



Bilingualism as a gradient measure modulates functional connectivity of language and control networks

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ABSTRACT

There is currently no agreement on which factor modulates most effectively and enduringly brain plasticity in bilingual individuals. Grouping heterogeneous linguistic profiles under a dichotomous condition (bilingualism versus monolingualism) may obscure critical aspects of language experience underlying neural changes, thus leading to variable and often conflicting findings. In the present study, we overcome these limitations by analyzing the individual and joint contribution of L2 AoA, proficiency and usage – all measured as continuous variables – on the resting-state functional connectivity of the brain networks mediating the specific demands of bilingual language processing: the language network and the executive control network. Our results indicate that bilingual experience – defined as a continuous and multifaceted phenomenon – impacts brain plasticity by modulating the functional connectivity both within and between language and control networks. Each experience-related factor considered played a role in changing the connectivity of these regions. Moreover, the effect of AoA was modulated by proficiency and usage. These findings shed new light on the importance of modeling bilingualism as a gradient measure rather than an all-or-none phenomenon.

It is well established that multiple languages are jointly activated and compete for selection in a bilingual mind (e.g., Guo and Peng, 2006; Marian and Spivey, 2003). Therefore, bilinguals must not only mentally store and instantiate the additional linguistic information acquired, but also selectively attend to one language and monitor from other languages' intrusions according to the given communicative circumstances. The neural bases of bilingual language control are largely overlapping with the neural infrastructure supporting domain-general executive control¹ functions (e.g., Branzi et al., 2016; Calabria et al., 2018). Both the acquisition and the context-dependent use of multiple languages may lead to functional and structural plastic changes in the brain. At the neuroanatomical level, bilingual experience and second language (L2) learning have been associated with volumetric and shape increases in several gray matter (GM) regions supporting language processing (e.g. Hosoda et al., 2013; Mårtensson et al., 2012) and bilingual language control (e.g. Abutalebi et al., 2012; Burgaleta et al., 2016), with early L2

learners and/or highly proficient L2 speakers showing greater GM density or maintenance than monolinguals (e.g., Del Maschio, Sulpizio, Gallo, Fedeli, Weekes and Abutalebi, 2018; Del Maschio, Fedeli, Sulpizio and Abutalebi, 2019; Klein et al., 2014; Mechelli, Crinion, Noppeney, O'doherty, Ashburner, Frackowiak and Price, 2004). In addition to local GM volume and shape, neuroimaging research has also focused on putative bilingualism-related effects on white matter (WM) structure, indicating, for instance, that proficient and highly immersed bilinguals display higher axonal density or myelination in WM tracts that connect regions which are critical for bilingual language processing, such as the bilateral inferior frontal gyrus (IFG), the left superior temporal gyrus (STG), and the caudate nucleus (e.g., Hosoda et al., 2013; Luk et al., 2011; Pliatsikas et al., 2015; Singh et al., 2018). Moreover, as an additional index of bilingualism-mediated plasticity, observed alterations in local GM and/or WM myelination have been investigated in relation to changes in brain function, with special reference to task- and

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¹ "Executive control" loosely refers to a multi-componential construct encompassing higher-order processes (e.g. inhibitory control, working memory, and attentional flexibility) that govern adaptive, goal-directed behavior.

context-independent (i.e., resting-state) functional connectivity. Although the available literature is limited, some recent evidence suggests that early (i.e., simultaneous) bilingualism affects the functional connectivity of language-related structures (Berken et al., 2016); it should be noted, however, that similar effects across both language- and control-related regions have also been ascribed to language proficiency (e.g., Li et al., 2015a,b).

Crucially, as the aforementioned findings suggest, being bilingual is not an all-or-none phenomenon that can be described as a dichotomous condition grouping extreme cases – e.g., people who have acquired an L2 before versus after a specific age threshold, or people who do or do not exhibit native-like L2 proficiency. L2 knowledge shows remarkable inter-individual variability and can dramatically change throughout the lifespan depending on personal experience. Learner-internal variables such as motivation, engagement in L2 culture, and degree of identification with L2 speakers are also well known to condition L2 learning and attainment (Dörnyei and Skehan, 2003). Accordingly, a better conceptualization of bilingualism should not only be centered on a *qualitative* perspective, but also take into account *quantitative* measures such as *the extent to which* individuals vary as bilinguals. This widening of perspective offers a more ecological description of bilingualism and can improve our understanding of bilingualism-associated brain plasticity. In the present study, we move along this direction and examine how inter-individual variability in bilingual experience predicts differences in the functional connectivity of brain networks responsible for language processing and control. In order to achieve this aim, we investigated a group of individuals ($N = 50$) who varied along the three main dimensions usually defining bilingual experience: (a) The age of L2 onset (i.e., L2 age of acquisition, AoA); (b) the level of mastery attained in L2 (i.e., L2 proficiency); (c) the relative frequency of daily use of first and second language (i.e., L1/L2 usage). We tested whether and to what extent bilingual experience impacts the functional organization of the language network and the control network using resting-state functional connectivity (rs-FC), which measures spontaneous correlations in fluctuations of the BOLD signal during task-independent neural activity (Fox and Raichle, 2007; Smith et al., 2013).

There is currently no agreement on which factor modulates most effectively and enduringly brain plasticity in bilingual individuals, and two opposing views have been argued for.

The first view suggests that L2 AoA is the main driving force of plasticity (e.g. Berken et al., 2016; Kousaie et al., 2017). Since the brain is extremely malleable during development, having an early experience with a second language would significantly contribute to shape the functioning of language-related and control-related networks. Berken et al. (2016) showed that, compared to sequential bilinguals (i.e., L2 acquired after the age of 5), simultaneous bilinguals (two languages from birth) had stronger functional connectivity between the left IFG and its right counterpart, as well as between the IFG and the right dorsolateral prefrontal cortex (DLPFC), the bilateral inferior parietal lobule (IPL) and the cerebellum. Similar effects of L2 AoA on the interhemispheric connectivity of frontal regions have been recently reported by Gullifer et al. (2018), who investigated rs-FC in French-English bilinguals. In addition, Liu et al. (2017) explored the topological properties of a distributed language network (encompassing phonology-, semantics- and syntactic-related modules) in early versus late proficient Cantonese-Mandarin bilinguals. Irrespective of L2 proficiency, late bilinguals (i.e., who learned L2 after the age of 6) were found to have weaker intra- and inter-modular functional connectivity.

The second view proposes that functional brain changes are enabled and constrained mainly by L2 experience, in terms of proficiency and usage. In particular, the organization of language- and control-related networks would be optimized by the relative use and maintenance of multiple languages (e.g., Calabria et al., 2018). Thus, the alleged effect of AoA, rather than a hard biological constraint, would be an epiphenomenon of language use, given that early bilinguals typically employ their two languages for a longer period than late bilinguals. Consistent with

this view, Li et al. (2015a,b) investigated rs-FC in monolinguals and highly proficient bimodal bilinguals who acquired Chinese sign language late in life (mean age: 19 years). Compared to monolinguals, bilinguals showed decreased connectivity between the anterior cingulate cortex (ACC), the left STG, and the left IFG, and increased connectivity between the left caudate nucleus and the right middle temporal gyrus, a region relevant for sign language processing. Moreover, Gullifer et al. (2018) reported that a balanced use of the two languages was associated with greater functional connectivity between the ACC and the putamen bilaterally, as well as between the left caudate and the STG bilaterally.

