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Brain Network Activity in Monolingual and Bilingual Older Adults

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Abstract

Bilingual older adults typically have better performance on tasks of executive control (EC) than do their monolingual peers, but differences in brain activity due to language experience are not well understood. Based on studies showing a relation between the dynamic range of brain network activity and performance on EC tasks, we hypothesized that life-long bilingual older adults would show increased functional connectivity relative to monolinguals in networks related to EC. We assessed intrinsic functional connectivity and modulation of activity in task vs. fixation periods in two brain networks that are active when EC is engaged, the frontoparietal control network (FPC) and the salience network (SLN). We also examined the default mode network (DMN), which influences behavior through reduced activity during tasks. We found stronger intrinsic functional connectivity in the FPC and DMN in bilinguals than in monolinguals. Although there were no group differences in the modulation of activity across tasks and fixation, bilinguals showed stronger correlations than monolinguals between intrinsic connectivity in the FPC and task-related increases of activity in prefrontal and parietal regions. This bilingual difference in network connectivity suggests that language experience begun in childhood and continued throughout adulthood influences brain networks in ways that may provide benefits in later life.

Keywords

Aging; Cognitive Control; Functional Connectivity; Frontoparietal Control Network; Default Mode Network; Language

1. Introduction

The concept of executive control (EC) comprises the ability to control attention, to inhibit distraction and to shift between goals (e.g., De Luca et al., 2003; Keys & White, 2000; Miyake et al., 2000; Vaughan & Giovanello, 2010). Many recent studies have shown that bilinguals outperform monolinguals in such EC tasks, and these effects have been found for infants growing up in bilingual homes (Kovacs & Mehler, 2009), for children (meta-analysis

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in Adesope et al., 2010), and for younger (Costa, Hernandez & Sebastian-Galles, 2008; Hilchey & Klein, 2011) and older adults (Bialystok, Craik, Klein & Viswanathan, 2004; Gold, Kim, Johnson, Kryscio & Smith, 2013; Salvatierra & Rosselli, 2010). However, this bilingual EC advantage is not always found, and is particularly weak in young adults (e.g., Paap & Greenberg, 2013; but see Baum & Titone, 2014, and Kroll & Bialystok, 2013, for discussion of the variability in these results). The bilingual advantage in EC presumably follows from the ongoing need to manage two language systems (Kroll, Dussias, Bogulski & Valdes-Kroff, 2012) for which EC is recruited (Bialystok, Craik, Green & Gollan, 2009). The results found in older adults indicate that age-related differences in performance on EC tasks are less severe in bilinguals than monolinguals (Bialystok et al., 2004). More dramatically, this cognitive advantage extends to dementia, where bilinguals show significantly later onset of symptoms for both Alzheimer's disease (Alladi et al., 2013; Bialystok, Craik & Freedman, 2007; Craik, Bialystok & Freedman, 2010) and mild cognitive impairment (Bialystok, Craik, Binns, Ossher & Freedman, 2014; Ossher, Bialystok, Craik, Murphy & Troyer, 2013), although in some studies this protection is restricted to specific cultural (Chertkow et al., 2010) or educational (Gollan, Salmon, Montoya & Galasko, 2011) groups.

