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Interference control at the response level: Functional networks reveal higher efficiency in the bilingual brain

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ABSTRACT

The bilingual advantage in interference control tasks has been studied with the Simon task, among others. The mixed evidence from the existing studies has led to contradictions in the literature regarding the bilingual advantage. Moreover, fMRI evidence on the neural basis of interference control mechanisms with the Simon task is limited. Previous work by our team showed that equivalent performance on the Simon task was associated with different activation maps in elderly bilinguals and monolinguals. This study aims to provide a more in-depth perspective on the neural bases of performance on the Simon task in elderly bilinguals and monolinguals, by adopting a network perspective for the functional connectivity analysis. A node-by-node analysis led to the identification of the specific topology that characterized the bilingual and monolingual functional networks and the degree of connectivity between each node across groups. Results showed greater connectivity in bilinguals in the inferior temporal sulcus, which plays a role in visuospatial processing. On the other hand, in monolinguals, brain areas involved in visual, motor, executive functions and interference control were more connected to resolve the same task. In other words, in comparison to the monolingual brain, the bilingual brain resolves visuospatial interference economically, by allocating fewer and more clustered regions. These results demonstrate a larger global efficiency in task performance in bilinguals as compared to monolinguals. Also, the provided evidence filters out the task-specific so-called bilingual advantage discussed in the literature and posits that bilinguals are strategically more efficient in a given performance than monolinguals, thus enhancing our understanding of successful aging.

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1. Introduction

Both the early and late acquisition of two or more languages have been related to an enhanced ability to exercise cognitive flexibility during multi-tasking (Ansaldo, Ghazi-Saidi, & Adrover-Roig, 2015; Bak, Vega-Mendoza, & Sorace, 2015; Bialystok,

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2009; Bialystok, Craik, & Luk, 2012; Hilchey & Klein, 2011). Learning two languages also provides building blocks for cognitive reserve and increases functional efficiency at older ages. Different life experiences are crucial for building cognitive reserve, including engaging in leisure activities, education, occupational attainment skills and bilingualism (Bialystok et al., 2012; Bialystok, Abutalebi, Bak, Burke, & Kroll, 2016; Scarmeas & Stern, 2003). Bilingualism is considered to reduce interference from irrelevant stimuli in the environment. Thus, in daily life situations that present a variety of stimuli, a bilingual individual can function effectively by attending to the relevant information and ignoring the irrelevant one. In experimental situations, the successful performance on a given interference task (i.e., Simon, Stroop, go/no-go, tasks) relies upon the establishment of goal representations when beginning the experiment, and upon maintaining them throughout the task (Bialystok et al., 2005; Bialystok, Craik, Klein, & Viswanathan, 2004; Rodriguez-Fornells, De Diego Balaguer, & Münte, 2006; Zied et al., 2004).

Lifelong practice at juggling with two or more languages is likely to modulate such goal-directed behavior, resulting in a specific-to-bilinguals expertise, which might lead to a more economical interference control mechanism in this population. From a behavioral perspective, this observation relates to the concept of the “bilingual advantage” and suggests that bilinguals may have more resources than monolinguals for dealing with interference. However, inconsistencies in the behavioral literature and the lack of sufficient neurofunctional evidence to support this claim call for a more in-depth analysis of this issue. The purpose of this work was to provide a network perspective on our previous claims regarding the different underlying neurofunctional bases of interference control observed in elderly bilinguals and monolinguals (Ansaldò et al., 2015).

The bilingual advantage resulting from knowing two or more languages has been studied across the life span (Adesope, Lavin, Thompson, & Ungerleider, 2010; Bialystok et al., 2004; Costa, Hernández, & Sebastián-Gallés, 2008; Gold, Kim, Johnson, Kryscio, & Smith, 2013; Hilchey & Klein, 2011), in different cognitive-communicative disorders (Alladi et al., 2013; Bialystok, 2007; Craik, Bialystok, & Freedman, 2010), and using different cognitive tasks. The Simon task has often been used to compare interference control mechanisms in bilinguals and monolinguals (Bialystok et al., 2005), as well as within bilinguals (categorized based on age of acquisition, language use or proficiency). The Simon task is based on stimulus-response compatibility and assesses the ability to attend to task-relevant nonspatial information (i.e., the color of the stimuli) and to ignore task-irrelevant spatial information (i.e., the stimuli position on the computer screen). In our study, the colored stimuli (yellow or blue boxes) were presented on either the left or the right side of the computer screen. Each color is assigned a response key on one side of the keyboard that is analogous to the stimulus's position on the computer screen. In congruent trials, the response key for the corresponding color was on the same side as the stimulus position; in incongruent trials, the response key was on the opposite side from the stimulus position.

The Simon effect – namely the difference between response times for the congruent and incongruent conditions of the Simon task – has been shown to be smaller in bilinguals than monolinguals (Bialystok et al., 2004, 2005; Blumenfeld & Marian, 2014; Yow & Li, 2015), and this difference is even larger for older adults than for younger adults (Bialystok et al., 2004). However, some studies have reported no differences between bilinguals and monolinguals on the Simon task (Ansaldò et al., 2015; Kirk, Scott-Brown, & Kempe, 2013; Paap & Greenberg, 2013; Prior & MacWhinney, 2010). Similar results – namely either a bilingual advantage or bilingual equivalence in terms of behavioral response time cost – have also been observed with the Stroop task (Bialystok, Craik, & Luk, 2008; Duñabeitia et al., 2015) and the Flanker task (Costa, Hernández, Costa-Faidella, & Sebastián-Gallés, 2009; Costa et al., 2008). Moreover, functional neuroimaging studies on the neural correlates of the purported bilingual benefits in interference control are limited (Abutalebi et al., 2012, 2015) and sparse regarding the Simon task.

