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Neuroplasticity across the lifespan and aging effects in bilinguals and monolinguals

Nicola Del Maschio[a], Simone Sulpizio[a], Federico Gallo[a], Davide Fedeli[a], Brendan S. Weekes[b, c], Jubin Abutalebi[a, b, *]

[a] Centre for Neurolinguistics and Psycholinguistics (CNPL), Vita-Salute San Raffaele University, Milan, Italy
[b] Department of Speech and Hearing Sciences, University of Hong Kong, Hong Kong
[c] School of Psychological Sciences, University of Melbourne, Parkville, Victoria, Australia

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ABSTRACT

Evidence that bilingualism protects against age-related neurocognitive decline is mixed. One relatively consistent finding is that bilingual seniors have greater grey matter volume (GMV) in regions implicated in executive control (EC) and language processing. Here, we compare the neuroplastic effects of bilingual experience on the EC network of young and aging populations directly, and for the first time we evaluate the extent to which such effects may predict executive control performance across age. We used GMV as an index of neural reserve and response time (RT) performance on the Flanker task for measuring EC efficiency. In the presence of age-related widespread GM deterioration, bilinguals had greater GMV than monolinguals in key regions of interest across age. Moreover, whereas EC performance in monolingual seniors was strictly related to GMV, this was not observed for bilingual seniors or younger participants in either group. Interactions between expected effects-of-age and language group on the relationships between GMV and RT suggested that bilingualism affords differential benefits across the lifespan. In younger participants, greater GMV offered no behavioral benefit on EC performance, whilst it did for seniors. It thus appears that age-related cognitive decline following GMV loss in the EC network is delayed in bilinguals.

1. Introduction

Average life expectancy in industrialized countries is projected to increase continuously in the coming years (Kontis et al., 2017). Extended longevity is likely to be associated with a higher prevalence of cognitive impairment and dementia, with an accompanying social and healthcare burden (Santosa, 2017; Winblad et al., 2016). The consequences of these projections are far-reaching and global, and suggest the need for maintaining brain health and cognitive efficiency across the lifespan, enabling older adults to function independently for longer periods. Ideally, these interventions will be non-pharmacological so that learning capacity is maximized. Non-pharmacological interventions such as environmental enrichment and cognitive stimulation have been linked to reduced risk of neurocognitive decline in animal studies (van Praag, Kempermann, & Gage, 2000) and in humans (Wilson, Scherr, Schneider, Tang, & Bennett, 2007), as well as to improved cognitive functioning in patients with mild-to-moderate dementia (Aguirre, Woods, Spector, & Orrell, 2013). As in domain-specific forms of cognitive stimulation such as working memory training (Jaeggi, Buschkuehl, Jonides, & Perrig, 2008; Karbach & Verhaeghen, 2014) and music training (Rogenmoser, Kernbach, Schlaug, & Gaser, 2017; White-Schwoch, Carr, Anderson, Strait, & Kraus, 2013), second language use (*i.e.,* bilingualism) is an environmental factor that seems to foster 'successful aging' (Bialystok, Abutalebi, Bak, Burke, & Kroll, 2016; Rowe and Kahn, 2015). It is not yet clear, however, what cognitive and neural mechanisms lead to putative beneficial effects, and few studies have tested this question directly. One hypothesis is that bilingualism acts to postpone neurodegeneration (see Baum & Titone, 2014; Bialystok et al., 2016; Calabria, Cattaneo, & Costa, 2017). Two distinct neurocognitive constructs have been advocated to explain the delay in cognitive decline in bilingual seniors, *i.e.*, 'neural reserve' and 'cognitive reserve' (see Perani & Abutalebi, 2015). Both mechanisms seem to be induced by the increased cognitive load for executive control functions that bilingualism entails across the lifespan (Perani & Abutalebi, 2015). In other contexts, neural reserve has been defined as the capacity for resilience to the expected age-related deterioration and pathology of the brain (Barulli & Stern, 2013; Stern, 2002). Anatomic indices

* Corresponding author at: Vita-Salute San Raffaele University, Via Olgettina, 58, 20132, Milan, Italy.
Email address: abutalebi.jubin@hsr.it (J. Abutalebi)

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such as brain size, grey matter density, synaptic count and dendritic branching have been identified as effective measures of neural reserve and associated with the risk, incidence and severity of dementing disorders (e.g. Mori et al., 1997; Satz, 1993; Stern, 2012). Cognitive reserve has been defined as the discrepancy between underlying levels of age-related deterioration or pathology and observed functional and/or cognitive efficiency (Barulli & Stern, 2013; Stern, 2002). Unlike neural reserve, cognitive reserve depends on active compensation for decline and pathology by recruiting spared brain networks and/or alternate cognitive strategies to maximize performance (Barulli & Stern, 2013; Stern, 2002), so that neural decline need not impact necessarily on the preservation of cognitive capacities in aging. Indeed, it is apparent that cognitive processing can be somewhat resistant to extensive neurodegenerative lesions in bilingual speakers with Alzheimer's disease (AD) as compared to monolinguals (e.g. Schweizer, Ware, Fischer, Craik, & Bialystok, 2012). Therefore, although it is possible that more neural reserve will very likely be associated with greater cognitive reserve in healthy aging, it is clear that cognitive and neural reserve are dissociable mechanisms in bilingual seniors.

