differs cognitively from the language-switching task of bilingual speakers. Clearly, caution is needed in interpreting our results given the likely difference in cognitive process that implement the 2 tasks. Controlling competing naming responses in different languages is arguably routine for the bilingual and involves mechanisms that allow the nontarget language to dominate. By contrast, verbs are typically recruited to express event information, and their selection is constrained by that requirement. However, the within-language task, like the between-language task, requires a switch in naming response conditional on a non-verbal cue. The contrast between switch and non-switch trials (pooled over noun and verb) is not confounded by any difference in difficulty in generating responses, and indeed, monolingual speakers also activated bilateral ACC (BA 32), although at an uncorrected threshold ($P < 0.001$).

Hence, it may be concluded that the ACC is one of the chief areas responsible for the cognitive processes underlying both between-language switching (common amongst bilinguals) and within-language switching in monolinguals. The conjunction analysis performed to detect whether language control processes (i.e., those involved in language switching) and cognitive control processes in general (i.e., those involved in resolving conflict in the flanker task) have a common neural substrate revealed bilateral activity in the dorsal ACC for both bilingual and monolingual groups. The bilingual group, in addition, showed activity in the pre-SMA (Fig. 3). Importantly, the pre-SMA is increasingly recognized for its role, along with the ACC, in the performance of demanding tasks such as the Trail Making Test-B, in terms of response control, performance monitoring, error detection, feedback, and related processes (Bush et al. 2000; Hester et al. 2005; Nachev et al. 2008). The peak activation in the pre-SMA is within a region identified as the rostral cingulate zone (Ridderinkhof, Ullsperger, et al. 2004; Ridderinkhof, van den Wildenberg, et al. 2004), which overlaps with anatomical loci labeled “dorsal ACC” in other studies on cognitive control and performance monitoring (MacDonald et al. 2000; Kerns et al. 2004; Brown and Braver 2005). We suggest therefore that the brain structure responsible for detecting and aiding the resolution of conflicts whether in the verbal or in the nonverbal domain is the dorsal ACC. Indeed, the stereotactic coordinates of the ACC activations fall in a region overlying the cingulate sulcus, within BAs 24 and 32, associated with the ACC response to conflict elicited in different processing domains and different response modalities (Barch et al. 2001; Beckmann et al. 2009).

Therefore, in line with the theoretical proposals of conflict monitoring theory (Botvinick et al. 2001), dorsal ACC fulfills a common function in language switching (Abutalebi and Green 2007) and in the flanker task: it detects and signals the presence of interference with the current task goal. The precise mechanisms invoked in cognitive control will depend

on the specifics of the task. Avoiding a visual distractor, for example, invokes inhibitory processes in the frontal eye fields (e.g., McSorley et al. 2006). We therefore do not claim that the mechanisms of language control completely overlap with those invoked in a visual attention task.

The Neurocognitive Advantage of Bilinguals

Given that dorsal ACC is crucially involved in monitoring cognitive conflicts (e.g., Carter et al. 1999; Fan et al. 2002; 2003; Kerns et al. 2004), and on the assumption of its use in language control (e.g., Abutalebi and Green 2007), we predicted that early bilingualism may “tune up” the ACC and make it more efficient at handling conflict. Indeed, the fundamental difference between the bilingual and monolingual groups in our study is that language control in bilinguals (as required in switching between languages or in avoiding inappropriate language switching) is a necessity in everyday life. Therefore, we hypothesized that the early bilingualism may induce experience-driven neurofunctional plastic changes in the dorsal ACC for the bilinguals. If this is the case, then we might expect a strong coupling between functional activity for resolving conflict in our region of interest and GM density. Likewise, we also postulated a strong correlation between the behavioral measure (i.e., RTs) of the conflict effect and GM density.

We used VBM to analyze the correlation of local GM density in the dorsal ACC with the functional conflict effect (as measured with fMRI) in the flanker task. Over both groups of subjects, we found a significant correlation between the functional conflict effect and GM volumes bilaterally in the dorsal ACC region of interest. A groupwise comparison of the association between structural and functional data confirmed that the positive correlation between conflict effect activity and ACC GM density (see Fig. 4) was significantly stronger for bilinguals than monolinguals. These data provide a direct link between morphometric adaptive changes induced by bilingualism, in a brain region known to support more general cognitive control, and the functional demand induced by nonverbal conflict. Remarkably, this functional/structural correlation was paralleled by the correlation between behavioral data (i.e., the conflict effect) and GM density. Indeed, higher values of GM volume in the ACC conflict effect region were significantly associated with a lower conflict effect in bilinguals but not in monolinguals.