The inconsistent findings that emerge from the rs-FC literature may have two sources: First, the variables under investigation, along with the focus on a single variable characterizing bilingual experience and not others; second, the characterization of bilingualism as a qualitative rather than quantitative phenomenon. In the present study, we overcome these limitations by analyzing the impact of L2 AoA, proficiency and usage – all measured as continuous variables – on the rs-FC of the two brain networks which are expected to mediate the specific demands of bilingual language processing: the language network and the control network. Since individual differences in bilingual experience may result from a combined effect of these variables, other than testing the effect of each variable *per se*, we also investigated their interactions. Our sample of Italian-English speakers collected in Milan is well suited for testing how different socio-linguistic factors interact to shape network plasticity. Indeed, while it increasingly represents an international economic hub where a multilingual environment is the rule rather than the exception, Milan continues to be characterized by a large variability in terms of bilingual experience, even among younger age groups. Whereas >95% of students attend foreign language classes during their compulsory education (and >98% learn English) (Eurostat, 2015), second language proficiency and usage vary broadly across individuals, largely depending on contextual and learner-internal factors.

With regard to language processing, we examined the contribution of bilingual experience to the functional connectivity of the core perisylvian language network, comprising the left IFG and the posterior part of the STG bilaterally. Even though abundant evidence has been provided that the neural substrate for language processing is not restricted to this network, all major neurocognitive models consider the IFG and the STG as the key components of language functioning (e.g., Friederici, 2011; Hagoort, 2016; Hickok and Poeppel, 2004). Moreover, although being bilingual does not change the core language network (i.e., the network involved in language processing is the same for mono- and bilinguals), especially poorly proficient and less exposed bilinguals are faced with higher language-processing demands than their monolingual peers (for a review, see Costa and Sebastián-Gallés, 2014), with potential alterations of the functional connections between language regions. Based on previous evidence (Grant et al., 2015; Yang et al., 2015), we hypothesize that both L2 proficiency and usage might increase the strength of connections between core language areas. Language use may also modulate the connectivity between language-related and control-related regions: According to the Adaptive Control Hypothesis (Green, 1998; Green and Abutalebi, 2013), the more a bilingual uses her/his two languages, the more she/he will be able to keep active the to-be-used language while inhibiting the to-be-ignored language (see, Li et al., 2015b). However, changes in the connectivity of the language network might also be driven by L2 AoA, with early acquisition enhancing the efficiency of language-related regions (see Berken et al., 2016; Liu et al., 2017). This hypothesis also follows from recent evidence on structural connectivity: Hämäläinen et al. (2017) have shown that, compared to a later L2 onset (i.e., after the age of 5), an earlier acquired language is associated with increased fractional anisotropy along the arcuate fasciculus, the path connecting the regions of the language network.

As far as language control is concerned, neuroimaging evidence indicates that bilinguals control and switch between languages by means of a cortico-subcortico-cerebellar network including: PFC, bilateral ACC, inferior parietal lobules (IPLs), thalamus, basal ganglia, and cerebellum

(see Abutalebi and Green, 2016). In this study, we tested the modulation effect of bilingual experience on the functional connectivity of these structures. If changes in connectivity are mainly driven by the long-term use of multiple languages – in accordance with Green and Abutalebi's Adaptive Control Hypothesis and findings in Li et al. (2015a,b) and Gullifer et al. (2018) –, then we can expect an increase in functional connectivity as a function of L2 usage. These changes would result from the extensive recruitment of regions underpinning bilingual language control as well as their interaction with perisylvian nodes. Enhanced functional connectivity between these structures may also correlate with practice in language control, here quantified by self-assessed measures of code-switching, the context-dependent tendency to alternate between or mixing two languages. However, if remodeling of functional networks is conditional on the timing of L2 acquisition – since the brain is maximally plastic during early development –, then the connectivity of control regions might be modulated only (or mainly) by L2 AoA; in such a perspective, only an early acquisition would guarantee the use of the same neurocognitive mechanisms for both languages (e.g., Abrahamsson, 2012; Ullman, 2016).

The effects of bilingualism on the functional connectivity of the language and control networks were explored by means of a seed-to-voxel approach and graph analysis. Whereas the selection of our seed regions was supported by prior research, the choice of a seed-to-voxel approach for the connectivity analysis was aimed at maximizing the variety of functional systems which these seed regions likely underpin. Graph analysis was used to explore possible modulations on within-network relationships.

1. Materials and methods

1.1. Participants

Fifty right-handed young adults ($M_{\text{age}} = 25.78$, $SD = 4.8$, 30 F) with no history of neurological or psychiatric disorder were included in the study. Socio-demographic variables – age, years of education and annual family income – were collected for all participants. Annual family income was measured using the MacArthur Scale of Subjective Social Status (<https://macses.ucsf.edu/research/psychosocial/subjective.php#measurement>), whose score ranges from 1 (<5000 €) to 5 (>75,000 €). Participants' fluid and verbal intelligence were also assessed using, respectively, the Raven's Standard Progressive Matrices for adults (the intelligence quotient was estimated following normative data for the Italian population; Basso et al., 1987) and the *Test Breve di Intelligenza* (TIB) (Colombo et al., 2002), the Italian equivalent of the National Adult Reading Test (NART; Nelson, 1982).

All participants were native Italian speakers who spoke English as an L2. In order to qualify participants' bilingual experience, L2 AoA, L2 proficiency, Language Entropy (a measure of language usage; for details, see below), and participants' language switching habits were collected for all participants. L2 AoA was measured by asking participants the timing of L2 acquisition. To establish L2 proficiency, the online Cambridge test for adult learners (<http://www.cambridgeenglish.org/test-your-english/general-english/>) was administered to all participants (see Sulpizio et al., 2019). The test is composed of 25-items that evaluate English grammatical and conversational knowledge. The score goes from 0 to 25 and provides an estimation of English proficiency in terms of the reference levels defined by the Common European Framework of Reference for Languages (i.e., A1, A2, B1, B2, C1, C2). To evaluate L2 vocabulary knowledge, participants also completed a second proficiency assessment consisting in a L1-to-L2 90-items translation task (i.e., 30 high-frequency, 30 medium-frequency, and 30 low-frequency words) (see Abutalebi et al., 2012).