fMRI studies on the Simon task have demonstrated a lack of consensus about the brain areas involved in task performance. Activity has been reported in the anterior cingulate cortex (ACC), the middle frontal gyrus, the inferior parietal cortex, and various frontal and temporal areas (Kerns, 2006; Maclin, Gratton, & Fabiani, 2001; Peterson et al., 2002). The variability of the neural areas related to Simon task performance can be attributed to the confounding variables across populations. Nevertheless, many studies provide only limited information on participant selection, namely number and type of languages known by the participants, socioeconomic status, etc. (Forstmann, Van den Wildenberg, & Ridderinkhof, 2008; Kerns, 2006; Lee, Dolan, & Critchley, 2008; Maclin et al., 2001; Peterson et al., 2002), all of which have been shown to influence cognitive processing. For example, in an fMRI study, Peterson et al. (2002) examined the performance of young bilingual adults ($M = 26.5$ years) on the Simon task with participants from different ethnic backgrounds (Caucasian, Asian-Americans) who had English as their native language. However, no information was reported on the type and level of the second languages spoken by participants or their socioeconomic status. The fMRI data showed that performance on the Simon task significantly activated the dorsolateral prefrontal cortex (BA 46), the ACC (BA 24 and 32), the supplementary motor area (BA 6), the visual association area (BA 19), the inferior temporal area (BA 37), and parietal (BA 40) and frontal areas (BA 44). Forstmann et al. (2008) reported quite different areas of activation for the Simon task, namely the superior parietal lobe, the middle occipital gyrus, the inferior parietal lobe, the inferior precentral sulcus, the superior temporal gyrus and sulcus calcarinus. Like in the Peterson's et al. study, no information was provided on the participants' linguistic background. Unlike the mentioned previous studies, Kerns (2006) highlighted the role of the ACC, the inferior parietal cortex and the middle frontal gyrus in the Simon task by observing the effect of a conflict in the previous trial on performance in the current trial. Thus, Kerns highlighted the global effect of cognitive control by post-trial adjustments induced by the ACC, which triggers the prefrontal cortex to minimize conflict. In distinguishing between the Stroop and Simon tasks using fMRI paradigms, several authors have highlighted the role of preprogrammed and hard-wired visuospatial-motor circuitry (Liu, Banich, Jacobson, & Tanabe, 2004; Peterson et al., 2002). In particular, Liu et al. (2004) account for the specific role of posterior processing regions in the middle occipital and inferior temporal cortices in attentional control. The only study carried out on bilinguals' performance on the

Simon task found significant activation of the left medial prefrontal areas (Bialystok et al., 2005). In that study, greater activity in the superior and medial temporal gyrus, the cingulate gyrus, the superior frontal gyrus and inferior frontal gyrus was also reported, predominantly on the left hemisphere.

So far, the so-called bilingual advantage reported in the literature has faced criticisms at two main levels: (1) the lack of homogeneity in the bilingual population; (2) the presence of a condition-nonspecific bilingual advantage (i.e., global advantage) in the absence of a condition-specific bilingual advantage (i.e., task-specific advantage).

Similar to the literature on the Simon task, studies related to bilingualism have produced varying results due to discrepancies in the selection of participants and in the use of different stimulus types and task designs (Costa et al., 2008; Ghazi-Saidi & Ansaldi, 2015; Grosjean, 1998; Hilchey & Klein, 2011; Paap & Greenberg, 2013). Paap and Greenberg (2013) reviewed various studies related to bilinguals' performance on different cognitive control tasks (i.e., Simon task, Flanker task, anti-saccade task, Stroop task, etc.), and reported a lack of the so-called bilingual advantage. One of the reported studies even showed a bilingual disadvantage.

Moreover, compelling studies are available reporting an overall advantage of bilinguals over monolinguals in the absence of condition-specific (i.e., congruent vs. incongruent) differences. Behavioral studies addressing the cognitive control performance in bilinguals suggest they have a nonspecific advantage over monolinguals (Costa et al., 2008; Hilchey & Klein, 2011). In general, the processing time required for task performance is faster for bilinguals, irrespective of the conditions being explored. Similarly, and based on a whole brain analysis, Abutalebi et al. (2014) reported a bilingual advantage irrespective of differences in a specific condition. Bilingualism-related experiential neurofunctional changes were reported in the left inferior frontal gyrus, left inferior parietal lobule, ACC, caudate nucleus and putamen. This data analysis method has potential for generalization of the findings in real-life situations.

Furthermore, whole brain analysis provides an ideal window to compare different task performances, given that this approach provides with more information on a global advantage rather than advantages related to task-specific conditions, and has the potential to provide a new perspective on the issue. We believe it is worthy of note that traditional approaches that compare cognitive abilities between bilingual and monolinguals cognitive rely predominantly on task-specific differences (e.g., congruent vs. incongruent or go vs. no-go conditions).

Recent work by our team on the behavioral and neurofunctional correlates of interference control in elderly bilinguals and monolinguals (Ansaldi et al., 2015) showed that equivalent performance on the Simon task across groups was supported by different neural substrates, suggesting a bilingual advantage at the neurofunctional level. Thus, unlike elderly monolinguals, who recruited frontal areas to resolve interference in the Simon task, elderly bilinguals recruited parietal areas – namely the left inferior parietal lobule – responsible for visuospatial processing. In other words, reliance on the right middle frontal gyrus, an area particularly vulnerable to healthy and pathological aging (Grady, Luk, Craik, & Bialystok, 2015), was observed only in monolinguals. This represents a bilingual advantage at the neurofunctional level, given that bilinguals seem not to need to rely on brain areas that are more likely to be affected by aging. This might cause the bilingual brain to be better equipped to face cognitive aging.

Despite the interest of these finding, the question of the underlying basis of this supposed neurofunctional advantage remains to be further explored. Brain function is better reflected in the study of networks: temporally and spatially structured complex systems supporting cognition, whose functional interactions can be measured and compared across distinct populations. Different approaches can be used to attain this goal. For example, graph theory analysis with small-world¹ network properties (Bullmore & Sporns, 2009; Reijneveld, Ponten, Berendse, & Stam, 2007; Sporns & Honey, 2006) can shed light on the particularities of brain networks characterizing specific populations.

Hence, on the basis of our previous work (Ansaldi et al., 2015), and with the aim of moving from a segregation perspective to an integration perspective that is more representative of brain function, the purpose of this work is to provide an in-depth perspective of the neurofunctional characteristics of the bilingual brain by revealing the neurofunctional networks that characterize the behavior of bilinguals and monolinguals using the Simon task.

2. Methods

An individually processed whole-brain functional connectivity analysis was performed on fMRI data collected during the Simon task on the elderly bilingual and monolingual participants recruited for our previous work (Ansaldi et al., 2015), so as to characterize the topology of these networks.

2.1. Participants

The sample of participants was described in a previous study by our research group (Ansaldi et al., 2015), in which we examined the neural substrates underlying interference control between monolinguals and bilinguals using a classical independent group comparison. As reported in the earlier paper, the monolinguals had French as their only language ($n = 10$, 4 males) and the bilingual participants were late French-English speakers ($n = 10$; first language, L1: French, 4 males).

¹ A small-world network is a large system in which each element can be reached from every other element in relatively few intermediate steps. In other words, small-world organization is intermediate between a random network and a clustered network.

Monolinguals and bilinguals were equivalent in terms of age (monolinguals = 74.5, SD = 7.1; bilinguals = 74.2, SD = 7.4) and years of education (monolinguals = 16.1, SD = 3.28; bilinguals = 17.2, SD = 3.1; see Table 1 for sociodemographic data). All of them were right-handed, as assessed by Edinburgh Handedness Inventory – French version (Oldfield, 1971) and were eligible for an fMRI study (see eligibility form, Appendix 1).