The goal of the current study is to investigate the hypothesis that lifelong bilingual experience is associated with greater neural and cognitive reserve in healthy aging by measuring the neurostructural changes in regions of interest that are known to subserve executive control in young and elderly bilinguals. This hypothesis will be tested by comparing bilingual speakers with age-matched monolingual controls. Given previous reports, the alternative outcomes are that neural reserve but not cognitive reserve or – conversely – cognitive reserve but not neural reserve will be observed in bilingual seniors as compared with monolinguals. The novel test here will be contrasting seniors who have greater cumulative bilingual experience with younger participants who are bilingual but may not develop an advantage in neural or cognitive reserve (see Valian, 2015 for discussion). Our main hypothesis is derived from theories of bilingual language experience that assume bilingual individuals to rely heavily on executive functions to speak one language while monitoring for potential interference from language(s) not in use but constantly active (Abutalebi & Green, 2007; Green, 1998). These theories are supported by a number of behavioral studies reporting superior performance by bilingual speakers on tasks that require conflict monitoring and resolution (Bialystok, Craik, & Luk, 2012; Valian, 2015), suggesting that executive control functions may be better 'trained' in bilinguals than monolinguals (but see Lehtonen et al., 2018). Most importantly, neuroimaging evidence shows that the extensive use of executive functions has structural and functional repercussions in regions of the cognitive control system that mediates the specific demands of bilingual language processing, such as the prefrontal cortex (PFC), the anterior cingulate cortex (ACC), the inferior parietal lobules (IPLs) and the dorsal striatum (Abutalebi & Green, 2007, 2016). In particular, studies comparing bilingual and monolingual seniors report that lifelong bilingualism is positively associated with grey matter density in these regions (Abutalebi, Guidi, et al., 2015; Pliatsikas, DeLuca, Moschopoulou, & Saddy, 2017) and microstructural integrity of the underlying white matter tracts (Luk, Bialystok, Craik, & Grady, 2011; Olsen et al., 2015), especially when high levels of second language (L2) proficiency and immersion are attained. Moreover, retrospective studies identify an association between bilingualism and a 4–5 year onset delay of clinical dementia symptoms, indicating bilingual experience as a potential buffer against neurodegeneration (Alladi et al., 2013; Bialystok, Craik, & Freedman, 2007; Gollan, Salmon, Montoya, & Galasko, 2011; Perani et al., 2017; Wilson, Boyle, Yang, James, & Bennett, 2015; Woumans et al., 2015). Overall, these findings have led to the proposal that bilingualism may render the brain more resistant to atrophy and prospective age-related disease, either because sufficient neural substrate remains to support normal function (*i.e.,* neural reserve) or because compensatory strategies are employed to optimize performance (*i.e.*, cognitive reserve). It cannot yet be assumed, however, that these mechanisms are necessarily related constructs at a functional level in bilingual healthy aging.

The claim that bilingualism protects the aging brain is controversial (Calvo, García, Manoiloff, & Ibáñez, 2016; Paap, Johnson, & Sawi, 2016). One reason for this controversy is that a number of studies failed to replicate the aforementioned critical findings (Crane et al., 2009, 2010; Sanders, Hall, Katz, & Lipton, 2012; Zahodne, Schofield, Farrell, Stern, & Manly, 2014). In a cross-sectional study by Ressel et al. (2012), for instance, both whole-brain and regions of interest (ROI) approaches were used to compare volumetric patterns of healthy Spanish-Catalan bilinguals and Spanish monolinguals. Whereas ROI analysis yielded greater GMV in Heschl's gyri for bilinguals, no significant difference between groups was detected when correcting for multiple comparisons across the whole brain. In an incidence study, Zahodne et al. (2014) reported that the onset of dementia symptoms was not significantly delayed for bilingual individuals, albeit older than monolingual controls at the time of diagnosis. Along similar lines, Crane et al. (2010) assessed a large sample of second-generation Japanese-Americans for dementia on three occasions over 6 years, and found that the use of a second language was not associated with lower cognitive decline in later life. Inconsistencies may be due to general sources of heterogeneity such as sample size and design, but also to the lack of control for variables known to affect brain and cognitive health across the lifespan, such as formal educational attainment (Meng & D'Arcy, 2012), socioeconomic status (SES) (Sattler, Toro, Schönknecht, & Schröder, 2012), sustained physical activity (Davenport, Hogan, Eskes, Longman, & Poulin, 2012) and general intellectual stimulation (Scarmeas & Stern, 2004).

Here, we intend to explore whether bilingualism is associated with neuroplastic changes in the executive control network of young and aging populations matched for education and SES, and the extent to which these changes may differentially predict executive control abilities in the groups under investigation. We used grey matter volume (GMV) as a structural indicator of neural reserve and response time (RT) performance on the Flanker task – a benchmark test in attention and conflict monitoring studies (Fan, McCandliss, Fossella, Flombaum, & Posner, 2005) – as a behavioral measure of cognitive efficiency.

We expect typical aging to be associated with diminished GMV and Flanker performance in all groups (bilingual and monolingual). However, we also expect to observe an interaction between age and group wherein the lifelong use of a second language would selectively protect bilingual seniors from the typical effects of aging. We therefore predict that bilingual speakers will exhibit better performance on the Flanker task (following results from e.g. Bialystok and colleagues) and greater neural reserve (following results from e.g. Abutalebi and colleagues) when compared to monolingual seniors, *i.e.*, greater GMV in key structures of the executive control network such as the PFC and the ACC. Moreover, we expect that greater GMV will be associated with higher cognitive efficiency on the Flanker task for the same group, *i.e.*, faster RTs and a much smaller Flanker or 'conflict' effect on the task. The prediction tested here for the first time is that cognitive and neural benefits derive from lifelong bilingual experience and therefore any association between greater cognitive and neural reserve will be restricted to seniors.