Language Entropy was measured by computing Shannon Entropy (H), which provides a continuous measure of how often one or the two languages are used (for a similar approach, see Gullifer et al., 2018). First, participants were asked to estimate how many hours per day they were

exposed to L1 and L2 on different in-class/work-related and out-of-class/extra-work language associated activities; then these measures were used to quantify a proportion of L1 and L2 use for each participant by dividing the use of a given language by the sum of the use of the two languages. Finally, Shannon Entropy (H) associated with proportional L1 and L2 use (i.e., Language Entropy) was computed using the following equation:

$$H = - \sum_{i=1}^n P_i \log_2(P_i)$$

Here, n represents the total possible languages (i.e., two in the present study) and P_i represents the proportion associated with the use of a given language. Language Entropy provides a continuous measure of language usage, ranging from 0 (i.e., a completely compartmentalized context, where only one language is used) to 1 (i.e., a fully integrated context, where each language is used equally).

In order to further qualify participants' bilingual experience, switching habits were estimated using the Bilingual Switching Questionnaire (BSWQ; Rodriguez-Fornells et al., 2012), a 12-items self-assessment questionnaire aimed to detect individual differences in language switching. The questionnaire can be decomposed into four constructs which measure different aspects of switching habits: L1 switching tendencies (L1s) and L2 switching tendencies (L2s) measure the tendency to switch, respectively, to L1 and L2; contextual switch (CS) assesses the frequency of switches in particular situations or environments; unintended switch (US) measures the lack of awareness of language switches. Participants were required to evaluate the degree to which a behavior characterized his/her language switching habits using a five-point scale (from 1-never to 5-always); the score goes from 0 to 15 for each component (three items for each construct). Details on demographic, cognitive, and linguistic measures are reported in Table 1.

The present study was conducted with ethical approval from the Human Research Ethics Committee of the Vita-Salute San Raffaele University (Milan, Italy). Written informed consent was obtained from all participants.

1.2. Image acquisition

Structural and functional data were acquired during the same session for each participant with a 3T Ingenia Philips MR scanner (Philips Medical Systems, Best, Netherlands), equipped with two multiband coils at C.E.R.M.A.C. (Centro Eccellenza di Risonanza Magnetica ad Alto

Table 1

Descriptive statistics of demographic, cognitive, and linguistic measures. Mean, standard deviation (SD), and range for each measure are reported. Scores of the *Test Breve di Intelligenza* (TIB) range from 0 to 50. Raven's matrices raw scores are corrected according to participants' age and years of education; corrected scores range from 0 to 36 (cut-off = 18). L2 AoA = L2 Age of Acquisition; BSWQ = Bilingual Switching Questionnaire; L1s = L2 > L1 switching tendencies; L2s = L1 > L2 switching tendencies; CS = contextual switch; US = unintended switch.

	Mean (SD)	Range
Age (years)	25.7 (4.8)	18–38
Education (years)	17.4 (1.8)	13–21
Annual family income	3.6 (1)	1–5
TIB	47.2 (2.1)	43–50
Raven's Matrices (corrected scores)	31.3 (2.8)	26–36
L2 AoA	8.4 (5.3)	3–28
Language Entropy	0.7 (0.2)	0–1
Cambridge test (score)	19.2 (4)	10–25
Translation task (L1 > L2) (% correct responses)	61 (14.3)	19–89
BASWQ – L1s	7 (1.7)	3–10
BASWQ – L2s	8.8 (1.8)	4–13
BASWQ – CS	7 (2.7)	3–15
BASWQ – US	7.9 (1.4)	4–11

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T1-weighted MPRAGE (Magnetization Prepared Rapid Gradient Echo) images were acquired with the following parameters: repetition time (TR) = 9.9 m s, echo time (TE) = 4.9 m s, flip angle = 8°, FOV = 260 mm, matrix size = 256 × 256, number of slices = 243, slice thickness = 1.4 mm, voxel size = 0.7 × 0.7 × 0.7 mm³.

Resting-state fMRI images were acquired using a T2*-weighted EPI sequence with the following parameters: TR = 1178 m s, TE = 33 m s, flip angle = 85°, field of view (FOV) = 250 mm, matrix size = 64 × 64, number of slices = 38, slice thickness = 3 mm, voxel size = 3.0 × 3.0 × 3.75 mm³. A total of 760 vol were obtained for each participant.

1.3. Preprocessing

Preprocessing of the structural and functional data was carried out using CONN-fMRI Functional Connectivity toolbox v18.b (<https://web.conn-toolbox.org/home>) (Whitfield-Gabrieli and Nieto-Castanon, 2012) based on SPM12 v7219 (www.fil.ion.ucl.ac.uk/spm/).

All images were anonymized and then visually inspected for the presence of any artifacts; no participant was discarded due to this reason. The origin of structural images was set to match the bicommissural line (AC–PC). The Tsdiffana toolbox (<https://www.fil.ion.ucl.ac.uk/spm/ext/>) based on SPM12 was used to assess the quality of image timeseries and to identify slices showing deviations from timeseries mean. No participant was discarded during this step. All images were slice-time corrected. Participants' motion estimation and correction were then carried out through functional realignment and unwarping and potential outlier scans were identified using the Artifact Detection Tool (ART) toolbox (https://www.nitrc.org/projects/artifact_detect). Structural images were segmented into Gray matter, White matter and Cerebrospinal Fluid tissues and normalized to the Montréal Neurological Institute (MNI) space with the unified segmentation and normalization procedure (Ashburner and Friston, 2005). Functional volumes were normalized and smoothed with a 8 mm Full Width at Half Maximum (FWHM) Gaussian kernel.

Preprocessing steps automatically create three first-level covariates: a “scrubbing” covariate containing the potential outlier scans for each participant, a “realignment” covariate containing the six rigid-body parameters characterizing the estimated subject motion for each participant and a covariate containing quality assurance (QA) parameters (i.e., the global signal change from one scan to another and the framewise displacement, a measure of how much the participant moved from one scan to another) for each participant. Realignment parameters, potential outlier scans, signal from white matter and cerebrospinal fluid masks and effect of rest (i.e. an automatically estimated trend representing potential ramping effects in the BOLD timeseries at the beginning of the sessions), were entered as potential confound regressors into the model in the denoising step of the CONN toolbox. Using the implemented anatomical CompCor approach (Behzadi et al., 2007) all of these effects were removed in a single linear regression step to obtain a clean signal. Functional images were then band-pass-filtered between 0.1 and 0.01 Hz to remove low-frequency drifts and physiological high-frequencies noise.

1.4. Functional connectivity measures

Graph theory. According to graph theory, the brain can be modeled as a graph whose nodes (functional brain regions) are interconnected by edges (functional connections) (Bullmore and Sporns, 2009). We used CONN to estimate the following topological properties of the language and control networks: global efficiency (i.e., the average of the inverse shortest path distance between each node and all other nodes in the graph) and local efficiency (i.e., the efficiency of a sub-graph consisting only of nodes neighboring a certain node) (Whitfield-Gabrieli and Nieto-Castanon, 2012). In order to compute these measures, the entire matrix of ROI-to-ROI functional connectivity values was computed for each participant. In ROI-to-ROI rs-FC analysis, Pearson's correlation

coefficients are first computed between the residual BOLD time course from the ROI and the time course of all the other ROIs within the same network, and then converted with the same procedure described for the seed-to-voxel analysis. Finally, participant-specific ROI-to-ROI connectivity matrix was thresholded at a cost value of $k = 0.4$, chosen as small world properties observed at this threshold (i.e., global efficiency greater than that of a lattice graph and local efficiency greater than that of a random graph) (Whitfield-Gabrieli and Nieto-Castanon, 2012). Negative functional connectivity values were disregarded in these analyses.

