Research report

Processing demands upon cognitive, linguistic, and articulatory functions promote grey matter plasticity in the adult multilingual brain: Insights from simultaneous interpreters

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ARTICLE INFO

ABSTRACT

Until now, considerable effort has been made to determine structural brain characteristics related to exceptional multilingual skills. However, at least one important question has not yet been satisfactorily addressed in the previous literature, namely whether and to which extent the processing demands upon cognitive, linguistic, and articulatory functions may promote grey matter plasticity in the adult multilingual brain. Based on the premise that simultaneous interpretation is a highly demanding linguistic task that places strong demands on executive and articulatory functions, here we compared grey matter volumes between professional simultaneous interpreters (SI) and multilingual control subjects. Thereby, we focused on a specific set of a-priori defined bilateral brain regions that have previously been shown to support neurocognitional aspects of language control and linguistic functions in the multilingual brain. These regions are the cingulate gyrus, caudate nucleus, frontal operculum (pars triangularis and opercularis), inferior parietal lobe (IPL) (supramarginal and angular gyrus), and the insula. As a main result, we found reduced grey matter volumes in professional SI, compared to multilingual controls, in the left middle-anterior cingulate gyrus, bilateral pars triangularis, left pars opercularis, bilateral middle part of the insula, and in the left supramarginal gyrus (SMG). Interestingly, grey matter volume in left pars triangularis, right pars opercularis, middle-anterior cingulate gyrus, and in the bilateral caudate nucleus was negatively correlated with the cumulative number of interpreting hours. Hence, we provide first evidence for an expertise-related grey matter architecture that may reflect a composite of brain characteristics that were still present before interpreting training and training-related changes.

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1.   Introduction

Bilinguals often outperform monolinguals in a variety of linguistic and non-linguistic tasks relying on different cognitive functions such as attention (Bialystok, Craik, Klein, & Viswanathan, 2004; Costa, Hernandez, & Sebastian-Galles, 2008), inhibition (Bialystok et al., 2004; Festman, Rodriguez-Fornells, & Munte, 2010), working memory (Morales, Calvo, & Bialystok, 2013), or set shifting (Festman & Münte, 2013). According to current knowledge, it is assumed that such behavioural advantages origin, at least in part, from the processing demands upon cognitive control mechanisms that are required for solving interactions between first language (L1) and second language (L2) during language production (Zou, Abutalebi, et al., 2012), selecting the language in use (Abutalebi et al., 2013; Luk, Green, Abutalebi, & Grady, 2012; Rodriguez-Fornells, Balaguer, Munte, 2006; Rodriguez-Fornells, Rotte, Heinze, Nosselt, & Munte, 2002), switching between languages (Garbin et al., 2011; Price, 2012; Quaresima, Colier, Van der Sluijs, Menssen, & Ferrari, 2001), producing words in the weaker-spoken language (Abutalebi et al., 2013; Hernandez, Martinez, & Kohnert, 2000), accomplishing translation (Price, Green, & von Studnitz, 1999; Quaresima et al., 2001) and interpreting tasks (Rinne et al., 2000), and for inhibiting the non-target language during speech production (Rodriguez-Fornells et al., 2002) as well.

In an extensive review of previous neuroimaging data, Abutalebi and Green (Abutalebi & Green, 2007) have described a set of neural devices that participate in regulating cognitive control and language production in the multilingual brain. These brain regions are the inferior frontal cortex, middle-anterior cingulate gyrus, caudate nucleus, and the inferior parietal lobe (IPL). The inferior frontal cortex is engaged in attention, inhibition, working memory (Fuster, 2001; Hickok, 2009; Rodriguez-Fornells et al., 2006) as well as in linguistic functions (Fiebach, Schlesewsky, Lohmann, von Cramon, & Friederici, 2005; Friederici, 2006; Friederici & Gierhan, 2013), whereas the middle-anterior cingulate gyrus is implicated in monitoring the language in use, allocating attention, conflict monitoring, and error detection (Abutalebi & Green, 2007; Hernandez, 2009). Notably, previous functional (Crinion et al., 2006), structural (Zou, Ding, Abutalebi, Shu, & Peng, 2012), and lesion (Abutalebi, Miozzo, & Cappa, 2000) studies have identified the caudate nuclei as being part of a neuronal network that contributes to language selection and switching mechanisms. In addition, previous work has shown that the IPL [i.e., angular and supramarginal gyrus (SMG)] can be structurally altered in bilinguals compared to monolinguals (Della Rosa et al., 2013; Mechelli et al., 2004), and that grey matter in this brain region correlates with L2 proficiency, age of L2 acquisition (Mechelli et al., 2004), or even with other biographical measures (Della Rosa et al., 2013). The IPL is involved in mediating attention (Elmer, Meyer, Marrama, & Jancke, 2011; Kiehl et al., 2005) and working memory functions (Buchsbaum, Olsen, Koch, & Berman, 2005; Hickok, 2009), and in mapping a sound's structure to its phonetic representation (Golestani & Zatorre, 2004; Ruff, Marie, Celsis, Cardebat, & Demonet, 2003; Turkeltaub & Coslett, 2010). Evidently, depending on the cognitive requirements necessary

for accomplishing a particular language task (for example translation versus sentence repetition), and on the degree of speech competence achieved by the speaker, the single neuronal devices of the cognitive control system are differentially engaged (Elmer, 2013).