2. Methods

2.1. Participants

2.1.1. Bilinguals

A group of 22 healthy seniors from Hong Kong (11 males; mean age = 62.32; SD ± 5.73) was drawn from the pool of subjects reported in Abutalebi et al. (2014), Abutalebi, Canini, Della Rosa, Green, and Weekes (2015), Abutalebi, Guidi, et al. (2015). Eleven spoke Cantonese as first language (L1) and English as second language (L2), 11 spoke

Cantonese and Mandarin. A group of 22 healthy young adults (11 males; mean age = 20.5; SD ± 1.74) was recruited from the University of Hong Kong. Participants spoke Cantonese as L1 and English as L2. No participant had a history of neurologic or psychiatric illnesses. Mini Mental State Examination (MMSE) (Cockrell & Folstein, 2002) was used to evaluate the cognitive state of senior bilinguals (inclusion threshold: ≥27 raw score) and no participant was excluded due to clinical signs of cognitive impairment (mean raw score = 28.41; SD ± 1.1).

Educational history in years (young adults: mean = 15.5; SD ± 1.76; seniors: mean = 13.41; SD ± 5. 23) and Socio-Economic Status (SES) (young adults: mean = 23.96; SD ± 2.64; seniors: mean = 22.18; SD ± 6.42) were collected for all bilingual participants, along with the age of acquisition (AoA) of the L2 (young adults: mean = 3.3; SD ± 1.53; seniors: mean = 20.14; SD ± 13.26). Proficiency in L1 and L2 was established with a picture-naming task and a translation task. Thirty-two colored pictures matched for familiarity and visual complexity were selected from a revised version of the Snodgrass and Vanderwart picture set (Snodgrass & Vanderwart, 1980) (L1 naming % accuracy: young adults: mean = 87; SD ± 7.3; seniors: mean = 79; SD ± 11.1; L2 naming % accuracy: young adults: mean = 82; SD ± 8.4; seniors: mean = 63; SD ± 15.5). Bilingual participants also performed an oral translation task from L1 to L2 comprising 66 words (see Abutalebi et al., 2012) (% accuracy: young adults: mean = 92.85 ± 4.2; seniors: mean = 81.05 ± 16.36).

The Human Research Ethics Committee at the University of Hong Kong approved the study and written informed consent was obtained from all participants.

2.1.2. Monolinguals

A group of 22 healthy seniors (12 males; mean age = 62.05, SD ± 5.88) was recruited in Milan and drawn from the pool of subjects reported in Abutalebi et al. (2014, Abutalebi, Canini, et al. (2015), Abutalebi, Guidi, et al. (2015). A group of 22 healthy young adults (8 males; mean age = 20.86; SD ± 1.64) was recruited from the Vita-Salute San Raffaele University in Milan. No participant had a history of neurologic or psychiatric illnesses. Mini Mental State Examination (MMSE) (Cockrell & Folstein, 2002) was used to evaluate the cognitive state of older monolinguals (inclusion threshold: ≥27 raw score) and no participant was excluded due to clinical signs of cognitive impairment (mean raw score = 28.73; SD ± 1.07).

Educational history in years (young adults: mean = 15.5; SD ± 1.29; seniors: mean = 13.27; SD ± 4.64) and Socio-Economic Status (SES) (young adults: mean = 28.73; SD ± 4.11; seniors: mean = 22.18; SD ± 6.42) were collected for all monolinguals.

Independent *t* tests were performed to assess that no significant difference was present between older groups (bilinguals and monolinguals) for the matching criteria of age ($p = .88$), education ($p = .93$) and MMSE scores ($p = .27$). The same tests were performed to assess that no significant difference was present between younger groups (bilinguals and monolinguals) in terms of age ($p = .48$) and education ($p = .34$).

The Human Research Ethics Committee at the Vita-Salute San Raffaele University approved the study and written informed consent was obtained from all participants.

2.2. Behavioral assessment

All participants performed a revised version of the Flanker Task (Fan et al., 2005) and were instructed to press the left or the right button of a mouse as quickly as possible depending on whether the target, a central arrow presented on computer screen for 1700 ms, pointed to left or right, respectively. Targets could be presented with additional arrows flanked to the same direction as the target (→→→→→) (*i.e.*, congruent condition), additional arrows flanked to the opposite direction of the target (←←→←←) (*i.e.*, incongruent condition), or additional neutral lines (-- -- → -- --) (*i.e.*, neutral condition). Congruent flankers favor the correct response and are normally associated with better performance (i.e. higher accuracy and lower RTs); incongruent flankers represent conflicting information with the correct response and generally yield performance decline (*i.e.* lower accuracy and increasing RTs); the neutral condition typically biases neither the correct nor the incorrect response. Congruent, incongruent and neutral trials (64 for each condition, overall = 192) were presented in a pseudo-randomized order. Prior to the experiment, participants had a practice run consisting of 24 pseudo-randomized trials. Stimulus presentation and data collection were controlled using the Presentation software system v.18 (www.neurobs.com).