In spite of substantial evidence from behavioral studies, much less is known about the influence of bilingualism on brain function. Neuroimaging studies with young bilinguals have demonstrated that cognitive performance on nonverbal EC tasks is associated with utilization of more distributed brain networks than those used by monolinguals (Garbin et al., 2010; Luk, Anderson, Craik, Grady & Bialystok, 2010). In older adults, there are reports that bilinguals have larger gray matter volumes in left temporal cortex than monolinguals (Abutalebi et al., 2014), and stronger white matter connectivity between left and right frontal cortex (Luk, Bialystok, Craik & Grady, 2011), although reduced white matter measures in bilinguals also have been found (Gold, Johnson & Powell, 2013). In terms of brain function, only two studies have examined differences due to language experience in older adults. One found more distributed patterns of resting functional connectivity between frontal and posterior brain areas in bilingual older adults, relative to monolinguals (Luk et al., 2011). The other study examined activation during task switching and found a general age-related increase in activation of frontal regions, but that bilinguals had less over-recruitment, showing activation that more closely resembled that of young adults (Gold, Kim, et al., 2013). Although the evidence is not extensive and there is some inconsistency in these results, all highlight the prominent role of frontal cortex in brain differences between monolinguals and bilinguals, a difference which is notable given the importance of frontal regions for the implementation of EC (e.g., D'Esposito et al., 1995; Fuster, 2000; Seeley et al., 2007; Stuss & Alexander, 2000). Both structural and functional differences may serve to maintain cognitive function as a consequence of lifelong naturally-occurring experience on the brain, although at present the nature of those differences is not clear. The purpose of the current study was to use a different approach to understanding the effects of language experience on brain network activity by focusing on specific networks that have been implicated in the ability to engage EC. The primary aim was to assess whether bilingual older adults would show stronger resting-state functional connectivity (patterns of covarying activity in networks rather than individual brain regions), and larger modulations of activity when participants switch from carrying out tasks to periods of fixation (transition between endogenous and exogenous states). This approach was adopted to demonstrate that bilingualism is associated with large-scale differences in brain networks and to contribute to our understanding of how the dynamic coherence of neural networks is influenced by language experience.

Previous work has shown that a number of brain networks are important for EC. One such network is the frontoparietal control network, or FPC, which includes dorsolateral and inferior frontal regions, as well as the inferior parietal lobes (Cole & Schneider, 2007; Spreng, Sepulcre, Turner, Stevens & Schacter, 2013; Vincent, Kahn, Snyder, Raichle & Buckner, 2008). The FPC is thought to act as a “switch” to flexibly control the engagement of other brain networks and thus support the EC processes needed to meet task demands (Cole et al., 2013; Spreng et al., 2013). Another network involved in the control of behavior is the salience network, or SLN (Seeley et al., 2007). The SLN is thought to integrate sensory data with internal states (e.g., visceral, autonomic, and hedonic “markers”) so that the organism can guide its behavior and adapt to changing demands in the environment (Ham et al., 2013; Seeley et al., 2007). Its major nodes are the anterior insula/inferior frontal area, dorsal anterior cingulate and supramarginal gyri (Downar, Crawley, Mikulis & Davis, 2002; Seeley et al., 2007). Regions in these two networks are active during such EC tasks as working memory, task switching, planning, and other goal directed behaviors (Dosenbach et al., 2007; Grady et al., 2010; Luks, Simpson, Feiwell & Miller, 2002; Owen, McMillan, Laird & Bullmore, 2005; Spreng, Stevens, Chamberlain, Gilmore & Schacter, 2010). These EC-related regions often show greater task-related increases of activity in older than younger adults (for reviews see Grady, 2012; Park & Reuter-Lorenz, 2009; Rajah & D’Esposito, 2005; Spreng, Wojtowicz & Grady, 2010), but the literature on age changes in functional connectivity within the FPC and SLN is inconsistent. Some studies have reported rather widespread age-related reductions of functional connectivity in these networks (Allen et al., 2011; Thomas, Brier, Snyder, Vaida & Ances, 2013), whereas others have found age reductions only in some regions (Campbell, Grady, Ng & Hasher, 2012; Onoda, Ishihara & Yamaguchi, 2012; Voss et al., 2010), or even increased functional connectivity among EC regions in older relative to young adults (Grady et al., 2010; Rieckmann, Karlsson, Fischer & Backman, 2011; Tomasi & Volkow, 2012).