The behavioral data are also consistent with the notion that experience may tune the efficiency of this structure. Bilinguals, but not monolinguals, revealed a marked decrease in the conflict effect in the second session of the flanker task suggesting that they are better able to adjust to conflict, hence, to adapt to conflicting situations. The neurofunctional data provide strong converging support.

The comparison of monolinguals with bilinguals yielded an extensive cluster of activity in the right ACC (BA 24/32) (Fig. 4). It is noteworthy that the reverse comparison (bilinguals vs. monolinguals) yielded no significant difference. This observation is consistent with the notion that bilinguals require fewer neural resources to monitor cognitive conflict in these regions and are consistent with other data (Luk et al. 2010) suggesting that bilingualism selectively affects the neural network involved in resolving nonverbal conflict or interference.

Our analysis of ACC activity in the 2 sessions of the flanker task extends the data on this point. As shown in Figure 2,

bilinguals activated the ACC less than monolinguals already in the first session. However, in the second session, they showed a radical and significant decrease in signal in the dorsal ACC ($x = 2, y = 22, z = 44$), whereas the monolingual group did not as reported in our interaction analysis. This decrease is correlated with the decreased conflict effect observed in the behavioral data.

In conclusion, from our combined findings, we suggest that practicing lifelong bilingualism has neurocognitive benefits. The fact that bilinguals learn early in life to resolve language conflicts and to avoid speaking in the nontarget language leads to beneficial plastic changes in the dorsal ACC. Bilinguals not only resolve cognitive conflicts with less neural resource but their brain also adapts better to conflicting situations as shown in our sessions effects analysis of the flanker task. The ACC conflict effect region is more tuned for conflict monitoring in bilinguals. Despite continuing misconceptions that early learning of 2 languages causes intellectual delay in childhood (see for critical review, Wei 2007), the neural evidence points in a different direction: early learning and use of an L2 tunes up the human brain.

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>

Funding

Stiftung Südtiroler Sparkasse, Bozen, Südtirol, Italy.

Notes

Conflict of Interest : None declared. The authors declare no competing financial interests.

References

- Abutalebi J, Annoni JM, Seghier M, Zimine I, Lee-Jahnke H, Lazeyras F, Cappa SF, Khateb A. 2008. Language control and lexical competition in bilinguals: an event-related fMRI study. *Cereb Cortex*. 18:1496-1505.
- Abutalebi J, Brambati SM, Annoni JM, Moro A, Cappa SF, Perani D. 2007. The neural cost of the auditory perception of language switches: an event-related functional magnetic resonance imaging study in bilinguals. *J Neurosci*. 27:13762-13769.
- Abutalebi J, Green DW. 2007. Bilingual language production: the neurocognition of language representation and control. *J Neuro-linguistics*. 20:242-275.
- Abutalebi J, Green D. 2008. Control mechanisms in bilingual language production: Neural evidence from language switching studies. *Lang Cogn Process*. 23:557-582.
- Ashburner J, Friston KJ. 2000. Voxel-based morphometry—the methods. *Neuroimage*. 11:805-821.
- Ashburner J. 2007. A fast diffeomorphic image registration algorithm. *Neuroimage*. 38:95-113.
- Barch DM, Braver TS, Akbudak E, Conturo T, Ollinger J, Snyder A. 2001. Anterior cingulate cortex and response conflict: effects of response modality and processing domain. *Cereb Cortex*. 11:837-848.
- Beckmann M, Johansen-Berg H, Rushworth MFS. 2009. Connectivity-based parcellation of human cingulate cortex and its relation to functional specialization. *J Neurosci*. 29:1175-1190.
- Bermudez P, Lerch JP, Evans AC, Zatorre RJ. 2009. Neuroanatomical correlates of musicianship as revealed by cortical thickness and voxel-based morphometry. *Cereb Cortex*. 19:1583-1596.
- Bialystok E. 2009. Bilingualism: the good, the bad, and the indifferent. *Bilingualism*. 12:3-11.