2.3. Image acquisition and processing

Images for bilingual participants were acquired at the 3T MRI Center at the University of Hong Kong and at the C.E.R.M.A.C. at University San Raffaele in Milan (Italy) for monolinguals with the same scanner model (3T Achieva Philips MR scanner) and exam card. For each participant, an axial high-resolution structural MRI scan was acquired (magnetization prepared rapid gradient echo, 150 slice T1-weighted image, TR = 8.03 ms, TE = 4.1 ms; flip angle = 8, FOV = 250 × 250, matrix = 256, TA = 9.35 min, mode = 3D FFE, sense factor = 1, NSA = 1, resolution = 1 1 1). The Computational Anatomy Toolbox (CAT12, r1113, http://dbm.neuro.uni-jena.de/cat/) within SPM12 (v6906) was used to obtain total amount of grey matter volume (GMV) within predefined brain regions and to perform a region-based morphometry for both groups. Images were first visually inspected to check for gross field distortions and movement artifacts and no participant was discarded for this reason. For each image, the origin was manually set to correspond to the AC-PC line. The following two-steps procedure was used for the GMV extraction. In Step 1, the raw structural image was segmented into Grey Matter (GM), white matter (WM) and cerebrospinal fluid (CSF) images. The segmentation routine implemented in CAT12 utilizes an adaptive Maximum A Posterior (aMAP) technique that reduces the need for *a priori* information of tissue probabilities (see Rajapakse, Giedd, & Rapoport, 1997) and also accounts for local variations and inhomogeneity of GM intensity (Dahnke, Ziegler, & Gaser, 2012). Following aMAP segmentation, CAT12 also carries out a Partial Volume Estimation (PVE) of mixed tissue-classes (GM-WM and GM-CSF) that results in a more accurate segmentation by estimating the fraction of pure tissue of each type within each voxel. The segmentation routine was further improved through the use of a spatial-adaptive non-local means (SANLM) denoising filter in a pre-segmentation step to reduce noise (Manjón, Coupé, Martí-Bonmatí, Collins, & Robles, 2010). After segmentation, the brains of all of the participants from Hong Kong were registered to the ICBM (International Consortium for Brain Mapping) template for East Asian brains, while the brains of participants from Italy were registered to the ICBM European brain space template by affine regularization. In Step 2, GMV values were extracted from ROIs in the executive control network (Abutalebi & Green, 2016): (1) Left and right anterior cingulate cortex (lACC, rACC); (2) left and right caudate (lC, rC); (3) left and right prefrontal cortex (lPFC, rPFC); (4) Left and right inferior parietal Lobules (lIPL, rIPL). The right primary Visual Cortex (rV1) was used a control region. The extraction was done using an in-built CAT12 function that allows for the estimation of GM volumes in non-normalized native space using maximum tissue probability labels derived from the Neuromorphometrics Atlas (2012) (http://Neuromorphometrics.com/). To control for any differences in brain sizes of the two groups, Total Intracranial Volume (TIV) was calculated for each participant by summing the native space global volumes of GM, WM and CSF.

2.4. Statistical analyses

2.4.1. The effects of aging and linguistic group on the executive control network

To investigate the prediction that bilingual speakers will exhibit greater neural reserve as compared to monolingual seniors, we ran linear models with the GMV of each ROI as dependent variables and Age (young vs. seniors) and Linguistic Group (bilingual vs. monolingual) as predictors. To control for overall differences among participants, total intracranial volume (TIV) was entered as a covariate in all models.

2.4.2. The role of GMV in modulating executive control performance

To test the prediction that greater GMV would be associated with a higher cognitive efficiency on the Flanker task for the same group, we ran a linear mixed-effects model (Baayen, Davidson, & Bates, 2008) for each ROI, with participants' RTs as the dependent variable, Age (young vs. seniors), Linguistic Group (bilingual vs. monolingual), GMV (as a continuous variable) and Flanker Condition (congruent vs. incongruent) as fixed effects, and by-participants and by-items random intercepts for the random part of the model. TIV was entered as a covariate in all models. The models were fitted with R using the *lmer* function (lmerTest package; Kuznetsova, Brockhoff, & Christensen, 2013).

3. Results

3.1. The effects of aging and linguistic group on the executive control network

Fig. 1 shows the mean values of GMV for all the ROIs under investigation. Table 1 reports the results of the models for each ROI. As expected, we observed a highly consistent pattern showing a main effect of Age for all ROIs (including rV1), with seniors having less GMV than young adults. As for the prediction that bilingual speakers will exhibit greater neural reserve than monolingual seniors, we observed a consistent pattern showing a main effect of Group for all ROIs excepted the bilateral Caudate (C) (and rV1), with more GMV in bilinguals than monolinguals. Moreover, although not expected, interactions between Age and Linguistic Group did not reach significance in any comparison. Both young and senior bilinguals are therefore shown to have greater neural reserve in all ROIs as compared to their monolingual peers.

3.2. The role of GMV in modulating executive control performance

Table 2 reports the descriptive statistics of the participants' behavioral performance on the Flanker task. Table 3 reports the results of the models for each ROI. As expected, bilingual seniors performed better on the Flanker task than age-matched monolinguals. As for the predicted association between greater GMV and higher cognitive efficiency on the Flanker for bilingual vs. monolingual seniors, the pattern of data that emerges across analyses is highly consistent: with the ex-