Seed-to-voxel functional connectivity. Analyses were performed using a seed-based approach with CONN toolbox. In seed-based rs-FC analysis, Pearson's correlation coefficients are computed between the residual BOLD time course from the seed and the time course of all the other voxels. Then, correlation coefficients are converted to normally distributed scores using Fisher's transform to allow for second-level GLM analysis. Key structures supporting language processing and bilingual language control were identified as target regions. The left inferior frontal gyrus (IFG) and the bilateral posterior superior temporal gyrus (pSTG) were selected as target regions of the language network. These areas, assumed to be at the core of language processing by the major neurocognitive models of language (e.g., Friederici, 2011; Hagoort, 2016; Hickok and Poeppel, 2004), were selected from the pre-defined network masks in CONN. For bilingual language control, target regions were selected based on Abutalebi and Green (2016) and defined through the Automated Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002). The following control areas were selected: bilateral superior frontal gyrus (SFG); bilateral middle frontal gyrus (MFG); bilateral inferior frontal gyrus pars opercularis (IFGop), pars triangularis (IFGtri) and pars orbitalis (IFGorb); bilateral supplementary motor area (SMA); bilateral anterior cingulate cortex (ACC); bilateral supramarginal gyrus (SMG); bilateral angular gyrus (AG); bilateral thalamus; left caudate nucleus; left putamen. All regions and their relative spatial coordinates are reported in Table 2.

1.5. Statistical analyses

Correlation analyses between linguistic, demographic and cognitive measures. Preliminary analyses were run to check for multicollinearity between linguistic, demographic and cognitive measures: L2 AoA, Language Entropy, Cambridge test, translation task, TIB and educational history. Pearson's correlations were run for all variables, except for those not normally distributed (according to the Kolmogorov-Smirnov test); in this latter case, Spearman's correlations were performed. When two measures were highly correlated ($r > 0.50$, cfr., e.g., Taylor, 1990), only one of them was used in the analyses.

Table 2

Regions entered as seeds in seed-to-voxel analysis. MNI centroid coordinates are based on the CONN's pre-defined network masks for the language network and on the Automated Anatomical Labeling (AAL) atlas for the control network.

Seed	Left MNI centroid coordinates (x, y, z)			Right MNI centroid coordinates (x, y, z)		
Language network						
IFG	−51	26	2	−	−	−
pSTG	−57	−47	15	59	−42	13
Control network						
SFG	−19	33	40	19	31	42
MFG	−35	29	33	36	32	34
IFGop	−47	10	13	48	14	18
IFGtri	−45	28	09	46	30	11
IFGorb	−35	28	−15	37	31	−14
SMA	−07	04	59	07	01	58
ACC	−05	33	11	07	35	15
SMG	−57	−37	28	56	−31	35
AG	−44	−63	35	43	−60	37
Th	−12	−20	07	12	−19	07
Caudate	−13	09	08	−	−	−
Putamen	−25	01	01	−	−	−

Since results showed a high significant correlation between the Cambridge test scores and the translation task scores ($r_s = 0.69$, $p < 0.001$), the former was chosen as an index of participants' proficiency for the subsequent analyses. We considered the Cambridge test as a more ecological measure which also evaluates participants' conversational abilities. No other significant correlation was found except for a low significant correlation between Cambridge test and Language Entropy ($r_s = 0.36$, $p < 0.05$).

Multiple regression analysis. The same models were used to analyze the topological properties of the networks and seed-to-voxel connectivity.

Two multiple regression analyses were performed to investigate the effects of bilingual experience on the language and control networks. Principal main effects of L2 AoA, L2 proficiency and Language Entropy were computed. As these measures did not strongly correlate with each other, the following interactions were performed: AoA by Proficiency, Language Entropy by Proficiency, and AoA by Language Entropy. Educational history, gender and TIB were included in the model as nuisance covariates. When computing the main effect of each linguistic measure (e.g., L2 AoA), the other two measures (L2 proficiency, Language Entropy) were entered as covariates. Following the same procedure, when computing each interaction effect between two linguistic measures (e.g., AoA by Proficiency), the other measure (Language Entropy) was entered as covariate in the model. Significant interactions, when present, were inspected by looking at one continuous variable at different levels of the other variable; in case AoA was involved in the interaction, it was divided in two levels (early: < 6 , late ≥ 6); in case Language Entropy was involved, it was divided in low, medium, and high levels ($0-30^\circ$, $31-60^\circ$, $>61^\circ$ percentiles).

For the analysis of the topological properties of the two networks, results were thresholded at $p < 0.001$. For seed-to-voxel analysis, results were thresholded at $p < 0.05$, with family wise error (FWE) correction for multiple comparisons at the cluster level.

Correlation analysis between switching habits and connectivity. As switching between languages requires control processes (e.g., disengaging from the old task and engaging with the new one; Green and Abutalebi, 2013), the relationship between switching habits and the rs-FC of regions involved in language processing and control was explored. To analyze this relation, Fisher-transformed correlation coefficients (i.e., connectivity values) between each pair of seed and suprathreshold cluster were extracted for each participant from CONN. Then, Spearman's correlation analyses were performed between connectivity values and switching measures (i.e., L1s, L2s, CS and US).

2. Results

2.1. Graph theory

The analysis of the networks' topological properties showed a main

effect of Proficiency. In particular, an increase of local efficiency on the control network was detected ($T = 2.19$, $p_{\text{unc}} = 0.034$). This finding indicates that, as proficiency increases, inter-connectedness among all nodes within a node neighboring sub-graph also increases.

2.2. Seed-to-voxel functional connectivity - language network

Results are reported in Tables 3a and 4a and Fig. 1. The analyses showed a main effect of AoA, with higher values of AoA (i.e., later AoA) associated with an increase of functional connectivity between the left pSTG and the left precuneus. A significant AoA by Proficiency interaction also emerged, modulating the connections of the left pSTG with the right temporal pole and the right precuneus. In both cases, an increase in proficiency was associated to an increase in connectivity in late bilinguals; moreover, only for the right precuneus, higher values of proficiency were associated to a decrease in connectivity in early bilinguals.

2.3. Seed-to-voxel functional connectivity - control network

Results are reported in Tables 3b and 4b, and Fig. 2. The analyses revealed both main effects and interactions affecting connections between several regions implicated in language control in both hemispheres. Specifically, at the cortical level: the right DLPFC, the left medial frontal cortex, and the IPLs; at the subcortical level: the left basal ganglia and the right thalamus.