Beside the undisputed contribution of cognitive control functions to multilingual speech processing [for an overview consider (Abutalebi & Green, 2007; Rodriguez-Fornells et al., 2006)], there is currently likewise evidence indicating that multilingual speech competence and expertise are associated with functional and structural changes in brain regions supporting articulation and sensory-to-motor coupling mechanisms, namely in the basal ganglia (i.e., caudate nucleus) (Abutalebi et al., 2008; Eickhoff, Heim, Zilles, & Amunts, 2009; Zou, Ding, et al., 2012) and in the left middle-anterior insula (Elmer, Hänggi, Meyer, & Jancke, 2011; Golestani, Molko, Dehaene, LeBihan, & Pallier, 2007; Golestani & Pallier, 2007). Such neuroplastic changes are supposed to arise as a consequence of the processing demands that are necessary for continuously adjusting the motor output while speaking (as a function of auditory feedback), this being a prerequisite for achieving a best possible pronunciation. In this context, Golestani and Pallier (Golestani & Pallier, 2007) reported that French speaking subjects who more accurately learnt to pronounce a Persian consonant that does not exist in French showed increased white matter volume in the left anterior insula. However, although the left anterior insula has repeatedly been identified as being crucial for articulation, phonation (Ackermann & Riecker, 2010; Baldo, Wilkins, Ogar, Willock, & Dronkers, 2011; Kurth, Zilles, Fox, Laird, & Eickhoff, 2010) and sensory-to-motor coupling mechanisms (Mutschler et al., 2007, 2009), this heterogeneous brain area participates in a variety of other brain functions (i.e., non-motor) as well (Flynn, Benson, & Ardila, 1999; Sterzer & Kleinschmidt, 2010).

Up to now, the majority of studies that have addressed functional and structural neuroplasticity, executive language control, and linguistic functions in the multilingual brain have focused on comparisons between bilinguals and monolinguals (Abutalebi et al., 2013, 2012; Zou, Abutalebi, et al., 2012; Zou, Ding, et al., 2012), bilinguals with high and low proficiency (Abutalebi et al., 2013), or even on bilinguals acting in both monolingual and bilingual contexts (Abutalebi et al., 2008). These previous studies have indisputably contributed to a better understanding of the brain regions supporting executive language control in the multilingual brain. However, it still remains unclear whether these brain regions are susceptible to structural changes as a function of training in early adulthood. Therefore, the investigation of professional simultaneous interpreters (SI) may constitute a fruitful and complementary approach for better understanding plastic adaptations in the adult brain in regions administrating cognitive control, linguistic functions, articulation, and sensory-to-motor coupling mechanisms [(Elmer, Hänggi, et al., 2011; Elmer, Meyer, & Jancke, 2010; Elmer, Meyer, et al., 2011), for a review consider (Elmer, 2013)]. This is related to the fact that simultaneous interpretation is trained as recently as in adulthood, and places heavier demands upon cognitive, linguistic, and articulatory functions than do multilingual subjects in everyday life.

Here, we used voxel-based morphometry (VBM), and compared grey matter volumes between professional SIs and multilingual control subjects within a-priori defined regions-of-interest (ROI). Based on the functional-anatomical framework proposed by Abutalebi and Green (2007) as well as on previous neuroimaging studies performed with SIs (Elmer, Hänggi, et al., 2011; Elmer, Meyer, et al., 2011; Rinne et al., 2000), between-group comparisons were evaluated in the following ROIs: inferior-lateral portion of the frontal operculum (pars triangularis and pars opercularis), middle-anterior cingulate gyrus, caudate nucleus, middle-anterior insula, SMG, and angular gyrus. Furthermore, in order to better differentiate between training-related grey matter changes and brain characteristics that were still present before training, we performed correlative analyses between the cumulative number of interpreting hours and grey matter volume in the a-priori selected ROIs.