Exclusion criteria for the sample were a history of any neurological condition, traumatic brain injury or cerebrovascular disease; use of drugs; history of intracranial surgery, encephalitis or meningitis; unstable medical or metabolic condition (e.g., uncontrolled diabetes, vitamin B12 or folic acid deficiency, hypothyroidism); evidence of psychiatric syndrome; history of alcoholism/drug addiction and/or excessive alcohol consumption; general anesthesia in the last six months; uncorrected hearing and/or vision problems; and use of cholinesterase inhibitors, antidepressants, and/or anxiolytics. In addition, a questionnaire regarding a number of socio-demographic and lifestyle variables whose contribution to cognitive reserve has been documented (Stern, 2009) was administered to all participants (see Table 1).

2.2. Language history and language of assessment

All bilinguals were born and also raised in the city of Montreal; thus, this sample did not include immigrants from other countries. They were recruited with a telephone interview during which they were given the Language Experience and Proficiency Questionnaire (LEAP-Q; Marian, Blumenfeld, & Kaushanskaya, 2007). The LEAP-Q identifies the percentage of second language (L2) use in everyday life, which in our sample amounted to at least 30%. Specifically, the LEAP-Q scores for L2 proficiency in speaking, listening, reading, and writing using a 0-to-10 scale, where 0 corresponds to no knowledge and 10 to perfect knowledge. Language proficiency in L2 was also assessed with Part C of the Bilingual Aphasia Test (BAT; Paradis & Libben, 1987). All participants included in the bilingual group considered themselves to be bilinguals, and all monolingual participants described themselves as monolinguals. Specifically, monolinguals affirmed that they neither were significantly exposed to L2 nor used it; further, they scored themselves below 4 (out of 10 points) in L2 speaking, listening, reading, and writing, thus below the cutoff of 7, which distinguishes between monolinguals and bilinguals (Marian et al., 2007). Therefore, the bilingual group outscored the monolingual group in terms of L2 proficiency, exposure, and usage (see Table 2 for information on language scores).

2.3. Neuropsychological assessment

In order to measure and to control for possible variables that might modulate the cognitive control abilities examined in the present work, all participants underwent a comprehensive neuropsychological assessment. All neuropsychological tests were administered in the participants' L1 (French). They included the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005); the Geriatric Depression Scale (GDS scale; Yesavage et al., 1983); verbal fluency (Controlled Oral Word Association Test, COWAT–FAS; Benton & Hamsher, 1976); the Boston Naming Test (Kaplan, Goodglass, & Weintraub, 2001); tests of executive control (Trail Making Test; Reitan, 1954); Brixton Test (Burgess & Shallice, 1997); Stroop Test (Jensen & Rohwer, 1966); Digit Span (Wechsler, 1999); a self-report 12-item questionnaire of cognitive flexibility (Cognitive Flexibility Scale, CFS; Martin & Rubin, 1995); and a measure of processing speed (Digit Symbol, WAIS-III; Wechsler, 1999). No significant differences between the two groups were observed in their formal test results (Table 3) or in their responses to the questionnaires.

2.4. fMRI task

Participants underwent a familiarization session in the simulator room. They were then tested with the Simon task during an event-related fMRI session at the Unité de Neuroimagerie Fonctionnelle. Event-related fMRI blood-oxygen level-dependent (BOLD) responses were collected with a 3T Siemens scan; accuracy rates (ARs) and response times (RTs) were recorded for the control, congruent and incongruent conditions of the Simon task. In the Simon task (Simon & Rudell, 1967), yellow or blue squares are presented on the left or right side of the screen, and participants are instructed to press one response key (left

Table 1
Sociodemographic characteristics of the sample of elderly participants.

	Monolingual	Bilingual	Min–Max	t (p)
Age	74.5 (7.1)	74.2 (5.2)	63–84	0.10 (n.s.)
Education	16.1 (3.2)	17.2 (3.9)	10–25	0.67 (n.s.)
MoCA	27.7 (1.2)	27.5 (1.6)	26–30	0.30 (n.s.)
GDS	1.5 (1.1)	1.2 (1.2)	0–4	0.55 (n.s.)
Days per week of exercise	3.7 (2.8)	3.3 (1.8)	0–7	0.34 (n.s.)
Hours per day of exercise	0.76 (0.5)	0.83 (0.3)	0–2	0.34 (n.s.)
Hours per day TV	2 (1.4)	1.8 (0.9)	.3–3.5	0.37 (n.s.)
Time awake (hours)	15.3 (1)	16.4 (1.2)	14–18	1.9 (0.07)

MoCA: Montréal Cognitive Assessment; GDS: Geriatric Depression Scale; *p < 0.05; **p < 0.01; ***p < 0.001.

Table 2

Language scores and contrasts between monolinguals and bilinguals.

	Monolingual	Bilingual	Min–Max	t (p)
Degree of bilingualism	21.4 (2.3)	40.5 (1.4)	18–42	22.1 (0.000)***
Age of acquisition	–	16.7 (8.5)	8–30	–
Speak L2	3.7 (2.05)	8.6 (1.6)	1–10	5.9 (0.000)***
Understand L2	4.5 (2)	9 (1.5)	2–10	5.5 (0.000)***
Write L2	3.9 (2.6)	8.4 (2.2)	1–10	4.2 (0.001)***
% speak L2 at home	0 (0)	30 (33)	0–100	2.9 (0.001)***
% speak L2 with friends	0.5 (1.1)	36.5 (36.8)	0–100	3.1 (0.006)***
% speak L2 at work	0.5 (0)	40 (41.1)	0–100	3 (0.007)***
Synonyms and antonyms L1	22.5 (0.03)	22.8 (0.88)	21–24	0.91 (0.38)
Synonyms and antonyms L2	13.1 (3.7)	19 (2.2)	4–20	4.2 (0.001)***
Lexical fluency L1	42 (10.7)	47.9 (19.4)	19–77	0.85 (n.s.)
Lexical fluency L2	21 (8.7)	39.4 (17.6)	6–75	2.96 (0.008)**
Categorial fluency L1	43.7 (7.9)	48.6 (10.8)	26–67	1.15 (n.s.)
Categorial fluency L2	17.7 (3)	39 (6.9)	13–50	8.9 (0.000)***
Boston naming test L1	13.1 (1.5)	13.2 (1.4)	11–15	0.15 (n.s.)
Boston naming test L2	7 (1.1)	12.6 (1.8)	5–15	6.9 (0.000)***

Speak L2: self-assessment of oral competence in L2; Write L2: self-assessment of written competence in L2; Understand L2: self-assessment of comprehension in L2; % speak L2 at home: percentage of time spent at home speaking in L2; % speak L2 with friends: percentage of time spent speaking in L2 with friends; % speak L2 at work: percentage of time spent speaking in L2 at work; *p < 0.05; **p < 0.01; ***p < 0.001.