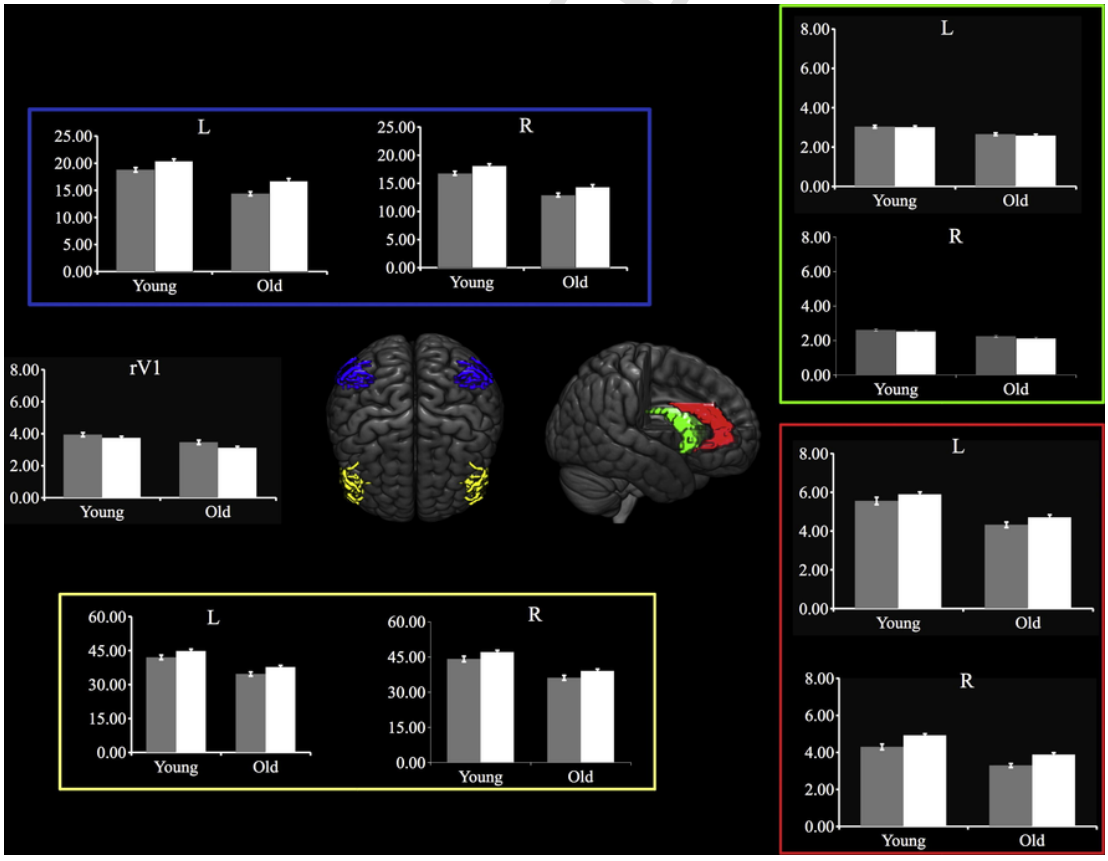

Fig. 1. The figure represents mean values of Grey Matter Volume (GMV) in each region of interest (ROI) under investigation for young and older bilinguals (white bars) and age-matched monolinguals (grey bars). The ROIs are highlighted in different colors: Prefrontal Cortex = yellow; Inferior Parietal Lobule = blue; Caudate nucleus = green; Anterior Cingulate Cortex = red. The right primary visual cortex (rV1) was used a control region. L/R = left/right hemisphere. Bilinguals show >GMV than monolinguals in all ROIs, with the exception of the caudate (and rV1). The pattern is stable from young adulthood to older adulthood, indicating that bilingual experience has neuroplastic effects across the life span. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Effects of Age and Linguistic Group (as well as their interactions) on the amount of Grey Matter Volume (GMV) in each region of interest (ROI) under investigation (ACC = Anterior Cingulate Cortex; C = Caudate nucleus; PFC = Prefrontal Cortex; IPL = Inferior Parietal Lobule). The right primary visual cortex (rV1) was used as a control region.

ROIs	Linguistic Group	Age	Linguistic group × Age
	t value	*t* value	*t* value
lACC	−4.214***	−7.123***	−0.159
rACC	−4.893***	−6.777***	−0.383
lC	−0.249	−4.426***	−0.538
rC	0.203	5.305***	−0.619
lPFC	−6.564***	−8.664***	−0.27
rPFC	−6.327***	−9.373***	−0.535
lIPL	−5.022***	−8.911***	−0.161
rIPL	−6.902***	−7.957***	0.812
rV1	1.27	−3.956***	−0.869

*** $p < .001$.

ception of the right ACC and the right Caudate, all models showed a significant four-way interaction between Flanker Condition, Age, Linguistic Group and GMV. Given these interactions, we split the data by Age group and ran separate models for young and older adults for each ROI where there was a significant four-way interaction.

For young adults, the interaction between Flanker Condition, Linguistic Group and GMV was not significant. The only significant interaction effects were the Flanker condition × GMV in the models including the following ROIs: the left PFC ($F = 5.66$, $p = .01$) and the left ACC ($F = 4.07$, $p = .04$), as well as the main effect of the ROI for the right IPL ($F = 4.65$, $p = .03$). Therefore, there is little evidence that young bilingual adults show an advantage on the Flanker task but there is some evidence of an association between Flanker performance and GMV in the expected regions of the cognitive control network. On the other hand, the analyses of data from seniors show a different pattern that is highly consistent across analyses. At all ROIs, there was a significant three-way interaction between Flanker condition, Linguistic Group and GMV (see Table 4), indicating a differential effect of bilingual experience on Flanker performance and the relationship between Flanker performance and GMV. As illustrated in Fig. 2, Flanker performance is not related to reduced GMV for bilingual seniors whereas Flanker performance is related with reduced GMV in monolinguals. Therefore, although we found evidence that reduced cognitive control is related to loss of GMV in critical ROIs (as expected with healthy aging), bilingualism protects against age-related performance decline, even though both senior groups showed a reduction in GMV as compared with young participants.

4. Discussion

We tested the hypothesis that lifelong bilingual experience is associated with greater neural and cognitive reserve in healthy aging. The results support this hypothesis in the following ways. There is greater neural reserve in bilingual vs. monolingual groups across age in key regions of the executive control network, supposedly resulting from bilingualism-induced neuroplastic changes. There is a performance advantage on the Flanker task for bilingual seniors compared with age-matched monolinguals, whereas there is no such advantage for younger bilinguals. In fact, although young bilinguals had greater GMV than young monolinguals, this did not lead to large cognitive differences between groups, at least as measured by executive control performance on the Flanker. Moreover, despite less GMV in bilingual seniors

Table 2
Participants' mean latencies for correct responses (with standard deviations) in the Flanker task.