2. Materials and methods

2.1. Participants

In the present work, we measured 12 professional SIs (all certified and graduated professional SI, eight women and four men, mean age = 37.9 years, standard deviation [SD] = 5.8 years, age range 28—48, mean cumulative number of practice hours = 5080 h, SD = 3505 h) and 12 multilingual control subjects (eight women and four men, mean age = 28.4 years, SD = 2.8 years, age range 25—38). None of the control subjects grew up in a bilingual context, and all subjects reported to speak at least three (2 subjects reported to speak 4 languages) languages fluently (the language of the region, a second national language, and English). Age of language acquisition (AA) and education time (ET) were estimated by taking into account regional differences in the Swiss scholar system: GER (mother tongue), FRE (AA ~ 8—11 years, ET ~ 8 years), ENG (AA ~ 11—14 years, ET ~ 6 years), ITA (AA ~ 14 years, ET ~ 4 years), SPA (AA ~ 14 years, ET ~ 4 years), POR (AA ~ 14 years, ET ~ 4 years). All other languages were acquired outside the context of school after the age of ~18—20 years.

All participants were consistent right-handers according to Annett's questionnaire (Annett, 1970), had a comparable level of education (i.e., university degree or were advanced university students), reported no past or current neurological, psychiatric, or neuropsychological problems, and denied illegal medication. Subjects were paid for participation, the local ethics committee (Zurich, Switzerland) approved the study and written informed consent was obtained from all participants. Table 1 provides an overview of the autobiographical data of the SIs investigated in the present study.

2.2. Imaging data acquisition

Magnetic resonance imaging (MRI) scans were acquired on a 3.0 T Philips Achieva whole body scanner (Philips Medical Systems, Best, The Netherlands) equipped with a transmit-receive body coil and a commercial eight-element sensitivity encoding (SENSE) head coil array. A volumetric 3D T1-weighted gradient echo sequence (TFE, turbo field echo) image was measured with a spatial resolution of $1 \times 1 \times 1.5$ mm (acquisition matrix 224×224 pixels, 180 slices) and reconstructed to a resolution of $.86 \times .86 \times .75$ mm^3 (reconstructed matrix 256×256 pixels, 180 slices). Further

Table 1 — Autobiographical data of the simultaneous interpreters and control subjects.

Subjects	Age	Spoken languages	Age of training commencement	Number of training years	Cumulative training hours
SI 1	42	ENG FRE ITA SPA POR DUT GER	39	3	1170
SI 2	36	FRE ENG POR GER	33	3	1014
SI 3	46	ENG FRE SPA ITA GER	24	22	13728
SI 4	48	GER ITA FRE ENG	33	15	8190
SI 5	32	GER FRE ENG POR	27	5	5265
SI 6	41	FRE ITA ENG SPA GRE GER	31	10	5200
SI 7	37	ENG SPA FRE GER	25	12	4805
SI 8	35	ENG FRE GER	30	5	1560
SI 9	39	ENG FRE SPA ITA GER	31	8	4160
SI 10	36	ENG ITA FRE GER ROM	27	9	3744
SI 11	35	FRE ENG GER	26	9	7020
SI 12	39	FRE ENG GER	29	10	5105
C 1	26	FRE ENG GER			
C 2	27	ENG DUT POR GER			
C 3	26	FRE ENG GER			
C 4	27	FRE ENG GER			
C 5	34	FRE ENG GER			
C 6	30	SPA ENG FRE GER			
C 7	28	FRE ENG GER			
C 8	38	FRE ENG GER			
C 9	28	FRE ENG GER			
C 10	26	FRE ENG GER			
C 11	25	FRE ENG GER			
C 12	25	FRE ENG GER			

Table 2 — MNI coordinates and maxima reflecting significant between-group differences within the a-priori selected regions-of-interest.

Contrast	Grey matter volume	Hemisphere	MNI coordinates (x, y, z)	Cluster size	t-value
Controls > interpreters	Middle insula	Left	−42, −4, −2	724	5.15
	Middle insula	Left	−42, 9, −12		3.84
	Middle-anterior cingulum	Left	−3, −9, 43	535	4.69
	Middle-anterior cingulum	Left	−9, −1, 43		4.45
	Middle-anterior cingulum	Left	0, 15, 40		4.34
	Supramarginal gyrus	Left	−50, −34, 51	138	4.21
	Broca pars triangularis	Left	−46, 38, 10	144	3.96
	Broca pars triangularis	Left	−48, 26, 13		3.34
	Broca pars opercularis	Left	−46, 11, 24	146	3.67
	Middle insula	Right	45, −1, −3	230	3.55
	Posterior insula	Right	38, −10, −3		3.34
	Broca pars triangularis	Right	50, 28, 0	173	3.43
	Broca pars triangularis	Right	51, 27, 12		3.24

imaging parameters were: Field of view FOV = 220 × 220 mm^2, echo-time TE = 2.3 msec, repetition-time TR = 20 msec, flip-angle α = 20°. Imaging data acquisition and behavioural testing took place at the same day. SI and control subjects were measured in an interleaved manner.