side) if a yellow square appears and another response key (right side) if a blue square is shown, irrespective of the position of the squares. Congruent trials (N = 30) are those in which the correct response key is on the same side as the stimulus; incongruent trials (N = 30) are those in which the reverse is true; and control trials have the same stimuli presented in the center of the screen. The mapping of stimulus-color to response key was counterbalanced across participants within each group. The response keys were placed comfortably, one under each hand, and participants placed their index fingers on the two keys, and were instructed to respond as quickly as possible without making errors. The event-related fMRI design included a total of 90 trials, all of them beginning with a fixation cross as a warning cue shown in the center of the screen for 150 ms, followed by a 500- to 600-ms interval (jittered). The stimulus (40 mm square) then appeared for 400 ms on the left or right side for experimental trials or in the center for control trials. A response was allowed for a maximum of 2000 ms post stimulus onset. After a jittered 1000- to 1400-ms blank interval, the warning cue for the next trial appeared. Consequently, the trial time ranged from 4050 to 4550 ms (including the response interval). The stimuli were projected onto a dark screen in the left or right visual field at 11.68° offset from a central fixation point. All cues and stimuli were reflected by mirrors inside the magnetically shielded room from a projection system outside the room. The trials were presented in a semirandom order. The total estimated time for this task was about 39 min. This study was approved by the ethics committee of the Réseau de Neuroimagerie au Québec.

2.5. Image acquisition and statistical analysis

High-resolution T1-weighted 3D anatomical images were acquired using a standard head coil and tilted coronal gradient echo sequence (time to repetition, TR = 3 s; echo time, TE = 4 ms; inversion time, TI = 250 ms; flip angle = 12°; field of view, FOV = 256° x 260; matrix size = 230° x 25; slice thickness = 1.1–1.5 mm). T2-weighted functional images were acquired using an echo planar imaging (EPI) pulse sequence, in an axial plane aligned with the AP-CP (circularly polarized) axis (TE = 44 ms; flip angle = 90°; FOV = 215 mm; matrix = 64° x 64).

2.6. Image preprocessing

MRI data were preprocessed using the statistical parametric mapping software (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8>). The fMRI volumes were corrected for slice timing and head motion then spatially smoothed with an isotropic Gaussian kernel (full-width at half-maximum 8 mm). For each participant, spatial registration was carried out using a rigid transformation of the fMRI data to the anatomical volume. This co-registration transferred the fMRI volumes into the native space of each patient.

2.7. Functional connectivity network analysis

A set of regions of interest (ROIs or nodes) was defined using FreeSurfer (Desikan et al., 2006). This software package provides a set of structural and functional MRI analysis tools and a fully automatic structural imaging stream for labeling brain regions. Thus, the cortical surface and the main subcortical brain structures were labeled on their T1-weighted anatomical image, providing a segmentation that retains the personal anatomy (Magalhães, Marques, Soares, Alves, & Sousa, 2015). Finally, the labeled volumes were re-sliced and resampled into the functional volume resolution in order to extract the EPI signal. Each functional network was set up with 160 selected ROIs, 80 for each hemisphere (See Table VI, Appendix 2.).

Table 3
Scores on neuropsychological tests and contrasts between monolinguals and bilinguals.

Bilinguals	Monolinguals	Bilinguals	Min–Max	t (p)
Paired associates total	12.4 (8.3)	15.9 (6.8)	1–26	1 (n.s.)
Paired associates (d–a)	4.1 (2.4)	4.3 (1.9)	0–7	0.2 (n.s.)
Logical memory A	14.4 (3.7)	14.1 (4.4)	8–20	0.16 (n.s.)
Logical memory A (themes)	5.6 (1.4)	5.8 (1.3)	3–7	0.32 (n.s.)
Logical memory B1	10.9 (3.4)	11.9 (3.1)	5–16	0.68 (n.s.)
Logical memory B1 (themes)	5.3 (1.4)	5.6 (1.5)	2–8	0.44 (n.s.)
Logical memory B2	12.9 (3.3)	16.3 (4.4)	7–23	1.94 (0.07)
Logical memory B2 (themes)	5.7 (1)	5.8 (1.9)	2–8	0.14 (n.s.)
Digits forward (WMS-III)	9.40 (1.17)	10.10 (1.96)	7–13	0.35 (ns)
Digits backward (WMS-III)	6.40 (1.95)	6.60 (2.37)	4–11	0.92 (n.s.)
Brixton test errors	19.5 (7.6)	19.6 (7.1)	12–33	0.3 (n.s.)
Trail Making Test-A	42.4 (16.25)	32.6 (7.53)	23–83	1.44 (0.10)
Trail Making Test-B	94.51 (39.72)	89.31 (32.44)	38–160	0.32 (n.s.)
Trail Making Test-B/A	2.25 (0.72)	2.84 (1.04)	1.13–4.43	1.46 (0.16)
Stroop interference (CW–CW')	1.27 (7.70)	–5.73 (9.17)	7.8–65.3	0.08 (n.s.)
Digit Symbol	58.6 (16.6)	59.1 (7.2)	31–83	0.1 (n.s.)
Finger tapping right hand	63.8 (7.8)	62.1 (3.6)	51–75	0.57 (n.s.)
Finger tapping left hand	59 (3.9)	56.3 (6.1)	45–67	1.13 (n.s.)
CFS	54.2 (6.8)	58.7 (7.2)	43–72	1.4 (n.s.)

Paired associates (d–a): score on the paired associates test (last attempt minus first attempt); Logical memory A: score on the logical memory test (WMS-III), first text read; Logical memory B: score on the logical memory test (WMS-III), second text read for the first time; Logical memory B2: score on themes on the logical memory test (WMS-III), second text read for the second time; CFS: Cognitive Flexibility Scale; *p < 0.05; **p < 0.01; ***p < 0.001.

The time series of all voxels within an ROI were spatially averaged to determine the representative intrinsic BOLD signal of that ROI. A time course corresponding to approximately 10.5 min of acquisitions was obtained for each ROI. To remove spurious sources of variance, linear and quadratic drifts, and motion parameters, averaged ventricular, white matter and global brain signals were regressed out (Fox, Zhang, Snyder, & Raichle, 2009; Van Dijk, Hedden, Venkataraman, Evans, Lazar, & Buckner, 2010).

The ROIs or nodes may be connected by a set of edges. Therefore, Pairwise inter-regional Pearson correlations were estimated between the BOLD time signals of each ROI, resulting in an individual correlation matrix (cM) with the *corr* function of the statistical toolbox of Matlab (MATLAB 8.0 and Statistics Toolbox 8.1, The MathWorks, Inc., Natick, MA). The hypothesis that a given correlation coefficient was null was tested to remove nonsignificant edges, and emphasize the network topology. This function also returns a matrix of p-values (pM) to test the hypothesis of no correlation against the alternative that there is a nonzero correlation between two nodes. Each element of pM is the p value for the corresponding element of the correlation matrix cM. If an element of pM is small, (less than 0.05) then the corresponding element of cM is significantly different from zero (Rubinov & Sporns, 2010). Thereafter the edges or nodes may be only compared to the same edges or nodes between the 2 independent groups with a *t*-test.