RT		Bilingual (Young) (N = 22)	Monolingual (Young) (N = 22)	Bilingual (Senior) (N = 22)	Monolingual (Senior) (N = 22)
Congruent trials	*Mean*	501.15	501.38	629.14	687.8
	SD	73.66	92.2	68.05	103.2
Incongruent trials	*Mean*	588.56	575.65	745.66	814.37
	SD	76.56	65.31	105.65	135.81

Table 3
Interactions for each region of interest (ROI) under investigation in young and older age groups (bilinguals and monolinguals). ACC = Anterior Cingulate Cortex; C = Caudate nucleus; PFC = Prefrontal Cortex; IPL = Inferior Parietal Lobule.

Effects	lACC	ROIs						
		rACC	lC	rC	lPFC	rPFC	lIPL	rIPL
Linguistic Group	–	–	–	–	–	–	–	–
Age	*	*	^	*	**	**	***	***
Flanker	***	***	***	***	***	***	***	***
ROI	–	–	–	–	–	–	–	–
Linguistic Group × Age	–	–	–	–	–	–	–	–
Linguistic Group × Flanker	*	–	–	–	–	–	–	*
Age × Flanker	***	***	^	**	***	***	***	*
Linguistic Group × ROI	–	–	*	–	–	–	–	–
Age × ROI	–	–	–	–	*	*	**	***
Flanker × ROI	–	–	–	**	–	–	–	–
Linguistic Group × Age × Flanker	*	–	*	–	*	*	*	^
Linguistic Group × Age × ROI	–	–	–	–	–	–	*	*
Linguistic Group × Flanker × ROI	**	–	–	–	–	–	–	*
Age × Flanker × ROI	**	***	–	–	***	***	**	^
Linguistic Group × Age × Flanker × ROI	*	–	**	–	*	*	*	*

^ $p < .1$.
* $p < .05$.
** $p < .005$.
*** $p < .001$.

Table 4
Significant interactions for each region of interest (ROI) under investigation in older age groups (bilinguals and monolinguals). ACC = Anterior Cingulate Cortex; C = Caudate nucleus; PFC = Prefrontal Cortex; IPL = Inferior Parietal Lobule.

Effects	lACC	lC	lPFC	rPFC	lIPL	rIPL
Linguistic Group	ˆ	*	_	ˆ	*	*
Flanker	***	***	***	***	***	***
ROI	_	_	_	_	_	_
Linguistic Group × Flanker	***	***	**	***	**	***
Linguistic Group × ROI	_	**	_	_	*	*
Flanker × ROI	**	_	***	***	***	**
Linguistic Group × Flanker × ROI	***	***	**	***	**	***

ˆ $p < .1$.
* $p < .05$.
** $p < .005$.
*** $p < .001$.

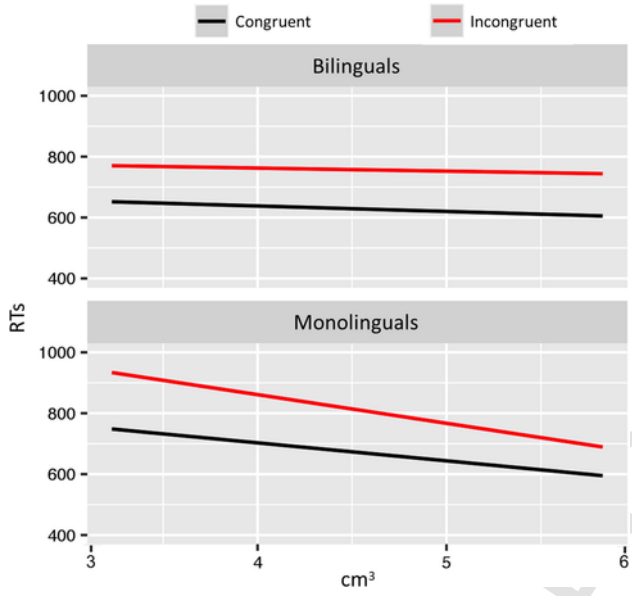

Fig. 2. The figure plots the predicted values for the three-way interaction between Linguistic Profile, Flanker Condition and left Anterior Cingulate Cortex (lACC) (selected as a representative region of interest). Whereas bilingual performance in both Flanker conditions (Congruent, Incongruent) is preserved against Grey Matter Volume (GMV) decline, the ability of monolinguals to deal with conflicting information is strictly related to the amount of available neural substrate, with < GMV associated with > Response Times (RTs).

compared to bilingual young adults, differences in performance between groups did not reach significance. Overall, despite the differential effects of bilingual experience on GMV and Flanker performance, we found evidence that cognitive reserve is not necessarily correlated with neural reserve.

By comparing seniors who have greater cumulative (lifelong) bilingual experience with younger bilingual participants directly, we can conclude that bilingual experience is a key to preserved cognitive efficiency even though brain restructuring is observed for bilinguals from an early age. We therefore contend that preserved executive control functioning may not be evident in all age groups even with greater neural reserve.