2.3. VBM

Between-group differences in grey matter volume were evaluated by using VBM (Ashburner & Friston, 2000; Good, Ashburner, & Frackowiak, 2001). All pre-processing steps were performed with the VBM8 toolbox (release 435, http://dbm.neuro.uni-jena.de/vbm/download/) that uses Statistical Parametric Mapping (SPM8, release 4667, http://www.fil.ion.ucl.ac.uk/spm/) software. The following pre-processing steps were realized: (1) the coordinate origin of each native image was manually set on the anterior commissure. (2) Intensity inhomogeneity (bias field) correction, tissue class segmentation, and spatial normalization (affine and warping) were performed using unified segmentation (Ashburner & Friston, 2005) combined with SPM8's "new segmentation approach". For spatial normalization, the diffeomorphic anatomical registration using exponentiated lie algebra (DARTEL) approach was used (Ashburner, 2007). Canonical a-priori maps (ICBM 152 T1-weighted) implemented in SPM8 were used as reference templates. (3) To enhance tissue class segmentation, Hidden Markov Random Field (HMRF) modulation was applied [(Cuadra, Cammoun, Butz, Cuisenaire, & Thiran, 2005), http://dbm.neuro.uni-jena.de/vbm/markov-random-fields/]. (4) To investigate absolute volumes, the warped images were voxel-wise multiplied with the Jacobian determinant of the deformations (linear as well as nonlinear terms were modulated). (5) The resulting Jacobian and HMRF modulated and segmented GM images were smoothed with a Gaussian kernel of full width at half maximum (FWHM) = 9 mm and the additional smoothing introduced during the modulation process was about FWHM = 3 mm.

2.4. Statistical analyses

Between-group comparisons were performed by using the general linear model (GLM) that implements an unpaired

t-test in SPM8. Global GM volume was used as nuisance variable in analyses of covariance of local GM volume. Furthermore, since the two groups significantly differed in age, this variable was implemented in the model as a co-variate of no interest. Grey matter volume differences between the two groups were evaluated in a set of a-priori defined bilateral ROIs, namely in the inferior-lateral portion of the frontal operculum (pars triangularis and opercularis), middle-anterior cingulate gyrus, caudate nucleus, supramarginal and angular gyrus, and in the middle-anterior insula. All these ROIs were added into a single, composite brain mask image and explicitly applied to restrict the statistical analysis to the voxels within this mask. The first five ROIs were taken from the functional-anatomical framework proposed by Abutalebi and Green (2007), and originated from the Harvard—Oxford cortical and subcortical structural atlases as implemented in the FSL software package (http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Atlases). The insula was selected based on previous neuroimaging studies performed with SIs (Elmer, Hänggi, et al., 2011) and also originated from the Harvard—Oxford cortical structural atlas. All ROIs were threshold at 30% probability. Since we had clear a-priori hypotheses, we used an uncorrected alpha error probability of $p < .005$ and a voxel extent threshold of 25 voxels. In addition, within the SIs group we performed linear regression analyses between grey matter volume in each ROI and the cumulative number of practice hours (corrected for the influence of age). Linear regressions were performed by using the GLM that implements the multiple regression in SPM8 (alpha error probability of $p < .01$ and voxel extent threshold of 15 voxels, uncorrected). Correlations were computed within a composite map of all ROIs as an explicit mask in SPM8. In addition, for reasons of completeness and as suggested by one anonymous reviewer, we performed explorative whole-brain group comparisons using the GLM that implements an unpaired t-test combined with the threshold-free cluster-enhancement approach (Smith & Nichols, 2009) (alpha error probability of $p < .001$, 5000 permutations, both FWE corrected and uncorrected, see FWE value in Table 3). However, since we did not have specific hypotheses concerning the grey matter volume relying outside the above-mentioned ROIs, the results of the whole-brain analysis are reported as

Table 3 – Montreal neurological institute (MNI) coordinates and maxima which negatively correlated with the cumulative number of practice hours within the simultaneous interpreters' group.

Grey matter volume	Hemisphere	MNI coordinates (x, y, z)	Cluster size	t-value
Broca pars triangularis	Left	−47, 29, 9	18	3.66
Middle cingulum	Left	−9, 5, 37	31	3.17
Caudate	Left	−9, 5, 6	31	2.99
Broca pars opercularis	Right	42, 12, 28	26	3.79
Caudate	Right	18, 20, 3	28	2.95

supplemental material (Supplemental Fig 1 and Supplemental Table 1) and these exploratory results are not discussed further.

3. Results

Between-group comparisons revealed reduced grey matter volume in SIs in the left middle-anterior cingulate gyrus, bilateral middle-anterior insula, left SMG, bilateral pars triangularis, and left pars opercularis. These anatomical results are shown in Fig. 1 (left column, blue colour) and summarized in Table 2. In addition, within the SIs group a correlative analysis revealed a negative relationship between grey matter volume and the cumulative number of practice hours in the right pars opercularis, left pars triangularis, middle-anterior cingulate gyrus, and left and right caudate (right column of Fig. 1, red colour, and Table 3). The results of the whole-brain analysis are reported as supplemental material (see Supplemental Figure S1 and Supplemental Table S1).