In terms of main effects, only AoA was found to modulate rs-FC, with the left caudate showing decreased connectivity with the right middle cerebellar lobe. More interestingly, AoA was found to interact both with Proficiency and Language Entropy. The AoA by Proficiency interaction modulated the connectivity of the left caudate with the right middle cerebellar lobe, with a negative relation between proficiency and connectivity (i.e., the higher the proficiency, the lower the connectivity) for early bilinguals only.

The AoA by Language Entropy interaction modulated the functional connectivity of different seed regions with different voxel clusters. In particular, the left putamen showed enhanced connectivity with the Rolandic operculum bilaterally and the left SMA: the inspection of the two interactions suggested, in both cases, a positive relationship between Language Entropy and connectivity (i.e., the higher the Language Entropy, the higher the connectivity) that was particularly pronounced for late bilinguals. A similar pattern of results was also found for the connectivity of the left SMA with the left caudate, and the connectivity of the bilateral SMG with the left paracentral lobule: in both cases, Language Entropy was associated to an increase in connectivity, but mainly in late bilinguals. Finally, there was a modulation of the connectivity between the right SFG and the right Rolandic operculum: while an increase of Language Entropy was associated with enhanced connectivity in late bilinguals, it was associated to a connectivity decrease when L2 was

Table 3

Seed-to-voxel results on the language (3a) and control (3b) networks. k = cluster size; p -FWE = p -family wise error (FWE) corrected.

Model	Seed	Target region	Direction of the effect	MNI coordinates (x, y, z)			k	t value	Equiv. Z score	p-FWE (cluster level)
AoA	L pSTG	L Precuneus	+	00	-56	38	377	4.59	4.12	.013
AoA*Proficiency	L pSTG	R Temporal Pole	+	38	18	-38	506	5.56	4.82	.003
AoA*Proficiency	L pSTG	R Precuneus	+	02	-56	36	591	4.98	4.41	.001
AoA	L Caudate	R Middle cerebellar lobe	-	18	-58	-24	691	-4.90	-4.34	<.001
AoA*Proficiency	L Caudate	R Middle cerebellar lobe	-	10	-60	-20	457	-4.48	-4.05	.007
LE*Proficiency	L Putamen	R Rolandic operculum	+	44	-14	18	648	4.49	4.05	<.001
LE*Proficiency	R Th	R Lingual gyrus	+	10	-70	00	457	4.54	4.09	.007
LE*AoA	L SMA	L Caudate	+	00	08	06	460	5.23	4.59	.007
LE*AoA	L SMG	L Paracentral lobule	+	-04	-28	72	411	4.98	4.41	.011
LE*AoA	R SMG	L Paracentral lobule	+	-02	-27	70	558	4.68	4.20	.002
LE*AoA	L Putamen	R Rolandic operculum	+	46	-18	16	1456	5.72	4.92	<.001
LE*AoA	L Putamen	L Rolandic operculum	+	-48	-12	14	666	4.74	4.24	<.001
LE*AoA	L Putamen	L SMA	+	-06	-06	58	386	4.71	4.22	.015
LE*AoA	R SFG	R Rolandic operculum	-	48	-02	10	314	-5.33	-4.65	.035

Table 4

Size effects, standard errors and confidence intervals of each predictor are reported for each significant result in the Language Network (4a) and Control Network (4b). β = size effect; St. Error = standard error.

Seed	Target region	Main/interaction effect	Nuisance variables	β	St. Error	Confidence Interval
L pSTG	L Precuneus	AoA		0.024	0.005	0.017
			Proficiency	0.002	0.007	0.025
			Language Entropy	-0.061	0.110	0.361
			Educational history	-1.77E-04	0.014	0.047
			Gender	0.045	0.055	0.182
L pSTG	R Temporal Pole	AoA*Proficiency	TIB	0.015	0.013	0.043
				0.001	2.43E-04	7.99E-04
			Language Entropy	-0.122	0.084	0.278
			Educational history	0.002	0.012	0.040
			Gender	-0.033	0.046	0.154
L pSTG	R Precuneus	AoA*Proficiency	TIB	0.002	0.011	0.036
				0.001	2.77E-04	9.12E-04
			Language Entropy	-0.171	0.096	0.317
			Educational history	0.003	0.014	0.046
			Gender	0.044	0.053	0.175
L Caudate	R Middle cerebellar lobe	AoA	TIB	0.016	0.012	0.041
				0.011	0.002	0.008
			Proficiency	5.55E-04	0.003	0.011
			Language Entropy	-0.062	0.050	0.167
			Educational history	-0.018	0.006	0.022
L Caudate	R Middle cerebellar lobe	AoA*Proficiency	Gender	0.009	0.025	0.084
			TIB	-0.006	0.006	0.020
				6.08E-04	1.36E-04	4.46E-04
			Language Entropy	-0.059	0.047	0.155
			Educational history	-0.020	0.006	0.022
L Putamen	R Rolandic operculum	LE*Proficiency	Gender	-0.032	0.026	0.086
			TIB	-0.005	0.006	0.020
				0.011	0.002	0.008
			AoA	0.010	0.003	0.010
			Educational history	-0.014	0.009	0.029
R Th	R Lingual Gyrus	LE*Proficiency	Gender	-0.047	0.034	0.113
			TIB	0.004	0.008	0.026
				0.015	0.003	0.011
			AoA	-0.001	0.004	0.013
			Educational history	5.89E-05	0.011	0.038
L SMA	L Caudate	LE*AoA	Gender	-0.024	0.044	0.145
			TIB	0.005	0.010	0.034
				0.015	0.003	0.009
			Proficiency	-0.006	0.003	0.012
			Educational history	-0.013	0.007	0.025
L SMG	L Paracentral lobule	LE*AoA	Gender	0.005	0.029	0.096
			TIB	0.003	0.006	0.022
				0.023	0.004	0.015
			Proficiency	-0.009	0.005	0.019
			Educational history	-0.010	0.012	0.039
R SMG	L Paracentral lobule	LE*AoA	Gender	-0.029	0.046	0.151
			TIB	0.002	0.010	0.035
				0.022	0.004	0.016
			Proficiency	-0.014	0.006	0.019
			Educational history	-0.008	0.012	0.041
L Putamen	R Rolandic operculum	LE*AoA	Gender	0.056	0.047	0.156
			TIB	-0.006	0.011	0.036
				0.019	0.003	0.011
			Proficiency	0.003	0.004	0.013
			Educational history	-0.010	0.008	0.028
L Putamen	L Rolandic operculum	LE*AoA	Gender	-0.034	0.032	0.107
			TIB	0.013	0.007	0.025
				0.018	0.003	0.013
			Proficiency	0.007	0.004	0.016
			Educational history	-0.007	0.010	0.033
L Putamen	L SMA	LE*AoA	Gender	0.014	0.038	0.127
			TIB	0.009	0.009	0.030
				0.016	0.003	0.011
			Proficiency	0.004	0.004	0.014
			Educational history	0.008	0.009	0.029
R SFG	R Rolandic operculum	LE*AoA	Gender	-0.020	0.034	0.113
			TIB	-0.002	0.008	0.026
				0.017	0.003	0.010
			Proficiency	4.52E-04	0.003	0.012
			Educational history	-7.86E-04	0.008	0.027
			Gender	-0.001	0.031	0.103
			TIB	-0.014	0.007	0.024