2.8. Graph theory

Graphs are mathematical structures used to model pairwise relations between objects. A graph is made up of nodes and edges that connect them. Functional brain connectivity networks can be modeled in graphs and examined with graph theory (Bullmore & Sporns, 2009). In a given graph, nodes correspond to the previously defined ROIs, and the edges are defined based on the value of the correlation matrix. If the correlation between two ROIs is different from zero, an edge is defined between these two nodes. Otherwise, there is no edge between them. Given that a Pearson correlation is a symmetric function (i.e., $corr(a,b) = corr(b,a)$), the edges can also be considered as undirected. In summary, the functional brain connectivity network is modeled by an undirected weighted graph of 160 regions, where the weight values are indicated in the correlation matrix. Fig. 1 represents the possible connectivity network for the Simon task in both groups, in axial, coronal and sagittal views.

2.9. Network analysis

Graph theory offers a set of metrics that analyzes the fine-scale functional properties of a network. Individual graph theory metrics were computed using MATLAB (R2011a, The MathWorks Inc., Natick, MA) software, in-house scripts and the Brain Connectivity Toolbox (<http://www.brainconnectivity-toolbox.net>).

In our study, participants were age-matched and showed equivalent behavioral performance. Therefore, we first checked whether the graph had the same properties to ensure that the model was stable across participants, and whether it reflected their behavioral equivalent performance. Furthermore, and in line with previous work (Rubinov & Sporns, 2010), we compared the properties of density and integration across groups, to see whether the metric calculated on the nodes was comparable across the two groups. Specifically, density is reflected by the ratio between the number of edges within a graph

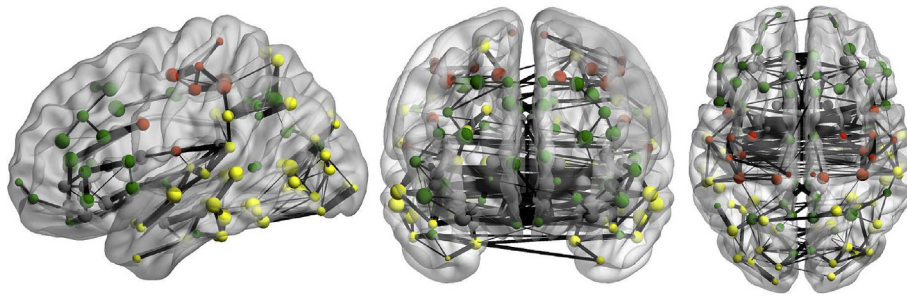


Fig. 1. Average functional network across all participants, in both groups, in the sagittal, coronal and axial planes (only for $r > 0.5$). Nodes are color-coded, based on the network function: yellow for the visual processing network; red for the motor processing network; green for the executive function network, and the rest of the regions are colored in grey. Edges (in black) represent the connectivity network for the Simon task in both groups. Edges between homologous brain regions across hemispheres were removed for a better visualization of the network. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and the theoretical maximum number of edges. Integration represents the amount of information flow; this concept comes from information theory and is a measure of the mutual dependence between two variables (Marrelec et al., 2008). Densities and integration were not statistically different between the two groups of subjects; thus, the two graphs were comparable for a deeper analysis at the ROI or node level.

To determine the specific topology that characterized the functional network of bilingual in contrast to the monolingual participants, functional connectivity was explored with the degree of connectivity (k). The degree of connectivity (k) is defined as the number of edges connecting the node within the graph. Following this, Student's t -tests were performed between both groups for the k value of each node. If the k value of a certain node is significantly higher in one group compared to the other, it is defined as a 'spotted node'. Moreover, in order to further explore the source of this higher degree of connectivity, statistical analyses were performed specifically on the edges that were linked to the 'spotted nodes' (see section 3.2 and Table 5).

3. Results

3.1. Behavioral results

A 2 (group: monolinguals, bilinguals) \times 3 (trial type: control, congruent, incongruent) ANOVA was performed on both RTs and ARs for the Simon task. Overall, there were main effects of condition in the sense of slower RTs and lower ARs for the incongruent condition than for the control and congruent conditions. However, bilinguals and monolinguals did not differ in any of the measured conditions and costs derived from the Simon task.

Specifically, there was a main effect of trial type for both RT ($F(1, 20) = 33.9, p < 0.0001$), and AR ($F(1, 20) = 15.15, p < 0.0001$). Post hoc contrasts revealed both slower RTs ($p < 0.0001$) and lower ARs ($p < 0.001$) for the incongruent condition than for the control and congruent conditions. As well, the congruent condition was characterized by faster RTs ($p = 0.013$) and greater ARs ($p = 0.026$) than the neutral condition. No main effects of group (RT ($p = 0.42$); AR ($p = 0.30$)) were observed. Similarly, the interaction between group and trial type did not reveal significant results in terms of RTs ($p = 0.64$) and ARs ($p = 0.96$). Speed-accuracy trade-offs, as measured by the inverse efficiency score (RT/AR, calculated for each subject and condition), did not reveal statistically significant differences between the two groups for any type of trial (all p s > 0.25).

In addition, two different costs were calculated for the Simon task; the first refers to the difference between the incongruent and congruent trials for both RT and AR and will be labeled as the "Simon effect." The second refers to the difference between the incongruent and control condition for both RT and AR and will be labeled as the "Simon cost." Both the Simon effect and the Simon cost were equivalent between monolinguals and bilinguals in terms of RT and AR in all blocks (all p s > 0.60).

3.1.1. Correlational analysis

A series of correlations between socio-demographic, executive (including the Simon task indexes), linguistic, and neuropsychological variables were performed (see Table 4). After correcting for multiple comparisons, a significant positive correlation was found between the years of formal education, phonological fluency in L2, and measures of logical memory. Also, there was a positive and significant correlation between the degree of bilingualism and naming, and between the degree of bilingualism and the production synonyms-antonyms in L2.

3.2. Neuroimaging results

Monolingual and bilingual speakers showed significantly different brain networks involved in the task with regards to the degree of connectivity (k) of each node across the two groups. Further, additional analyses confirmed different network structures (i.e., different correlation values among nodes) for the bilingual and monolingual groups.

Table 4

Correlation matrix between sociodemographic, linguistic and neuropsychological scores in several domains, and scores on the Simon task.