- Bialystok E, Craik FIM, Grady C, Chau W, Ishii R, Gunji A, Pantev C. 2005. Effects of bilingualism on cognitive control in the Simon task: evidence from MEG. *Neuroimage*. 24:40-49.
- Botvinick MM, Cohen JD, Carter CS. 2004. Conflict monitoring and anterior cingulate cortex: an update. *Trends Cogn Sci*. 8:539-546.
- Botvinick MM, Nystrom LE, Fissell K, Carter CS, Cohen JD. 1999. Conflict monitoring versus selection for-action in anterior cingulate cortex. *Nature*. 402:179-181.
- Brett M, Anton JL, Valabregue R, Poline JB. 2002. Region of interest analysis using an SPM toolbox. *Neuroimage*. 16:1140-1141.
- Brown JW, Braver TS. 2005. Learned predictions of error likelihood in the anterior cingulate cortex. *Science*. 307:1118-1121.
- Bush G, Luu P, Posner MI. 2000. Cognitive and emotional influences in anterior cingulate cortex. *Trends Cogn Sci*. 4:215-222.
- Carter CS, Botvinick MM, Cohen JD. 1999. The contribution of the anterior cingulate cortex to executive processes in cognition. *Rev Neurosci*. 10:49-57.
- Costa A, Hernandez M, Sebastian-Galles N. 2008. Bilingualism aids conflict resolution: evidence from the ANT task. *Cognition*. 106:59-86.
- Costa A, Santesteban M. 2004. Lexical access in bilingual speech production: Evidence from language switching in highly proficient bilinguals and L2 learners. *J Mem Lang*. 50:491-511.
- Crinion J, Turner R, Grogan A, Hanakawa T, Noppeney U, Devlin JT, Aso T, Urayama S, Fukuyama H, Stockton K, et al. 2006. Language control in the bilingual brain. *Science*. 312:1537-1540.
- Dale AM. 1999. Optimal experimental design for event-related fMRI. *Hum Brain Mapp*. 8:109-114.
- Fan J, Flombaum JI, McCandliss KM, Thomas BD, Posner MI. 2003. Cognitive and brain consequences of conflict. *Neuroimage*. 18:42-57.
- Fan J, McCandliss BD, Fossella J, Flombaum JI, Posner MI. 2005. The activation of attentional networks. *Neuroimage*. 26:471-479.
- Fan J, McCandliss BD, Sommer T, Raz A, Posner MI. 2002. Testing the efficiency and independence of attentional networks. *J Cogn Neurosci*. 14:340-347.
- Friston KJ, Penny WD, Glaser DE. 2005. Conjunction revisited. *Neuroimage*. 25:661-667.
- Garbin G, Costa A, Sanjuan A, Forn C, Rodriguez-Pujadas A, Ventura N, Belloch V, Hernandez M, Ávila C. Forthcoming. Neural bases of language switching in high and early proficient bilinguals. *Brain Lang*. doi:10.1016/j.bandl.2011.03.011.
- Garbin G, Sanjuan A, Forn C, Bustamante JC, Rodriguez-Pujadas A, Belloch V, Hernandez M, Costa A, Avila C. 2010. Bridging language and attention: brain basis of the impact of bilingualism on cognitive control. *Neuroimage*. 53:1272-1278.
- Genzel G, Kerkhoff G, Scheffter S. 1995. PC-gestuetzte Standardisierung des Bildmaterials von Snodgrass & Vanderwart (1980). *Neurolinguistic*. 9:41-53.
- Good CD, Johnsrude IS, Ashburner J, Henson RNA, Friston KJ, Frackowiak RSJ. 2001. A voxel-based morphometric study of ageing in 465 normal adult human brains. *Neuroimage*. 14:21-36.
- Guo T, Liu H, Misra M, Kroll JF. 2011. Local and global inhibition in bilingual word production: fMRI evidence from Chinese-English bilinguals. *Neuroimage*. 56:2300-2309.
- Hester R, Foxe JJ, Molholm S, Shpaner M, Garavan H. 2005. Neural mechanisms involved in error processing: a comparison of errors made with and without awareness. *Neuroimage*. 27:602-608.
- Kerns JG, Cohen JD, MacDonald AW, Cho RY, Stenger VA, Aizenstein H, Carter CS. 2004. Anterior cingulate conflict monitoring and adjustments in control. *Science*. 303:1023-1026.