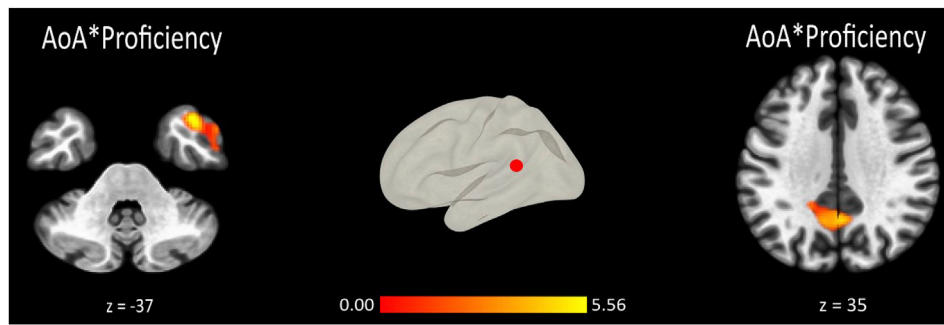


Fig. 1. Significant interaction effects between AoA and Proficiency. Axial slices show suprathreshold clusters for left pSTG as seed region (red circle on the central rendering). The color bar indicates positive T-values.

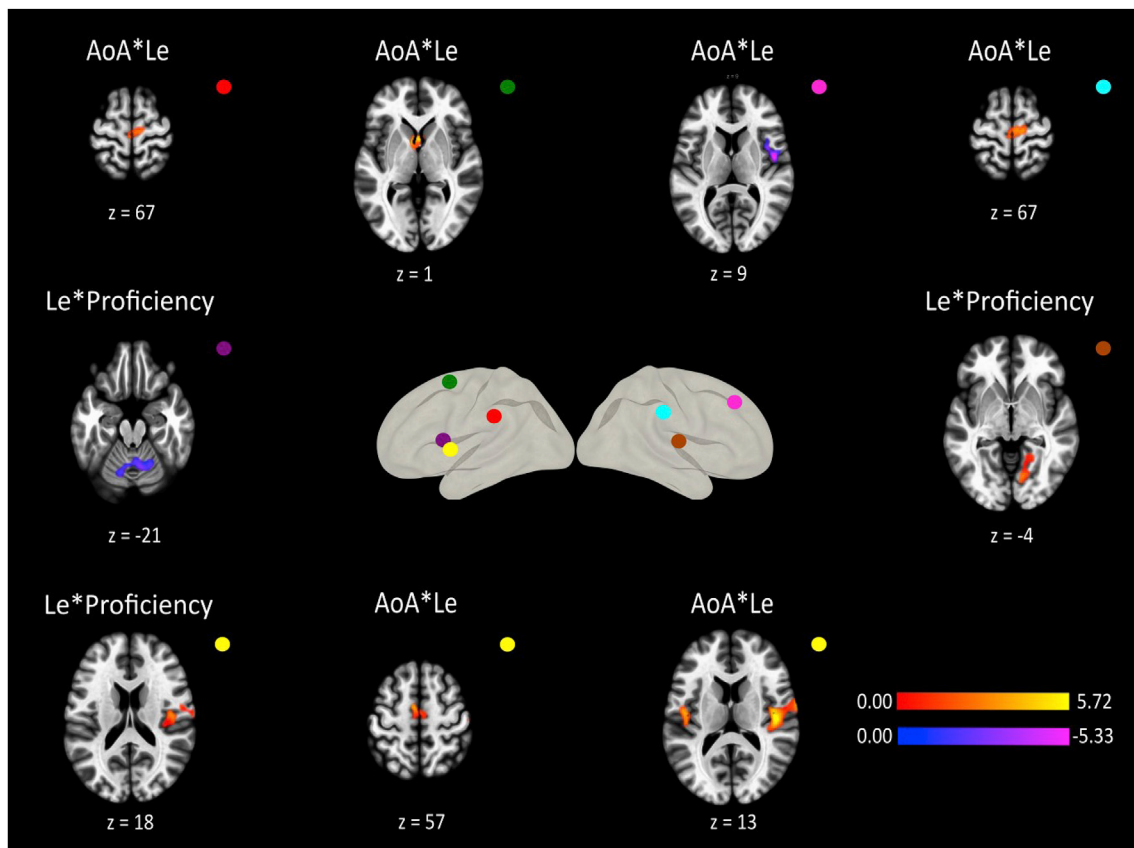


Fig. 2. Seed regions of the control network (colored circles on the central renderings) showing significant effects. Each color denotes a seed region: left Supplementary motor area (green), left Supramarginal gyrus (red), left Putamen (yellow), left Caudate nucleus (purple), right Superior frontal gyrus (pink), right Supramarginal gyrus (blue), right Thalamus (brown). Axial slices show suprathreshold clusters for the different seeds. Clusters' color denotes increased (red-yellow) or decreased (blue-purple) connectivity. Color bars indicate positive and negative T-values.

acquired earlier.

The Language Entropy by Proficiency interaction showed significant effects as well, modulating the connectivity between the left putamen and the right Rolandic operculum, as well as between the right thalamus and the right lingual gyrus. The inspection of these interactions showed that, as proficiency increased, the connectivity between the left putamen and the right Rolandic operculum also increased, but only for individuals with high values of Language Entropy. Moreover, the connectivity between the right thalamus and the right lingual gyrus increased in all participants, but especially for those with high values of Language Entropy.

Since the inspection of all the interaction effects showed similar patterns, only three representative examples are reported in Fig. 3.

Overall, seed-to-voxel analyses showed that all the three variables considered (AoA, L2 proficiency, and Language entropy) modulated the connectivity patterns of seed regions in the language network (left pSTG) and the control network (left SMA, bilateral SMG, left Putamen, left Caudate, right SFG, right Thalamus), as well as clusters in cortical, subcortical and cerebellar regions. These effects were driven both by the specific contribution of each variable and their joint action.