	Age	Educ.	MoCA	Bilingualism
<i>Executive functioning</i>				
Simon effect (RT)	0.28	−0.04	−0.41 (0.07)	0.02
Simon effect (AR)	−0.13	0.11	−0.17	−0.04
Simon cost (RT)	0.58	0.03	−0.38	−0.17
Simon cost (AR)	−0.15	−0.13	0.24	−0.03
Stroop interference (CW−CW')	−0.18	−0.13	0.22	−0.48
Trail Making Test B	0.47	−0.48	−0.40 (0.08)	−0.15
Trail Making Test (B/A)	0.30	−0.38	0.07	0.33
Brixton errors	0.51	−0.30	−0.49	−0.06
<i>Language</i>				
Boston naming (French)	−0.50	0.30		−0.018
Boston naming (English)	0.09	0.21		0.84 ^a
Phonological fluency (French)	−0.24	0.56	0.19	0.20
Phonological fluency (English)	0.04	0.68 ^a		0.59
Semantic fluency (French)	−0.45	0.51	0.42	0.24
Semantic fluency (English)	−0.03	0.31		0.89 ^a
Synonyms-antonyms (French)	0.07	−0.05	0.20	0.24
Synonyms-antonyms (English)	−0.40	−0.40	0.03	0.72 ^a
<i>Memory</i>				
Logical memory score (WMS-III)	−0.30	0.68 ^b	0.47	0.13
Digits forward (WMS-III)	0.07	0.17	0.09	0.22
Digits backward (WMS-III)	−0.40	0.10	0.04	0.07
Logical memory – themes (WMS-III)	0.09	0.47	0.30	0.11
Paired associates (d−a) (WMS-III)	−0.33	0.55 ^b	0.17	0.14
<i>Processing speed</i>				
Trail Making Test A	0.23	−0.14	−0.50	−0.38
Digit Symbol	−0.47	0.29	0.60	−0.08
Simon_control (RT)	0.20	0.10	−0.10	−0.12

MoCA: Montréal Cognitive Assessment; Bilingualism score is a compound measure of language tasks – see [Method](#) section for a more detailed description; Simon effect: difference between the incongruent and congruent conditions; Simon cost: difference between the incongruent and control conditions; Simon_control: response times to the control condition in the Simon task; RT: response time; AR: accuracy rate.

^a $p < .0062$ (after correction for multiple comparisons in executive control and language measures).

^b $p < .0010$ (after correction for multiple comparisons in memory measures).

Differences in degree of connectivity values between graphs of the bilingual and monolingual groups are represented in [Fig. 2](#). Results showed a series of “spotted nodes,” namely brain areas whose degree of connectivity was significantly higher in one group than the other. Specifically, in bilinguals, a single brain area showed a higher connectivity value than in monolinguals, namely the left inferior temporal sulcus (k_B : 115; k_M : 104). In monolinguals, several brain areas showed higher connectivity values than in bilinguals, namely: the left superior frontal gyrus (k_M : 106.6, k_B : 92.5), the left lateral orbital sulcus (k_M : 110.3, k_B : 95), the right inferior opercular frontal gyrus (k_M : 109, k_B : 95), the right medial lingual occipito-temporal gyrus (k_M : 114, k_B : 98) and the right parieto-occipital sulcus (k_M : 105, k_B : 90). These five brain areas were more connected to other brain areas in monolinguals than in bilinguals (i.e., they showed higher k values).

To further investigate the differences driving connectivity across the 2 groups, the correlation values of edges for each spotted node were across the two groups using a t -test. These analyses showed the differences between the correlation values of the spotted nodes and the other brain areas (i.e., connected nodes) for each group of participants. Results reflected differences in network structure across groups. [Table 5](#) shows differences in spotted nodes and their corresponding connected nodes between monolinguals and bilinguals; these are listed from the highest to the lowest mean correlation value.

In order to determine whether the spotted nodes could be considered as hubs, all ROIs were ranked according to their respective mean connectivity (k), [Table VI \(Appendix 2\)](#) shows the areas included in the ROI rank, according to their respective mean connectivity value (k) in monolinguals and in bilinguals. The spotted nodes are highlighted.

3.3. Correlational analysis

A set of correlational analysis between functional connectivity values of the left inferior temporal sulcus (i.e. identified hub) and the neuropsychological measures collected from all participants was performed. In monolinguals, there was significant correlation between the left inferior temporal sulcus K value, and both the Trail Making test-A (TMT-A) and the Trail Making Test-B (TMT-B). These tests measure visuo-motor speed of processing (TMT-A) and alternating attention (TMT-B), respectively ([Salthouse, 2011](#); [Sánchez-Cubillo et al., 2009](#)). In bilinguals, there was a significant correlation between the left inferior temporal sulcus K value, and both digit span-forward and digit-span backward measures. Digit span measures short-term memory, and working memory processing ([Woods et al., 2011](#)). These results are in line with the connectivity patterns observed in this study, as well as the activation maps observed in our previous study ([Ansaldò et al., 2015](#)). More specifically, this pattern of correlations reflects that bilinguals keep in mind the instruction and respond to the task, whereas monolinguals are resorting attention shift abilities.

Table 5

Significant correlation value between each spotted node and other brain regions (nodes). Spotted nodes are brain areas whose degree of connectivity (k) was significantly higher in one group than in the other. Nodes are arranged by value of correlation from high to low.

Spotted nodes in the Bilingual group and degree of connectivity	Correlation value		Nodes	p value
	Mono < bilingual			
Left inferior temporal sulcus	0.4965	0.6137	R. S_temporal_inf	p = 0.0355
$k_B = 115.5$	-0.1202	0.2759	R. G_temp_sup-G_T_transv	p = 0.0028
$k_M = 104.4$	-0.1225	0.2601	R. S_temporal_transverse	p = 0.0389
p = 0.0397	-0.0754	0.1954	L. insular gyrus	p = 0.0214
Spotted Nodes in the Monolingual group and Degree of connectivity	Correlation Value		Nodes	p value
	Mono > Bilingual			
Left superior frontal gyrus	0.5849	0.2829	R. precentral gyrus	p = 0.0013
$k_M = 106.6$	0.5584	0.3293	L. precentral gyrus	p = 0.0234
$k_B = 92.5$	0.4818	0.3556	L. paracentral gyrus and sulcus	p = 0.0376
p = 0.0483	0.4480	0.249	L. postcentral gyrus	p = 0.0147
	0.3710	0.2269	R. front middle Sulcus	p = 0.029
	0.3556	0.1065	L. cingulate Mid-Ant gyru and sulcus	p = 0.0178
	0.2307	0.3913	L. transv frontopol gyrus and sulcus	p = 0.0224
Left lateral orbital sulcus	0.5429	0.3222	L. lateral Fissure -ant-Vertical	p = 0.0012
$k_M = 110.3$	0.4826	0.2418	R. lateral anterior horizontal Fissure	p = 0.0164
$k_B = 95$	0.4512	0.3138	R. front inf-Triangul gyrus	p = 0.0199
p = 0.0414	0.4219	0.2468	R. Lateral Fanterior vertical fissure	p = 0.0014
	0.3068	0.0528	R. Accumbens-area	p = 0.0368
	0.2266	-0.0939	R. circular_insula_sup	p = 0.0457
	0.1757	-0.2191	R. subcentral gyrus and sulcus	p = 0.038
Right inferior opercular frontal gyrus	0.6499	0.54736	L. front inf-Opercular gyrus	p = 0.0437
$k_M = 109.8$	0.231	-0.0544	R. orbital-Shaped sulcus	p = 0.0379
$k_B = 98.4$	0.1614	-0.1532	L. transv frontopol gyrus and sulcus	p = 0.0491
p = 0.0483				
Right medial lingual occipito-temporal gyrus	0.6618	0.4914	R. oc-temp med and Lingual sulcus	p = 0.0229
$k_M = 114.8$	0.5698	0.4117	L. oc-temp lat-fusifor gyrus	p = 0.0486
$k_B = 98.3$	0.5418	0.3687	R. Pole occipital	p = 0.0293
p = 0.0364	0.4950	0.2603	R. temporal sup sulcus	p = 0.0212
	0.4742	0.2714	R. parieto occipital sulcus	p = 0.0292
	0.4454	0.1997	L.-Hippocampus	p = 0.0304
	0.3825	0.1844	R. temporal middle gyrus	p = 0.0276
	0.2876	0.0487	L. oc-temp med-Parahip gyrus	p = 0.0427
	0.2193	-0.0133	R. Pole temporal	p = 0.0443
Right parieto-occipital sulcus	0.5796	0.3539	L. calcarine sulcus	p = 0.0145
$k_M = 105.3$	0.4742	0.2714	R. oc-temp med-Lingual gyrus	p = 0.0292
$k_B = 90.36$	0.3457	0.0985	R. oc-temp med & Lingual sulcus	p = 0.0135
p = 0.0382				