The regular use of multiple languages has been proposed to protect the aging brain by fostering neural and/or cognitive reserve. An increasing body of evidence addressing structural neuroplasticity in bilingualism has begun to emerge (see García-Pentón, Fernández García, Costello, Duñabeitia, & Carreiras, 2016; Li, Legault, & Litcofsky, 2014), although results are heterogeneous and conflicting. Whereas some studies report a number of brain regions that consistently differ between bilinguals and monolinguals (Abutalebi et al. 2012, Abutalebi, Canini, et al. (2015); Mechelli et al., 2004; Olulade et al., 2016; Pliatsikas et al., 2017), others report differences in areas that are inconsistent across studies (see García-Pentón et al. 2016) or even failed to detect any bilingualism-induced effect (Gold, Johnson, & Powell, 2013; Grogan et al., 2012). Inconsistencies would benefit from neural models that account for bilingual language processing as modulated by age-related changes in brain and language functions (see Rossi & Diaz, 2016 for discussion). Most recently, based on the classic Posterior-to-Anterior Shift with Aging (PASA) in response to task demands (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2007), Grundy, Anderson, and Bialystok (2017) proposed the Bilingual Anterior to Posterior and Subcortical Shift model (BAPSS) with the aim to provide a unitary framework for the neural and cognitive effects of bilingualism across the lifespan. By integrating functional, structural and electrophysiological data, the model proposes that aging bilinguals would rely less than their monolingual peers on attentional resource demands associated with frontal lobe activity and more on automatic processes underpinned by posterior and subcortical structures, thereby contrasting with more efficiency than monolinguals the consequences of cognitive aging in terms of frontal lobe deterioration. Inconsistencies among structural data being granted, it is noteworthy that most previous MRI investigations did not compare different age groups in the same study or did not correlate brain data with relevant measures of cognitive processing, thus resulting in lack of specificity. The novel finding presented here is that these mechanisms are dissociable across age.

4.1. The effects of aging and linguistic group on the executive control network

As expected, voxel-based morphometry (VBM) revealed widespread atrophy in all regions of interest for seniors (including rV1). These findings agree with substantial evidence from post-mortem and in vivo studies reporting whole-brain deterioration due to chronological age (Jernigan et al., 2001; Kalpouzos et al., 2009; Raz et al., 2005; Tisserand et al., 2004), with prefrontal regions being more affected than other cortical regions (Cabeza & Dennis, 2012; Jernigan et al., 2001). We confirmed previous reports showing that bilingual individuals have greater GMV than their monolingual peers in regions of interest that are known to be affected in healthy aging, with the exception of the caudate nucleus (and rV1). Remarkably, greater GMV in bilinguals was observed from young adulthood to older adulthood, indicating that speaking and controlling for multiple languages has early neurostructural consequences that can extend across the lifespan. These results are in line with previous neuroimaging studies that report greater neural reserve for young and/or senior bilinguals in executive control regions such as the ACC, the PFC and the IPL bilaterally (e.g. Abutalebi et al. 2012, Abutalebi, Canini, et al. (2015), Abutalebi, Guidi, et al. (2015); Felton et al., 2017; Mechelli et al., 2004; Olulade et al., 2016). Abutalebi et al. (2012), for instance, showed that greater GMV for young bilinguals in the bilateral ACC was positively correlated with

their performance on the Flanker, but failed to detect such correlation in young monolinguals. Greater GMV in the ACC has also been reported for senior bilinguals (Abutalebi, Guidi, et al. (2015)). The ACC is widely assumed to be a core component of the executive control network that underpins conflict and error monitoring (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999, Botvinick, Braver, Barch, Carter, & Cohen, 2001) both in verbal and non-verbal domains (Branzi, Della Rosa, Canini, Costa, & Abutalebi, 2016; De Baene, Duyck, Brass, & Carreiras, 2015). Bilinguals are assumed to develop greater GMV in the ACC due to the continuous challenge of coordinating between languages while avoiding cross-linguistic interference (Abutalebi & Green, 2007). One outcome from the present study is that neural reserve may build up early in bilingual speakers, *i.e.*, that early acquisition of a second language leaves a neural signature from a relatively young age and that greater neural reserve depends on lifelong bilingualism. It is however noteworthy that cumulative exposure does not seem to have any demonstrable effect on neural reserve as chronological age increases, although this conjecture would require a longitudinal approach to be tested directly. A recent study by Olulade et al. (2016) reported increased GMV for young bilinguals as compared with age-matched monolinguals in a widespread network of cortical regions, including the dorsolateral PFC bilaterally and the right IPL. Growing evidence shows that the PFC is associated with response selection and inhibition in contexts that present interfering information (e.g. Collette et al., 2005; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). In particular, while the left PFC seems to support response selection, the right counterpart is arguably related to response inhibition (see Aron, Robbins, & Poldrack, 2004, 2014). Bilingual speakers are assumed to develop more GMV in the PFC because they are continuously engaged in overriding prepotent responses from the dominant language. On the other hand, based on clinical (Pötzl, 1925) and functional neuroimaging evidence (Price, Green, & von Studnitz, 1999), greater neural reserve for bilinguals in the IPL bilaterally may be attributed to the role of this region in language switching contexts, with the left IPL being involved in biasing language selection away from the unintended language, and the right IPL being responsible for addressing selection towards the language in use. Again, our findings suggest that GMV reflects bilingual experience from an early age and may reach asymptote with increasing age. This must be interpreted within the data showing no group differences across age, qualified by the fact that healthy aging induces GM deterioration. Importantly, there was evidence that GMV was reduced for bilingual seniors compared to young bilinguals but this had a minimal impact on cognitive performance.