Another network whose activity can influence EC, although it does not subserve EC directly, is the default mode network (DMN). The DMN shows reduced activity during externally-driven tasks such as those typically used in fMRI experiments (e.g., encoding or recognizing visual stimuli) and increased activity during rest or fixation (e.g., Buckner, Andrews-Hanna & Schacter, 2008; Gusnard, Akbudak, Shulman & Raichle, 2001). The DMN involves posterior cingulate, ventromedial prefrontal cortex, angular gyri and parahippocampal gyri (for reviews see Andrews-Hanna, 2012; Buckner et al., 2008; Spreng, Mar & Kim, 2009) and is thought to underlie self-reference and projection of the self through the past (memory) and future (planning), as well as having a role in social cognition, such as theory of mind (Buckner et al., 2008; Grigg & Grady, 2010; Harrison et al., 2008; Spreng & Grady, 2010). Importantly, the modulation of DMN activity is related to EC more generally because greater reduction of DMN activity during tasks and stronger functional connectivity among DMN nodes are related to better performance on EC tasks (Dang, O’Neil & Jagust, 2013).

DMN functional coupling with the FPC also supports goal-directed behaviors, such as planning and problem solving (Gerlach, Spreng, Gilmore & Schacter, 2011; Spreng, Stevens, et al., 2010). Finally, both modulation of activity and strength of functional connectivity in the DMN are reduced with aging (Andrews-Hanna et al., 2007; Damoiseaux et al., 2008; Grady et al., 2010; Lustig et al., 2003; Park, Polk, Hebrank & Jenkins, 2010), and those older adults with stronger DMN connectivity perform better on cognitive tasks (Andrews-Hanna et al., 2007).

An interesting property of the DMN and EC-related networks, such as FPC and SLN, is that they often show anti-correlated activity. That is, activity in DMN regions is negatively correlated with activity in FPC and SLN areas at rest (Fox et al., 2005; Grady et al., 2010), and the strength of this anti-correlation is positively related to better or more consistent performance on EC tasks (Kelly, Uddin, Biswal, Castellanos & Milham, 2008). Thus, the evidence to date suggests that modulation of activity in multiple networks and functional connectivity within and between networks, all of which are ways of assessing the dynamic range of network activity, are important for EC. Since managing two languages is demanding and requires EC, bilingual experience may have an impact on domain-general networks that could be observed in these brain network measures.

In general, evidence for effects of bilingualism on these network measures will contribute to an understanding of the brain differences that are related to the behavioral differences between monolinguals and bilingual performing EC tasks. Moreover, given the importance of network dynamics for general cognitive performance, understanding these dynamics in monolingual and bilingual older adults has broader implications for cognitive aging.

1.1 The Current Study: Bilingualism and Network Dynamics

Taken together, the evidence for reduced network functional connectivity and reduced dynamic brain activity in older adults, along with our prior finding of better maintained white matter connectivity in older bilinguals, lead to several predictions regarding differences between monolingual and bilingual older adults in network activity.

1. Bilinguals will have stronger functional connectivity within the three networks of interest (FPC, SLN and DMN) than monolinguals. There should be no group differences in functional connectivity within brain networks that are primarily involved in cognitive domains other than EC.
2. Bilinguals will show stronger modulation of activity in DMN and EC regions (i.e., FPC and SLN) when comparing fixation to task (i.e., more activity in the DMN during fixation and more activity in FPC and SLN during tasks). That is, bilinguals will show greater modulation of activity within the networks in response to changing task demands.
3. Bilinguals will show stronger correlations among these brain measures than monolinguals, suggesting tighter links between different measures of network activity.