4. Discussion

The aim of the present study was to provide an in-depth perspective on the underlying mechanisms and neural correlates supporting performance on the Simon task in elderly bilinguals and monolinguals by adopting a network approach. The literature on the neurofunctional basis of the Simon task is inconclusive; thus, although several studies have reported on the areas activated during the task, none of them has controlled for factors such as degree of bilingualism, socioeconomic status, education, leisure activities, age, and age of L2 acquisition.

Following our previous work with two highly controlled samples, we wanted to explore global network properties for the bilingual and monolingual groups, in the presence of similar behavioral performance. To attain this aim, a whole brain scale network analysis in terms of ROIs was performed, and network configuration, composition and connectivity value (k), across the two target samples were examined. This type of analysis allowed us, for the first time, to reveal the specific functional connectivity patterns in elderly monolingual and bilingual speakers performing the Simon task.

The respective networks for the monolingual and the bilingual groups showed identical properties at the global network level; however, network differences were observed across groups, at the node level in reference to these ROIs. Specifically, the monolingual brain network included a larger set of connected areas than the bilingual group network. This is in line with previous fMRI evidence showing that monolinguals recruit a larger number of areas than bilingual speakers on a set of cognitive tasks (Abutalebi et al., 2014; Grady et al., 2015). In this regard, Abutalebi et al. (2014) made two key observations in their neurofunctional study: a lesser decrease in grey matter volume in the anterior temporal lobe in bilingual speakers, and a more extended pattern of brain activity in monolingual participants (as measured by the number of activated voxels).

Similarly, in a MEG study with the Simon task Bialystok et al. (2005) compared a monolingual group (English) with two groups of bilinguals (French-English and Chinese-English). Two completely different activation patterns were observed in the

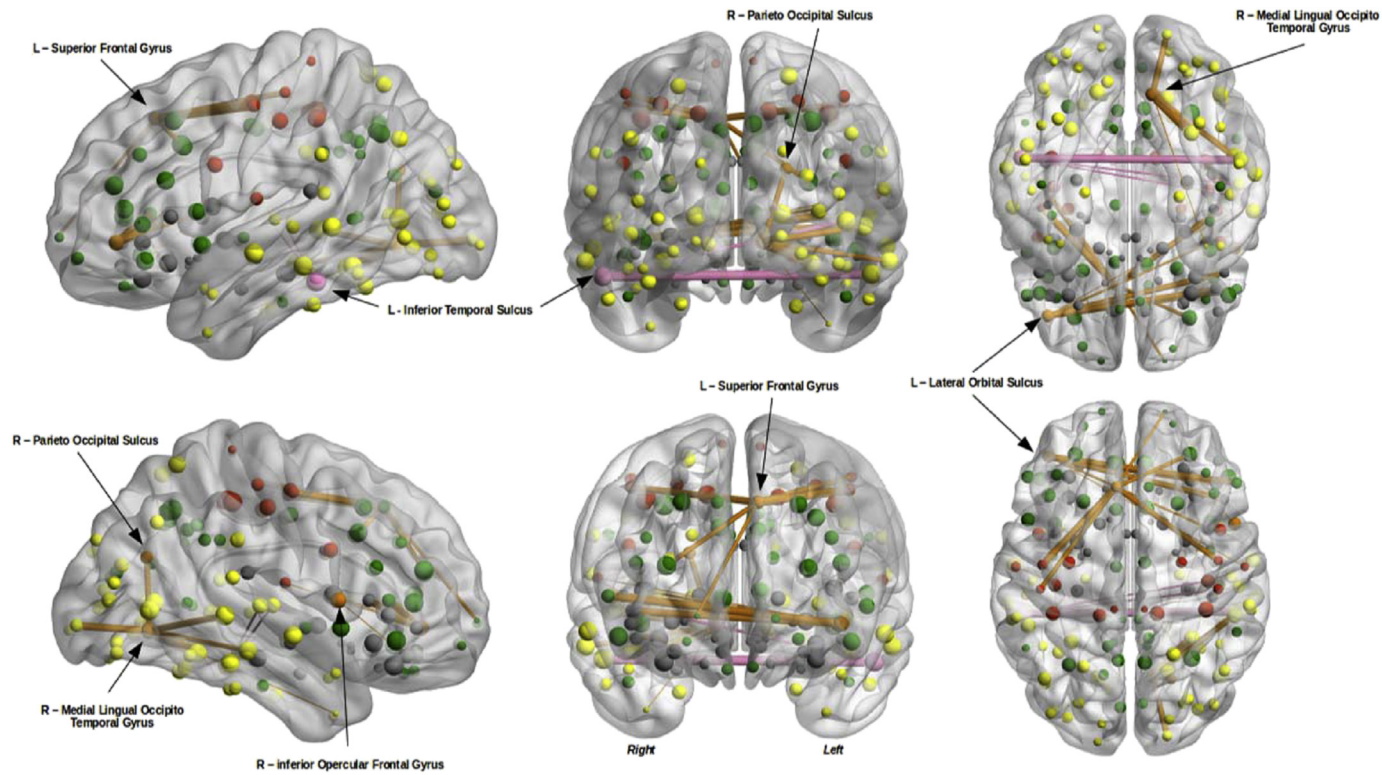


Fig. 2. Spotted nodes and the edges in the monolingual and bilingual groups, presented in the sagittal, coronal and axial planes (2 views per plane). Spotted nodes and edges in monolinguals are color-coded in orange. Orange edges correspond to correlation values (or the connectivity degree for nodes) that are higher in the monolingual group. Spotted nodes and edges in the bilingual group are color-coded in pink. Pink edges correspond to correlation values (or the connectivity degree for nodes) that are higher in the bilingual group. The strength of the correlation is represented by the thickness of the edge: the thicker the edge, the stronger the correlation. Nodes are color-coded based on the network function: yellow for the visual processing network; red for the motor processing network; green for the executive function network; the rest of the regions colored grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

monolingual (middle frontal regions) and the two bilingual groups (left superior and middle temporal, left cingulate, and left superior and inferior frontal regions) (Bialystok et al., 2005).