4. Discussion

4.1. Grey matter architecture and plasticity in brain regions supporting cognitive aspects of language control

Meanwhile, it is widely accepted that cognitive functions fundamentally contribute to control multiple language systems [for an overview consider (Abutalebi & Green, 2007)]. However, to date only few studies have investigated structural neuroplasticity in brain regions supporting neurocognitional aspects of language control as a function of training in adulthood (Abutalebi et al., 2012; Elmer, Hänggi, et al., 2011; Golestani, Price, & Scott, 2011). Therefore, in the present work we compared grey matter volume between professional SIs and multilingual control subjects in a-priori defined ROIs. Results revealed reduced grey matter volumes in SIs, compared to controls, in the left pars triangularis and opercularis, right pars triangularis, left SMG, bilateral middle-anterior cingulate gyrus, and in the bilateral middle-anterior insula. Moreover, within the SIs group grey matter volume in right pars opercularis, left pars triangularis, left middle-anterior cingulate gyrus, and in the bilateral caudate nucleus negatively correlated with the cumulative number of practice hours. Since not all of the brain regions showing significant group differences correlated with training parameters, results are interpreted as indicating a composite of grey matter characteristics that still persisted before training and training-

related changes. In turn, we will discuss these results in a more comprehensive manner by focussing on each of the single neuronal devices previously proposed to be implicated in language control mechanisms in the multilingual brain (Abutalebi & Green, 2007).

4.1.1. Middle-anterior cingulate gyrus

The grey matter differences we revealed between the two groups in the middle-anterior cingulate gyrus are compatible with previous results showing functional (Abutalebi et al., 2008, 2012; Luk et al., 2012) and structural changes in this brain region in bilinguals compared to monolinguals (Abutalebi et al., 2012; Zou, Ding, et al., 2012). Furthermore, in a recent work Abutalebi and colleagues (Abutalebi et al., 2012) reported reduced blood oxygen level dependent (BOLD) responses in bilinguals compared to monolinguals during a conflict monitoring task (i.e., flanker task) in a similar region as we found, namely in the cognitive division of the cingulate gyrus (Bush, Luu, & Posner, 2000). Interestingly, in the same study the authors also found a relationship between conflict effect during the flanker task (measured as the difference in reaction time between incongruent and congruent trials) and grey matter volume in the middle-anterior cingulate gyrus, suggesting a contribution of this brain region to conflict monitoring functions. However, Abutalebi and colleagues did not reveal any structural between-group differences in the cingulate gyrus between groups (Abutalebi et al., 2012).