It is worth underlying that we did not find significant differences in the participants' caudate region as a function of language group membership, a result which partially conflicts with previous anatomical MRI studies comparing bilingual and monolingual subjects (e.g. Burgaleta, Sanjuán, Ventura-Campos, Sebastian-Galles, & Ávila, 2016; Grogan, Green, Ali, Crinion, & Price, 2009; Zou, Ding, Abutalebi, Shu, & Peng, 2012). Left caudate activity has been linked to language switching based on clinical (Abutalebi, Miozzo, & Cappa, 2000; Mariën, Abutalebi, Engelborghs, & De Deyn, 2005) and functional neuroimaging evidence (Branzi et al., 2016; Crinion et al., 2006; Lehtonen et al., 2005). To a certain extent, however, the role of the caudate nucleus in multiple language control remains puzzling, as some studies did not report its activation during language switching tasks (e.g. Hernandez, Dapretto, Mazziotta, & Bookheimer, 2001; Hernandez, 2009; Wang, Kuhl, Chen, & Dong, 2009). Of special relevance to the present findings, when examining structural differences between bilinguals with a varying degree of second language immersion and monolinguals, Pliatsikas et al. (2017) found a volumetric increase in the left caudate in low-immersion bilinguals only, and independently of the level of attained second language proficiency, which was equally high in all participants (see also Burgaleta et al., 2016). Elmer, Hänggi, and Jäncke (2014) even reported a reduced bilateral caudate volume for simultaneous multilingual interpreters – *i.e.*, experienced language switchers – compared to multilingual controls, suggesting that GMV increase in the caudate region may not apply to situations in which a more automated and 'bottom-up' code-switching has taken over the initial effort of learning and controlling for multiple languages. Rather than ubiquitous in language control, the caudate nucleus seems to play a role in the processing of low proficient or unfrequently used languages, or during the initial stages of second language learning. Hence, a plausible explanation for the lack of caudate differences in the present study is that the bilinguals in our sample are proficient in both their languages and highly immersed in a multilingual environment such as Honk Kong, which may require extensive situational code-switching on a daily basis.

4.2. The role of GMV in modulating executive control performance

When testing the role of GMV in modulating executive control performance in young and aging groups, our results showed significant interactions for young adults restricted to the left ACC and the left PCF. On the other hand, a differential effect of GMV on bilingual and monolingual seniors for each ROI (rV1 excluded) indicated that while performance in both Flanker conditions (congruent, incongruent) was largely independent of the decline in GMV for bilinguals, it was clearly related to the decline in GMV for monolinguals. This is particularly relevant as increased chronological age has been associated with lower executive control efficiency due to disproportional deterioration of frontal lobe function (Mahoney, Verghese, Goldin, Lipton, & Holtzer, 2010; West, 1996). The lack of significant interactions between Linguistic Group, Age, Flanker and ROI in the right ACC and right caudate may indicate that these regions, differently from their left counterparts, do not modulate differences in performance between bilinguals and monolinguals as age increases. Overall, our findings suggest that by virtue of their lifelong experience using a second language, bilinguals retain greater cognitive reserve despite neural decline. Hence, we contend that lifelong bilingual experience fosters cognitive reserve in senescence, enabling seniors to maximize their task performance and mitigate typical GMV loss. The frontal lobes were disproportionately affected by cortical volume loss. We speculate that cognitive compensation arises due to recruiting premorbidly larger brain networks in the critical ROIs, thus allowing development of cognitive strategies that are less vulnerable to age-related decline. The scope of VBM analysis, however, does not allow us to make conclusive statements. Enhanced functional connectivity has been reported previously in the executive control and default mode networks of healthy senior bilinguals (Grady, Luk, Craik, & Bialystok, 2015) and senior bilinguals with AD vs. healthy senior monolinguals and AD monolingual controls (Perani et al., 2017). It could be that a strengthening of connections between areas and circuits of the executive control network may allow bilinguals to adjust more efficiently to normal brain aging.

A potential limitation to the results of this study is the cultural differences between bilinguals from Hong Kong and monolinguals from Milan. We cannot exclude that monolinguals and bilinguals differed on non-identified lifestyle variables with an influence on cognitive performance and neural capacity, driving the differences in neural and cognitive reserve between groups. However, besides the fact that a single study can hardly eliminate all the potential confounds associated with bilingual experience (Bak, 2016), the monolingual control group was selected from the aging population in Milan because of the relative difficulty of finding comparable monolinguals in Hong Kong. Usually, the few monolinguals in Hong Kong and surrounding areas have a much lower level of education and SES than the local bilingual population. Moreover, the aging population in Milan is hardly exposed to second languages, whereas in Hong Kong even alleged monolinguals are potentially exposed to other languages such as English, Mandarin and numerous other dialects. As argued by Abutalebi and colleagues in previous studies, Milan and Hong Kong are similar cities in that they are both densely populated global economic hubs located in a network of

states defined by a common ethnic and historical identity (*i.e.*, Hong Kong in China and Milan in Italy). It is because of these similarities that, although not ideal, we believe the monolingual control group from Milan is a better control than a potentially socioeconomically and educationally mismatched monolingual group from Hong Kong, especially given the possible confounding effects of SES on a putative bilingual advantage (Morton & Harper, 2007; see also Calvo & Bialystok, 2014).

5. Conclusion

Our results suggest – on the one hand – that bilingualism fosters neuroplasticity from a relatively early age and is sustained across the lifespan, and – on the other – that it promotes cognitive reserve in healthy aging, thus pointing to bilingual experience as an environmental variable that mitigates against neural decline in senescence. When compared to younger bilinguals and to monolinguals in general, senior bilinguals appear to be capable of optimizing their performance despite clear deterioration to GMV in widespread brain regions related to executive control. These findings are supportive of previous studies showing that bilingual patients with AD vs. monolingual patients exhibited greater amounts of neural substrate in regions associated with pathology when the groups were matched for education (e.g. Schweizer et al., 2012). Specifically, bilingual speakers can have significant cerebral atrophy without suffering the concomitant loss of cognitive function that accompanies healthy aging in monolingual speakers. More detailed report and analysis of the diversity in experience-dependent mechanisms are needed to further advance research on bilingualism and cognition.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.bandc.2018.06.007.

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