2.4. Correlations between switching habits and connectivity

When considering data from the language network, a positive correlation emerged between L2-switch scores and the left pSTG-left Precuneus connectivity, modulated by the interaction between AoA and

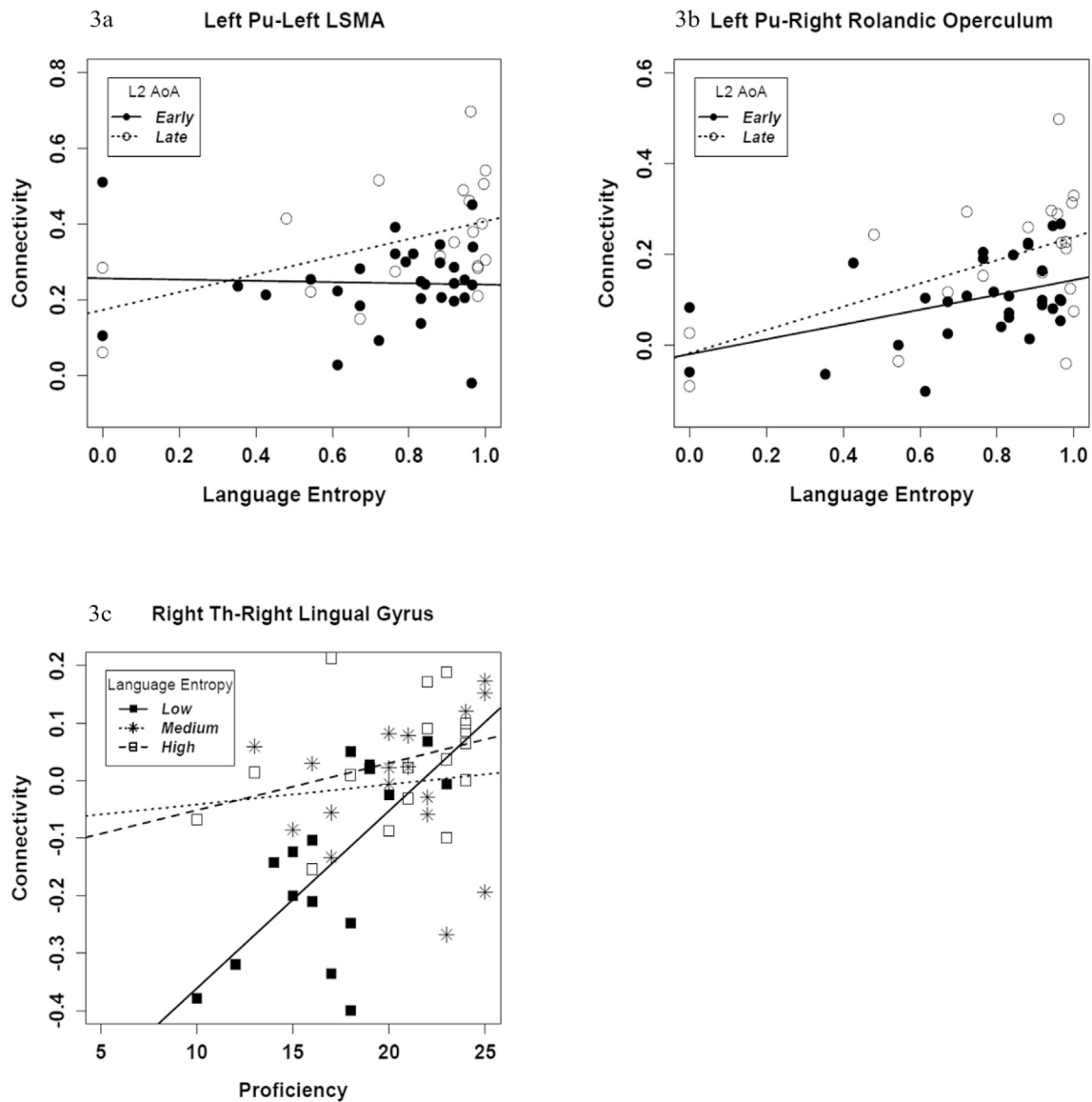


Fig. 3. Plots of representative interactions between: (3a) Language entropy and AoA on the left Putamen-left Supplementary motor area connectivity; (3b) Language entropy and AoA on the left Putamen-right Rolandic Operculum connectivity; (3c) Language entropy and Proficiency on the right Thalamus-right Lingual gyrus connectivity. For Figs. (3a) and (3b), 6 was used as a cut-off age for splitting AoA (early: L2 acquired earlier than 6); for Fig. (3c), 0–30°, 31–60°, and >61° percentiles were used as cut-off for splitting Language Entropy in low, medium, and high, respectively.

Proficiency ($r_s = .41$, $p < 0.05$). The correlation indicates that a larger tendency to switch to L2 in late bilinguals was associated to an increase in the strength of functional connections between left pSTG and right Precuneus associated with higher proficiency. No other correlation between switching measures and connectivity values was significant ($p > 0.05$ for all other correlations).

Turning to the control network, there was a positive correlation between L1-switch scores and the functional connectivity between right thalamus and right lingual gyrus modulated by the interaction between Language Entropy and Proficiency ($r_s = 0.34$, $p < 0.05$). A further positive correlation emerged between the L2s scores and the left SMA-left caudate connectivity ($r_s = .32$, $p < 0.05$). As the connectivity between these regions was modulated by the interaction between AoA and Language Entropy, the correlation indicates that the larger tendency to switch to L2 was linked to a Language Entropy-related increase in connectivity mainly in late bilinguals. No other correlation between switching measures and connectivity values was significant ($p > 0.05$ for all other correlations).

3. Discussion

In the present study, we investigated the impact of bilingual experience on the functional connections of brain networks responsible for the processing and control of two languages. In order to achieve this goal, a renovated conceptualization of bilingualism was adopted which frames the phenomenon as a gradient and composite measure encompassing both static (i.e., L2 AoA) and dynamic factors (i.e., L2 proficiency and usage). We explored the individual and joint contribution of these factors in shaping the functional organization of the language and control networks. In what follows, we first discuss the results for each network separately; then, we discuss the general implications of our findings for bilingualism research.

3.1. Language network

We found that L2 AoA modulated the functional connectivity between the left pSTG and the left precuneus, with a later onset age of L2 associated with enhanced connectivity within the language network.

Moreover, the interaction between AoA and proficiency of L2 was found to bolster the inter-hemispheric connectivity of the left pSTG with the right precuneus and the right temporal pole. In particular, in late bilinguals, a higher level of proficiency was associated with stronger connections between left pSTG and the other two regions.

The left pSTG, a critical region for word comprehension, integrates auditory-phonological and conceptual processing (e.g., Bonilha et al., 2017; Hickok and Poeppel, 2004). Testing interpreting students, Mårtensson et al. (2012) reported that a 3-months foreign language training program led to increased GM volume in the left STG, with a positive association between volume and learners' proficiency. Since the precuneus has been found to contribute to attentional operations (e.g., Cavanna and Trimble, 2006; Utevsky et al., 2014) and has been repeatedly associated with language switching in bilinguals (e.g., Garbin et al., 2011; Reverberi et al., 2015), the modulation of the functional connections between pSTG and precuneus may be linked with the ability to successfully direct attention to the lexico-phonological representations of the to-be-used language. In such a perspective, as AoA increases, the more a bilingual becomes proficient, the more she/he would be able to efficiently integrate phonological and semantic representations of the language in use, resulting in stronger connectivity between pSTG and precuneus. Supporting evidence for this interpretation comes from the positive correlation between the pSTG-precuneus connectivity and L2-switch, which requires bilinguals to focus on the lexico-phonological representation of the second (typically weaker) language. An early L2 onset *per se*, however, irrespective of L2 proficiency, may be associated with increased efficiency in handling lexico-phonological representations from active languages that compete for selection, resulting in a more efficient lexical mapping (Hernandez et al., 2005). This would explain the lack of a significant association between higher L2 proficiency and stronger integration among language- and control-related systems in bilinguals who acquired their L2 at an earlier age.