Our results are relevant in that we provide evidence for the fact that subjects extremely engaging cognitive control mechanisms in everyday life are characterized by differential grey matter architecture in the middle-anterior cingulate gyrus. In addition, the architecture of this brain region was related to the cumulative number of practice hours. Taking into account the functional–anatomical relationship reported by Abutalebi et al. (2012) as well as the spatial location of the cluster showing reduced grey matter in SIs, we may speculate whether the anatomical changes we revealed have been, at least partially, driven by the processing demands upon conflict monitoring functions during translation. Certainly, the intensive usage of other cognitive functions than conflict monitoring may likewise account for such grey matter changes in SIs. In fact, the middle-anterior cingulate gyrus also mediates error detection and attention functions (Bush et al., 2000), the latter being for example necessary for monitoring both the speech input and its respective translation (Elmer, 2013). Certainly, further longitudinal studies combining behavioural, functional, and anatomical measurements are required for better comprehending the relationship between grey matter changes, cognitive functions, and training.
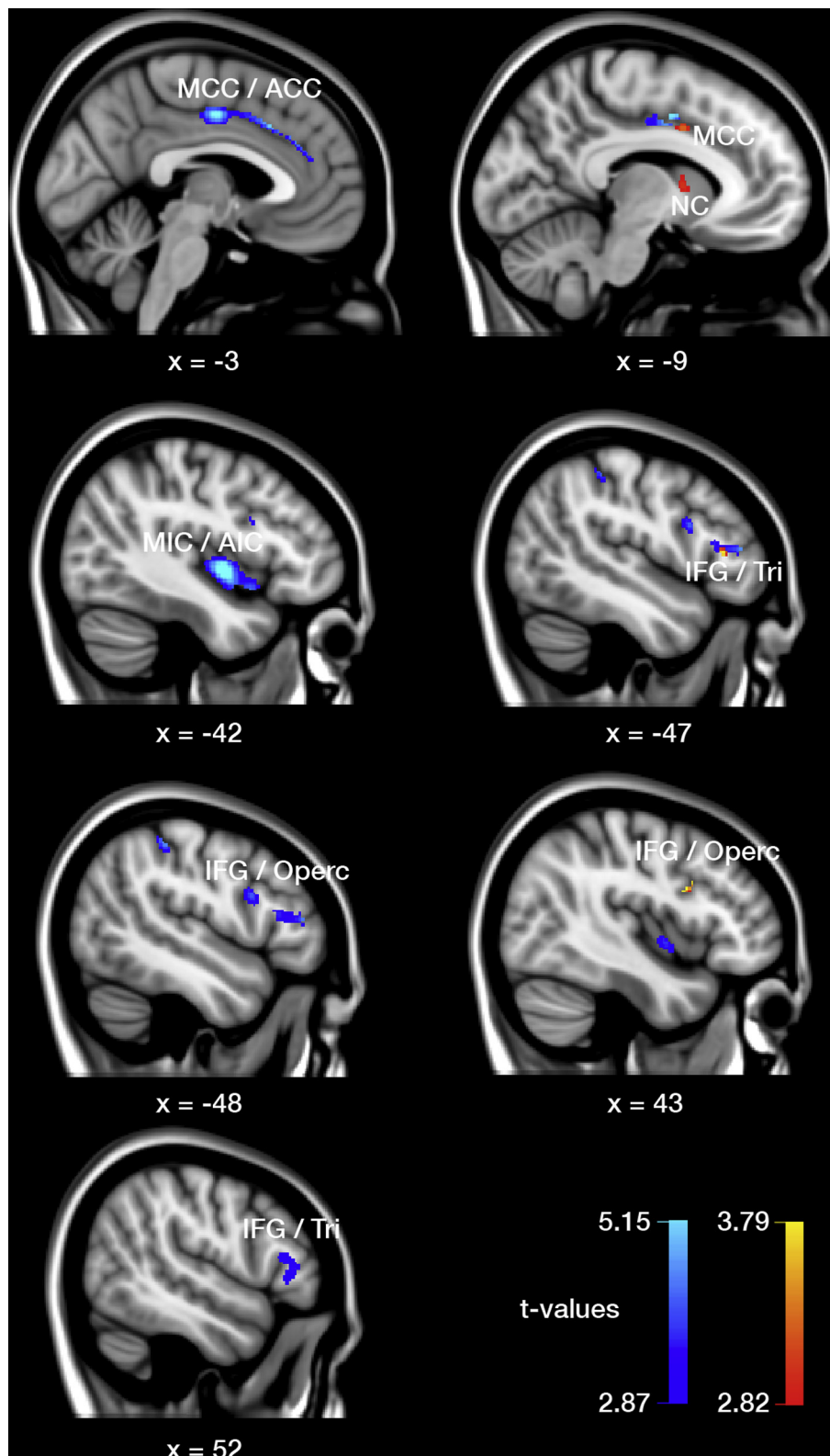
Fig. 1 — This figure shows grey matter differences between the two groups (blue, left part of the figure) as well as significant correlations between grey matter volume and the cumulative number of practice hours within the interpreters group (red, right part of the figure). MCC = middle cingulate cortex, ACC = anterior cingulate cortex, MIC = middle insular cortex, AIC = anterior insular cortex, IFG = inferior frontal gyrus, Operc = pars opercularis, Tri = pars triangularis, NC = nucleus caudatus.

4.1.2. Caudate nucleus

A recent meta-analysis provided clear evidence for a bilateral functional involvement of the caudate nucleus in bilinguals during language switching (Luk et al., 2012). Currently, there is even evidence showing functional (Abutalebi et al., 2013; van Heuven, Schriefers, Dijkstra, & Hagoort, 2008) and structural (Zou, Ding, et al., 2012) changes in this brain region in bilinguals compared to monolinguals. In addition, a recent imaging study could show that professional SIs are characterized by a reduced fractional anisotropy in the head of the right caudate nucleus compared to multilingual control subjects (Elmer, Hänggi, et al., 2011). However, in the present work we did not reveal structural between-group differences in the caudate nuclei, possibly because of the rather small sample size and the low statistical power. Nevertheless, within the SIs group we found a negative relationship between grey matter volume in the bilateral caudate nucleus and the cumulative number of practice hours, suggesting a relationship between grey matter characteristics and interpreting training. It is important to mention that this result partially diverge from that of a previous study by Zou and colleagues (Zou, Ding, et al., 2012) who reported increased (and not decreased) grey matter volume in the head of the left caudate in bilinguals compared to monolinguals. However, bilinguals principally differ from SIs in that the former more intensively practice language control mechanisms during childhood, whereas the latter acquire language-related cognitive skills as recently as in adulthood. Therefore, we may speculate whether the processing demands upon language control mechanisms may differently affect grey matter volume depending on the interaction between training onset and cortical development (a more detailed discussion about this issue is implemented in the section "Interpretation of reduced grey matter volume in simultaneous interpreters").