To test the first of these predictions, we examined intrinsic functional connectivity of the FPC, SLN and DMN in resting state data from bilingual and monolingual older adults. We used a multivariate, seed-based approach that assessed functional connectivity in these networks simultaneously by including a seed for the DMN (the posterior cingulate cortex, or PCC) and one that has been linked to both the FPC and SLN (the anterior insula/frontal operculum, or aIFO). This two-seed approach is useful for distinguishing network activity between groups of participants, and for distinguishing connectivity patterns that differ across brain regions (Campbell, Grigg, Saverino, Churchill & Grady, 2013). Here, we used it to identify the networks of interest and to test whether bilingual older adults have stronger functional connectivity than monolinguals in any or all of them. As comparison analyses, we assessed functional connectivity of two regions involved in processes that would not be expected to differ between monolinguals and bilinguals, and hence would allow us to assess the specificity of group differences for networks that influence EC. The first comparison region was in the medial temporal lobe (MTL), under the assumption that the MTL is more involved in memory than EC (Moscovitch, 1992; Nyberg, McIntosh, Houle, Nilsson & Tulving, 1996; Squire & Zola, 1998; Strange, Otten, Josephs, Rugg & Dolan, 2002; Yonelinas et al., 2007) and so should not show a group difference in functional connectivity. Although the MTL is sometimes considered to be a part of the DMN, it also shows a pattern of functional connectivity distinct from the major DMN nodes (Andrews-Hanna, Reidler, Sepulcre, Poulin & Buckner, 2010; Campbell et al., 2013) and it is this pattern that we address here. The second region was in extrastriate visual cortex, which is functionally connected to other visual areas (Allen et al., 2011), and involved in perceptual processes that would not be expected differ between language groups (Laird et al., 2011). We assessed changes in brain activity across tasks and fixation to test the second hypothesis of greater dynamic changes in network activity when participants shift between internal (fixation periods) and externally-driven cognitive demand (task periods). Finally, we calculated correlations among all the brain measures within each group. In this way we were able to obtain a multi-faceted picture of network dynamics and the influence of bilingualism in supporting network activity.

2. Methods

2.1 Participants

Twenty-eight right-handed healthy older adults (mean age = 70.5 yrs, SD = 3 yrs) participated in the study. Fourteen participants were monolingual speakers of English (7 males and 7 females) and 14 had lifelong bilingual experience (6 males and 8 females). Participants provided informed consent and underwent a behavioral and a scanning session. The two groups had comparable demographic backgrounds and neuropsychological performance but different language experience. The monolinguals had an average age of 70.6 yr; they had received 16 yr of education on average, and had a mean short MMSE score of 16.9 (out of 17). Their mean Shipley Vocabulary score was 88%, and 86% of this group had been born in Canada. Members of the bilingual group had an average age of 70.3 yr; they had received 17.7 yr of education on average, and had a mean short MMSE score of 17.0. Their mean Shipley vocabulary score was 84%, and 43% of this group had been born in Canada. All procedures were approved by the Research Ethics Board of the Baycrest Centre in Toronto, Canada. Monolingual older adults reported English to be their only communicating language, whereas the bilingual older adults reported that they had used both

English and another alphabetic language regularly since childhood (before age 11). Participants in the two language groups were matched on age, gender and English proficiency. All participants were active community members, reported no known psychiatric or health issues that may affect neurological health, no experience of concussion and no contraindication with MR scanning. Two-tailed *t*-tests showed no statistically significant difference between the monolinguals and bilinguals in age, years of education and weekly hours spent using a computer, *t*s(24) < 2, *ns.*

2.2 fMRI Scanning and Preprocessing

Approximately two weeks after the behavioral testing session, participants returned for the scanning session. Diffusion and functional resting-state data were acquired on a 3-Tesla Siemens Trio scanner with a 12-channel head coil. For DTI, two sets of whole-brain 30-direction diffusion weighted data were collected with the following parameters: TR = 9000s, TE = 90ms, b = 900s/mm^2, 32 oblique-axial slices with 5 mm thickness, FOV = 242mm. For the resting-state data, thirty gradient-EPI oblique axial slices with 5-mm thickness were obtained for the entire brain using a T2*-weighted pulse sequence during a six minute and twenty second resting state. Participants were instructed to keep their heads still, keep their eyes open, and not fall asleep. After the resting-state scan, participants confirmed that they had complied with these instructions. The scanning parameters were TR = 2s, TE = 30ms, FOV = 200mm, 64 × 64 matrix. These parameters also were used for four runs of task scans, which were each 5 minutes and 52 seconds in length. We also collected 160 1mm thick oblique axial slices of 3D-MPRAGE T1 images with TR = 2s, TE = 2.63ms, FOV = 256mm to create a sample-specific anatomical image for registration and overlay.