3.2. Control network

The analysis of the topological properties of the control network showed that a higher L2 proficiency was associated with higher levels of local efficiency. Local efficiency is typically associated to the fault tolerance of a network to the elimination of random nodes (Achard and Bullmore, 2007), that is the ability of a subgraph to transmit information at a local level. This finding may suggest that an increase in L2 proficiency enhances the functional segregation of clusters within the control network, thereby optimizing local information processing.

Seed-to-voxel analysis showed changes in functional connectivity between control regions and areas both within and outside the control network. Within the control network, the main findings come from the interaction between AoA and Language Entropy, which modulates the connectivity between left putamen and left SMA (as seed regions) and left SMA and left caudate, respectively. Higher values of Language Entropy (i.e., living in a fully integrated context, where each language is used equally) were associated to enhanced connectivity, especially in late bilinguals. These data support the view that the degree of language usage shapes the strength of connections among control regions (e.g., Perani and Abutalebi, 2005; Perani et al., 2017). Moreover, the positive correlation between left SMA-left caudate connectivity and L2-switch in late bilinguals seems to indicate the bolstering of control-related networks as a result of selecting the target language and/or inhibiting the non-target language.

A further result is the modulation of connectivity between the left caudate and the right cerebellum which emerges from the AoA by Proficiency interaction. This finding may suggest that, the earlier participants become bilinguals, the more a higher level of proficiency is associated with weaker connections. The left caudate has been proposed to support language control, by keeping track of the language in use and controlling for lexical interference (Ali et al., 2010; Crinion et al., 2006). The degree of left caudate involvement in language control has been

inversely related to language proficiency (i.e., the higher the proficiency, the lower the caudate involvement: see Abutalebi et al., 2013a,b). Since the cerebellum plays a role in producing a fluent speech (e.g., Tyson et al., 2014) and resolving conflicting linguistic input (e.g., comprehending a sentence in L2 while listening to an interfering sentence in L1; Filippi et al., 2011), the weaker left caudate-cerebellum connectivity in early proficient bilinguals may be associated with the ability of these bilingual profiles to efficiently minimize the cross-linguistic interference.

The modulation of connectivity among control regions as a function of the interaction between static (L2 AoA) and dynamic variables (L2 proficiency and usage) is in line with the Adaptive Control Hypothesis (Green and Abutalebi, 2013), which posits that the control network essentially adapts to the demands of language control.

With regard to connectivity changes between control regions and regions outside the control network, the AoA by Language Entropy interaction modulated the functional integration of the bilateral SMG with the left paracentral lobule, and that of the right SFG with the right rolandic operculum. Specifically, higher values of Language Entropy were found to be associated with a stronger connectivity between these regions, especially in bilinguals who acquired their L2 later in life. The connectivity of the right rolandic operculum with the left putamen was also shaped by the Proficiency by Language Entropy interaction, with higher Proficiency associated to a higher connectivity, but only in case of high Language Entropy (i.e., in a context characterized by a balanced use of the two languages). The rolandic operculum is involved in speech articulation, and plays an important role in motor control and subvocal rehearsal (e.g., Behroozmand et al., 2015; Brown et al., 2009; Vallar et al., 1997). Recently, evidence has been provided that this region is more extensively recruited during L2 speech processing in late than early bilinguals or monolinguals, suggesting that the rolandic operculum may support subvocal rehearsal of L2 sounds "which likely remain less interconnected than the sounds of the first language" (Archila-Suerte et al., 2015, p. 45). The putamen is known to be involved in the control of articulatory processes as well, in terms of motor implementation for both internal and external speech (Calabria et al., 2018). In bilinguals, its engagement has been attributed to the motor control of complex articulatory repertoires from multiple languages (e.g. Abutalebi et al., 2013a,b). Of note, in the present study an increased functional coupling between putamen and rolandic operculum was detected mainly in contexts of high Entropy.

3.3. Methodological considerations

Resting-state functional connectivity studies are characterized by a high variability of functional data due to multiple factors: Within-participants variability (e.g., Chen et al., 2015; Sämann et al., 2010; Wong et al., 2012), brain atlas selection (e.g., Arslan et al., 2018; Wu et al., 2019), and preprocessing steps choices (e.g., Murphy and Fox, 2017). These factors can potentially jeopardize the reproducibility of a study. The choice of using the AAL atlas (Tzourio-Mazoyer et al., 2002) and following the CONN's standard preprocessing pipeline, both widely used and publicly available, increases the reproducibility of this study by making our data comparable to others' findings. Future investigations may validate our results either by replicating them in different contexts or by employing reproducibility metrics (e.g. split-half or leave one out methods; Li et al., 2015a,b; Su et al., 2016).

3.4. Toward a continuous and multifaceted approach to bilingualism

Broadly speaking, and in accordance with recent trends in bilingualism research (e.g., DeLuca et al., 2019; Kousaie et al., 2017; Thomas-Sunesson et al., 2018), envisioning bilingualism as a gradient and composite phenomenon opens up new opportunities to investigate the impact of inter-individual variability in language experience on brain functioning. The operationalization of bilingualism as a continuum has two main advantages: First, it is more ecological, since it mirrors the

intrinsic nature of bi-/multilingualism (i.e., heterogeneous across individuals and dynamic throughout life). Second, it allows for a more precise modeling of the effects of bilingual experience on the brain. The dichotomization of a continuous variable (e.g., proficiency or use) is in fact well-known to potentially reduce the amount of variance that can be explained, resulting in loss of statistical power and reliability (e.g., Baayen, 2004; Cohen, 1983).

Another general observation emerging from our findings is the need to simultaneously consider the multiple experiential factors characterizing bilingualism. The results here reported suggest that all the variables considered – AoA, L2 proficiency, L1/L2 usage – play a role, but also that the impact of static variables such as AoA may be modulated by more dynamic factors such as proficiency and usage. As the Adaptive Control Hypothesis entails (Green and Abutalebi, 2013), a lifelong experience with bilingualism, which implies the continuous engagement in a cognitively stimulating activity, seems to be the main driving force which plastically shapes resting state functional connections. Note that the effect different experiential factors have on plasticity may be influenced by other sources of inter-individual variability, such as the linguistic distance between languages at the various levels of processing, or social factors such as cultural diversity and immigration status (cf. Bak, 2016). Our sample is highly homogeneous in this respect, but research on bilingualism should not neglect socio-linguistic variables that may contribute to better characterize both bilingualism and its neural consequences (cf. Surrain and Luk, 2019).

To conclude, the results of our study show that bilingual experience – defined as a continuous and multifaceted phenomenon – impacts brain plasticity by modulating the functional connectivity both within and between language and control networks. All the experience-related factors considered played a role in changing the connectivity patterns of our regions of interest, with the more dynamic factors of proficiency and usage modulating the effect of AoA. The findings here provided substantiate the emerging approach to bilingualism as a gradient measure and advocates for a mind change in bilingualism research.

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