4.1.3. Pars triangularis

Remarkably, we also found between-group differences in the grey matter volume enclosing bilateral pars triangularis, a brain region which comprises several histological subdivisions (Amunts et al., 2010, 1999) and has often been associated (mainly in the left hemisphere) with syntactic processing (Friederici & Gierhan, 2013; Gold & Buckner, 2002). However, there is likewise evidence showing that language-selective and domain-general regions lie side by side within Broca's area (Fedorenko, Duncan, & Kanwisher, 2012). Consequently, this observation leads to suggest that the left pars triangularis is not selective for language processing per se, but more likely supports general cognitive functions. This is compatible with the view that language switching, attention, and working memory tasks share, at least in part, the same neuronal substrate (Fedorenko et al., 2012; Price et al., 1999; Rodriguez-Fornells et al., 2002; Rogalsky & Hickok, 2011; Santi & Grodzinsky, 2012).

Interestingly, the grey matter differences we revealed between the two groups in pars triangularis were bilaterally distributed and not restricted to the left hemisphere. In addition, within the SIs group the left but not the right pars triangularis was negatively correlated with the cumulative number of interpreting practice hours. Hence, results are interpreted as indicating that the left pars triangularis more

likely adapted as a function of training, probably for facilitating the intensive demands upon executive functions and/or syntactic processing during interpreting, the latter being indeed more strongly lateralized to the left hemisphere (Herrmann, Obleser, Kalberlah, Haynes, & Friederici, 2012). In contrast, since grey matter volume in the right pars traingularis was not at all related to practice parameters, we propose that this expert-specific architecture more likely reflects differences that were still present before training and that possibly may be advantageous for becoming professional SIs rather than neuroplasticity per se.

4.1.4. SMG

In the present work, we also revealed grey matter differences between the two groups in the left SMG, a brain region situated in the IPL. In addition, within the SIs group grey matter volume in the left SMG was negatively correlated with the cumulative number of practice hours, suggesting a training-related modulation of grey matter in this specific brain region. This result is in line with previous work showing structural changes in the IPL in bilinguals compared to monolinguals (Della Rosa et al., 2013; Mechelli et al., 2004) as well as with a previous fMRI study providing first evidence for an increased responsiveness of the left IPL in SIs compared to multilingual controls while performing an auditory attention task (Elmer, Meyer, et al., 2011). Certainly, the IPL does not only supports attention functions but also a variety of other cognitive functions which are all strongly engaged during simultaneous interpreting such as, for example, working memory (Baldo & Dronkers, 2006; Buchsbaum et al., 2005; Hickok, 2009) and phonetic processing (Golestani & Zatorre, 2004; Ruff et al., 2003; Turkeltaub & Coslett, 2010). In fact, for performing simultaneous translations SIs have to perceive and decode the phonetic structure of the input language, to keep the meaning in working memory while formulating the output in the target language, and to additionally allocate attention resources, which are necessary for monitoring both the speech input and its respective translational output (Elmer, 2013).

4.2. Speech production, articulation, and sound-to-motor mapping mechanisms

A second main purpose of this study was to evaluated grey matter architecture and plasticity in brain regions previously proposed to be engaged in supporting speech production and sensory-to-motor coupling mechanisms (Ackermann & Riecker, 2010; Baldo et al., 2011; Dronkers, 1996; Elmer, Hänggi, et al., 2011; Eickhoff et al., 2009; Golestani et al., 2007; Golestani & Pallier, 2007; Mutschler et al., 2007). These regions included the caudate nucleus, left pars opercularis, and the left middle-anterior insula. Anatomically, the pars opercularis is bounded by the inferior precentral sulcus, the inferior frontal sulcus, and the ascending ramus of the Sylvian fissure, and has previously been shown to support, among other functions (Grodzinsky & Friederici, 2006; Heim, Opitz, & Friederici, 2003), overt speech production (Eickhoff et al., 2009; Richardson, Fillmore, Rorden, LaPointe, & Fridriksson, 2012). From a histological perspective, this brain region has more likely the characteristics of a motor than a sensory cortex