The first 10 TRs of the resting-state functional data were excluded from the analysis to avoid signal instability. Subsequent data were corrected for slice timing, motion artifacts, and physiological signal, as well as spatially normalized to standard Montreal Neurological Institute (MNI) space using the 152-subject template. White matter signal was removed as a nuisance variable using regression, and the time course for each run was “scrubbed” by eliminating images that exceeded pre-set criteria for excessive motion (Campbell et al., 2013), given the demonstrated influence of motion on functional connectivity measures (Power, Barnes, Snyder, Schlaggar & Petersen, 2012; Van Dijk, Sabuncu & Buckner, 2012). These processed images were smoothed with an 8-mm FWHM resulting in isotropic voxel size of 4mm for subsequent analysis. These preprocessing steps were carried out using Analysis of Functional Neuro-Images (Cox, 1996). All the coordinates reported subsequently are in MNI space.

2.3 Data Analysis

To examine the three networks we used regions identified as major nodes in these networks. For the DMN we used a PCC region (X, Y and Z MNI coordinates: −4, −48, 28) using coordinates from previously published data (Grady, Grigg & Ng, 2012; Grigg & Grady, 2010, 2010), and which are very similar to coordinates published by other groups (e.g., Buckner et al., 2009; Leech, Kamourieh, Beckmann & Sharp, 2011; Toro, Fox & Paus, 2008). For the SLN and FPC we used a single region, the aIFO, because this area is strongly coupled to both networks (Allen et al., 2011; Seeley et al., 2007; Vincent et al., 2008). To obtain the seed region we averaged the coordinates for the right aIFO (36, 24, −8) from three papers looking at the SLN or the FPC (Seeley et al., 2007; Spreng, Stevens, et al., 2010; Vincent et al., 2008). Data extracted from both regions over the time course of the resting state run were entered into the analysis so that we could directly contrast the functional connectivity patterns of the two networks (for the location of the PCC and aIFO seeds, see Figure 1b). To determine the MTL network we used a region (−28, −40, −12) that previously has been used to identify regions correlating specifically with the MTL, such as posterior and medial parietal cortex and occipitotemporal areas (Andrews-Hanna et al., 2010; Campbell et al., 2013). The extrastriate seed was in the lingual gyrus and coordinates for this region (28, −76, −8) were taken from a study by Allen et al. (2011) that identified a number of resting-state networks in a large sample of individuals.

To assess functional connectivity, the preprocessed resting-state data were analyzed with seed Partial Least Squares (PLS, Krishnan, Williams, McIntosh & Abdi, 2011; McIntosh, Chau & Protzner, 2004) following the procedures reported by Grigg and Grady (2010) for resting-state functional connectivity analysis. Seed PLS is a data-driven multivariate statistical technique that reveals functional activity across the entire brain that correlates with some external variable, such as activity in a seed voxel (or region) chosen a priori. The covariance between activity in the seed and other brain voxels is decomposed into latent variables (LVs) that can identify multiple patterns of functional connectivity. The advantage of using PLS is the consideration of the entire resting-state (resampled to 32 blocks of 5 consecutive volumes) simultaneously, thereby reflecting both the temporal and spatial characteristics of intrinsic brain activity at rest. Furthermore, the decomposition and associated resampling techniques consider all time points and voxels simultaneously, thus avoiding the problem of multicollinearity and post-hoc multiple correction of the p-values. Because of its ability to identify groups of brain regions with covarying functional connectivity, this technique is appropriate for the investigation of large-scale brain networks (McIntosh, 2000). Activity in each seed voxel (see results for seed location) was extracted and correlated (across participants) with all other brain voxels for each of the 32 time blocks in the resting run; PLS then was used to identify patterns of correlation that differed between bilinguals and monolinguals. Significance of the LVs was determined by 500 permutation tests, using resampling without replacement. Robustness of each voxel's contribution to a LV was provided by a bootstrap that resampled the data 100 times (with replacement) to estimate the standard error of the weight of each voxel on the LV. A bootstrap ratio, calculated as the ratio of each weight to its standard error, was thresholded at ± 3, equivalent to $p \leq 0.0027$. Significant clusters were further thresholded to include at least 10 voxels.