Differences in connectivity in the Default Mode Network (DMN) pattern have been reported across bilingual and monolingual speakers (Grady et al., 2015). Specifically, Grady et al. (2015) reported that bilinguals showed better correlations and functional connectivity values in the executive control network, and in the modulation between task and rest periods. As well, the authors (Grady et al., 2015) reported stronger connections in the DMN (right and left angular gyrus, right and left superior frontal gyrus, ventromedial prefrontal, and right and left middle temporal gyrus), and in the fronto-parietal control network (right and left intraparietal sulcus, precuneus, right anterior cingulate gyrus, right precentral gyrus, right and left middle frontal gyrus and left insula) for bilingual participants than for monolinguals.

The results of the present study show that only one region displayed higher degree of connectivity in the bilingual group, and this is the LITS, whereas in monolinguals, five regions presented higher connectivity, namely the Left superior frontal gyrus, the Left lateral orbital sulcus, the Right inferior opercular frontal gyrus, and the Right medial lingual occipital temporal gyrus, Right parietal occipital sulcus. Further, the ITS showed a high degree of connectivity in both groups, but ITS connectivity was significantly higher in bilinguals than in monolinguals, which makes the ITS a distinctive hub of the bilingual group (see Table 5).

Previous evidence shows that the superior temporal sulcus plays a role in shape, location and color processing (Baizer, Ungerleider, & Desimone, 1991; Beauchamp, Lee, Argall, & Martin, 2004). Further, significant activation in the superior and the inferior temporal cortices has been reported in relation to performance on the Simon task (Forstmann et al., 2008; Peterson et al., 2002). Moreover, activity in these areas has not specifically been attributed to attentional control (Liu et al., 2004; Peterson et al., 2002). Furthermore, the significant activation of the inferior temporal cortex (a component of the ventral stream) has been related to the detection of objects as opposed to locations (Mishkin, Ungerleider, & Macko, 1983). Evidence from rhesus monkey studies (Li, Miller, & Desimone, 1993), shows that a subpopulation of the inferior temporal cortex plays a role in short- and long-term memory for visual patterns, based on stimulus familiarity, with increased inferior temporal activation being associated with the occurrence of any new event. Hence, Li et al. (1993) argue that the inferior temporal cells act as an “adaptive mnemonic filter” or communication channel between attention and memory, to ensure economical functioning. Such results suggest that the temporal cortices play a role in interference control that is tuned by experience. This is particularly relevant to this study, as the ITS represents a distinctive hub in a population of lifelong bilinguals.

A comparison of the global structure of the networks reported in the present study, with the set of ROIs described in earlier literature on the Simon task, shows converging evidence, in regards to the type of areas involved, namely motor, visual and executive processing areas. However, the variety and number of cognitive control processing areas mentioned in the previous literature is quite large compared to our findings. More specifically, according to previous work, the significantly activated areas can be grossly grouped into three clusters: (1) brain areas supporting interference suppression (ACC, inferior frontal, dorsolateral prefrontal cortex); (2) brain areas supporting motor performance (supplementary motor areas); and (3) brain areas supporting visuospatial processing (superior parietal and visual association areas) (Bialystok et al., 2005; Forstmann et al., 2008; Kerns, 2006; Lee et al., 2008; Maclin et al., 2001; Peterson et al., 2002). It is to be noted that, apart from the MEG study by Bialystok et al. (2005), the studies reporting these activations did not control for bilingualism. Considering the sociolinguistic characteristics of many of the research sites where these studies were carried out (Forstmann et al., 2008; Lee et al., 2008), and based on the information that can be inferred from sample descriptions in those studies (Kerns, 2006; Maclin et al., 2001; Peterson et al., 2002), it is likely that the samples examined in those studies were highly heterogeneous, in terms of number of languages spoken and levels of L2 proficiency, use and exposure. This would introduce a bias in the fMRI results, thus lowering the validity on the neural basis of interference control on the Simon task.

Conversely, the sample assessed in the present study is quite exceptional in terms of experimental control for language-related factors, as the two groups are equivalent in respect of several factors that are known to modulate cognitive control abilities (i.e., education level, socioeconomic status, leisure activities, etc.), while being clearly distinct in their L2 knowledge. We argue that, given the well-known impact of bilingualism on cognitive control, and considering that bilingualism status might not have been strictly controlled in previous work on the neural basis of the Simon task, the earlier results should be considered with caution, as the reported results may reflect the neurofunctional profile of the specific sample examined in either paper.

Overall, the evidence of the present study suggests that bilinguals rely on a highly connected network devoted to visuospatial processing. These findings support the notion that the bilingual brain is able to deal with interference by allocating fewer and more task-specific resources, as reflected by the support of a smaller, more integrated visuospatial hub. In contrast, monolinguals, whose performance is sustained by a larger, and multifunctional network which includes a wide set of processing nodes dedicated to executive processing.

The results of the present work suggest that lifelong juggling with two languages in competition impacts the brain at a network level, and they provide information about the role of experience as a source of cognitive efficiency (Peterson, van Mier, Fiez, & Raichle, 1998). The evidence suggests that interference control tasks consume more neurofunctional resources in monolinguals, and that this is so even in the context of a nonverbal interference control task.

Previous work has suggested that the bilingual and the monolingual brain may show distinct ways of approaching cognitive complexity (Kroll & Chiarello, 2015); the present data provide evidence supporting this hypothesis at the level of network configuration. This neurofunctional evidence has implications for the role of bilingualism as a neurofunctional brain-

shaping factor, and its potential impacts morbidity compression, in the context of cognitive decline, with potential implications on Health policies both in healthy elderly and clinical populations (Ghazi-Saidi & Ansaldo, 2015). Future studies with larger population samples will provide further understanding of the impact of bilingualism on brain connectivity.

To conclude, this work argues for the value of a whole brain functional connectivity approach in the study of the neural bases and underlying processes supporting cognitive operations in bilinguals and monolinguals. This approach filters out the task-specific so-called bilingual advantage discussed in the literature, and shows that bilinguals tend to be strategically more efficient at performing a given task than monolinguals even in the presence of an equivalent performance. This furthers our understanding of how to foster successful aging.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jneuroling.2016.09.007>.

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