(Amunts et al., 1999; Anwander, Tittgemeyer, von Cramon, Friederici, & Knosche, 2007; Kelly et al., 2010) because the pars opercularis shows only a rudimentary developed cortical layer IV. In addition, the pars opercularis (but not pars triangularis) has been shown to be connected to the posterior and middle superior temporal gyrus via the arcuate fasciculus, a fibre bundle that is an important prerequisite for sensory-to-motor transformations (Friederici & Gierhan, 2013). Meanwhile, there is likewise evidence showing that the caudate nucleus (Eickhoff et al., 2009) and the left anterior insula (Ackermann & Riecker, 2010; Dronkers, 1996; Eickhoff et al., 2009) are important for supporting overt speech production and articulation. Even though the insula is engaged in a variety of cognitive, emotional, and motor functions as well (Kurth et al., 2010; Sterzer & Kleinschmidt, 2010), at least its left middle-anterior part has been repeatedly shown to support overt speech, articulation, phonation, as well as to be engaged in the regulation of ventilation during speech production (Ackermann & Riecker, 2010; Baldo et al., 2011; Dronkers, 1996). In addition, the insula has been reported in association with sensory-to-motor transformations (Mutschler et al., 2007, 2009). Such transformations are for example necessary for coupling phonetic representations with articulation. In line with our hypothesis, we provide evidence for expertise-dependent grey matter architecture in the left and right insula and in the left pars opercularis. Grey matter volume in these regions did not correlate with training parameters. Furthermore, grey matter volume in the right pars opercularis and in the bilateral caudate nucleus inversely correlated with the cumulative number of practice hours, leading to suggest training-related plastic adaptations.

4.3. Interpretation of reduced grey matter volume in SI

In the present work, we consistently revealed reduced grey matter volumes in SIs compared to multilingual control subjects. By contrast, most of the previous studies that investigated language expertise revealed increased grey matter volumes in bilinguals compared to monolinguals (Della Rosa et al., 2013; Mechelli et al., 2004; Zou, Ding, et al., 2012). Although this divergence of results seems contra intuitive, it is important to mention that a main biographical difference between bilinguals and SIs is that the former still train executive control during childhood, whereas in the latter group the demands upon cognitive control mechanisms principally emerge and increase during early adulthood. Meanwhile, it is generally acknowledged that brain maturation until early adolescence is associated with increased grey matter volume, whereas during adulthood cortical grey matter is influenced by synaptic "pruning" and decreases in order to promote functional specialization (Giorgio et al., 2010; Gogtay et al., 2004; Paus, 2005). Therefore, we may speculate whether the training of languages-related skills during childhood may additionally increase grey matter volume. Consequently, more nerve cells will survive pruning, resulting in increased grey matter volume when comparing bilinguals and monolinguals during adulthood by using cross-sectional approaches. In contrast, by considering cortical pruning as a process of removing inefficient nerve cells, we may speculate whether the intense training of language control in early

adulthood may additionally promote pruning in adulthood and therefore improve functional specialization, leading to more efficient processing (Kanai & Rees, 2011). This reasoning further implies that the grey matter architecture underlying language expertise and control can fundamentally diverge depending on the time of acquisition of specific skills during different periods of cortical development. Finally, it should also be mentioned that the training of specific skills is not always associated with increased grey matter volume (James, Oechslin, Van De Ville, Descloux, & Lazeyras, 2013; Takeuchi et al., 2011). In fact, there is growing evidence from longitudinal studies showing that grey matter volume can decrease as a function of cognitive training. For example, Takeuchi and colleagues (Takeuchi et al., 2011) showed that after intensive working memory training grey matter volume bilaterally decreased in frontal and parietal regions in a sample of young adults.

5. Limitations

Here, we evaluated grey matter differences between professional SIs and multilingual controls. Thereby, we only focused on brain anatomy (and not function) in a set of a-priori defined ROIs. Consequently, it results difficult to draw accurate conclusions about structure–function relationships. A further shortcoming of the present work is that we dissociated training-related changes and training-unrelated differences based on correlative analyses. However, it is definitely possible that some between-group differences were attributed to grey matter differences that were still present before interpreting training instead of plastic changes. For example it has been shown that anatomical constraint in mesiotemporal brain areas are most important in determining improvement of cognitive functions after practising (Supekar et al., 2013). This may be related to the fact that our sample, and therefore the statistical power, was rather small. Furthermore, future studies comparing professional SIs and bilinguals as well as longitudinal studies may provide important information for better comprehending how the training of language-related skills may influence grey matter architecture during different periods of cortical development. A further shortcoming of the present work is that the paradigm we used does not enable to assess whether interpreting training additionally drives grey matter plasticity in regions that are already modulated by multilingualisms or rather shapes the architecture of additional brain regions. Further studies comparing multilinguals, monolinguals, and SIs may constitute a fruitful approach for better comprehending this issue. Finally, we want to emphasize that even though the subjects who participated in the present study reported to fluently speak the foreign languages in a conversational context, we cannot exclude that some differences in linguistic skills may have influenced the data in some direction.

6. Conclusions

Our results provide first evidence for an expertise-specific grey matter architecture in professional SIs which is assumed to be

driven by the cognitive, linguistic and articulatory requirements necessary for simultaneously translating a source language into a target language during adulthood.

Authors' contributions

Competing interests

The authors declare that they have no competing interests.

Acknowledgements

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2014.02.014.

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