- Laudanna A, Thornton AM, Brown G, Burani C, Marconi L. 1995. Un corpus dell'italiano scritto contemporaneo dalla parte del ricevente. In: Bolasco S, Lebart L, Salem A, editors. III Giornate Internazionali Analisi Statistica Dati Testuali, Vol. 1. Rome: CISU. p. 103-109.
- Luk G, Anderson JAE, Craik FIM, Grady C, Bialystok E. 2010. Distinct neural correlates for two types of inhibition in bilinguals: response inhibition versus interference suppression. *Brain Cogn*. 74:347-357.
- MacDonald AW, Cohen JD, Stenger VA, Carter CS. 2000. Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science*. 288:1835-1838.
- Maguire EA, Gadian DG, Johnsrude IS, Good CD, Ashburner J, Frackowiak RSJ, Frith CD. 2000. Navigation-related structural change in the hippocampi of taxi drivers. *Proc Natl Acad Sci U S A*. 97:4398-4403.
- Manjon JV, Coupé P, Martí-Bonmatí L, Collins DL, Robles M. 2010. Adaptive non local means denoising of MR images with spatially varying noise levels. *J Magn Reson Imaging*. 31:192-203.
- McSorley E, Haggard P, Walker R. 2006. Time course of oculomotor inhibition revealed by saccade trajectory modulation. *J Neurophysiol*. 96:1420-1424.
- Mechelli A, Crinion JT, Noppeney U, O'Doherty J, Ashburner J, Frackowiak RS, Price CJ. 2004. Structural plasticity in the bilingual brain. *Nature*. 431:757.
- Nachev P, Kennard C, Husain M. 2008. Functional role of the supplementary and pre-supplementary motor areas. *Nat Rev Neurosci*. 9:856-869.
- Nichols T, Brett M, Andersson J, Wager T, Poline JB. 2005. Valid conjunction inference with the minimum statistic. *Neuroimage*. 25:653-660.
- Perani D, Paulesu E, Sebastian-Galles N, Dupoux E, Dehaene S, Bettinardi V, Cappa S, Fazio F, Mehler J. 1998. The bilingual brain: proficiency and age of acquisition of the second language. *Brain*. 121:1841-1852.
- Pernet C, Andersson J, Paulesu E, Demonet JF. 2009. When all hypotheses are right: a multifocal account of dyslexia. *Hum Brain Mapp*. 30:2278-2292.
- Rajapakse JC, Giedd JN, Rapoport JL. 1997. Statistical approach to segmentation of single-channel cerebral MR images. *IEEE Trans Med Imag*. 16:176-186.
- Ridderinkhof KR, Ullsperger M, Crone EA, Nieuwenhuis S. 2004. The role of the medial frontal cortex in cognitive control. *Science*. 306:443-447.
- Ridderinkhof KR, van den Wildenberg WPS, Segalowitz J, Carter CS. 2004. Neurocognitive mechanisms of cognitive control: the role of prefrontal cortex in action selection, response inhibition, performance monitoring, and reward-based learning. *Brain Cogn*. 56:129-140.
- Rodriguez-Fornells A, Rotte M, Heinze HJ, Noesselt T, Munte TF. 2002. Brain potential and functional MRI evidence for how to handle two languages with one brain. *Nature*. 415:1026-1029.
- Schneider P, Scherg M, Dosch HG, Specht HJ, Gutschalk A, Rupp A. 2002. Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. *Nat Neurosci*. 5:688-694.
- Snodgrass JG, Vanderwart M. 1980. A standardized set of 260 pictures: norms for name agreement, image agreement, familiarity and visual complexity. *J Exp Psychol Hum Learn*. 6:174-215.
- Wang Y, Kuhl PK, Chen C, Dong Q. 2009. Sustained and transient language control in the bilingual brain. *Neuroimage*. 47:414-422.
- Wang Y, Xue G, Chen C, Xue F, Dong Q. 2007. Neural bases of asymmetric language switching in second-language learners: an fMRI study. *Neuroimage*. 35:862-870.
- Wei L. 2007. *The bilingualism reader*. 2nd ed. New York: Routledge.
- Zou L, Ding G, Abutalebi J, Shu H, Peng D. Forthcoming. Structural plasticity of the left caudate in bimodal bilinguals. *Cortex*. doi:10.1016/j.cortex.2011.05.022.