To obtain summary measures of each participant's expression of each LV pattern, we calculated 'brain scores' by multiplying each voxel's weight on the LV by the BOLD signal in the voxel, and summing over all brain voxels for each participant. This resulted in a brain score for each participant in each condition, for each LV. To provide a measure of how strongly seed activity covaried with the whole-brain pattern of activity, correlations between brain scores and seed activity were computed for each group, for each block. For each LV of interest we obtained a pattern of brain activity characterizing the regions with functional connectivity to the seeds and four sets of 32 correlations (one correlation per block): one set for each seed in the bilingual group and one for each seed in the monolingual group.

Between-group differences in the correlation distributions were assessed with independent-group *t*-tests[1]. The analysis of the PCC and aIFO seeds identified patterns of functional connectivity consistent with the three networks of interest, i.e., DMN, FPC and SLN.

To assess changes in task-positive and task-negative activity in the two groups, we measured activity during a version of a Simon task (Bialystok et al., 2005) and fixation, and the images were preprocessed as described above. For the current task we used colored or gray-scale pictures of abstract figures (Ryan & Villate, 2009), with instructions to respond with a button press to a colored stimulus using either the right or left hand and a gray stimulus with the other hand. On one-third of the trials the stimulus appeared in the center of the display so that its position was neutral relative to the mapping of right/left responses. On other trials the cue appeared on the right or left side of the display, either on the side corresponding to the hand that should be used to respond to the stimulus based on its color (congruent), or on the side of the display opposite to the hand that should be used to respond to the stimulus (incongruent). Each trial consisted of a fixation for a jittered duration of 250, 750 or 1250 ms, followed by the abstract figure presentation for 2550 ms or until response (whichever was shorter). Four scanning runs consisted of alternating six task blocks containing all three trial types (42 sec each) and five fixation blocks (20 sec each).

To analyze the task and fixation data we used task-PLS to identify brain patterns related to the two conditions. As with seed-PLS, task-PLS uses singular value decomposition to extract patterns of activity that characterize the covariance between activity in all voxels and the experimental conditions. In task-PLS, each latent variable (LV) contains a spatial activity pattern depicting the brain regions that, as a whole, show the strongest relation to (e.g. are covariant with) the task contrast identified by the LV. Brain scores were calculated as described above, and were then mean-centered (using the grand mean across groups) and confidence intervals (95%) for the mean brain scores in each condition were calculated from the bootstrap. Differences in activity between conditions within groups, as well as differences between groups per condition, were determined via a lack of overlap in these confidence intervals.

To compute correlations among all the brain measures within each group, we first needed to obtain individual measures of functional connectivity within each of the networks. To do this, we extracted the time courses for the major nodes in each network (i.e., those nodes shown in Table 1) over the 32 blocks of the resting state scan, computed pair-wise correlations among all the nodes within a network for each participant, and then averaged these correlations to obtain a single measure of functional connectivity for each participant, for each of the three networks. As a measure of modulation of network activity during task vs. fixation, we calculated the difference between the task brain score and the fixation brain score for each participant; the larger the difference score, the larger the distinction between task-negative activity during fixation and task-positive activity during the task. These measures were then included in a series of six correlations within the bilingual and monolingual groups separately. Each correlation was submitted to a bootstrap procedure (using 1000 bootstraps) to calculate the 95% confidence interval for each correlation,

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[1] Note that the same results as those reported below were obtained with independent sample non-parametric tests.

because of the relatively small sample size in each group. To be conservative, we considered as significant those correlations with $p < 0.05$ *and* confidence intervals that did not include zero (du Prel, Hommel, Röhrig & Blettner, 2009).

3. Results

3.1 Resting Functional Connectivity

Two LVs from the seed-PLS analysis on the resting data showed regions where activity was correlated with the PCC and aIFO seeds that were consistent with the three networks of interest, as well as clear language group differences in the strength of these whole-brain patterns of correlation. The first of these LVs (explaining 5.9% of the covariance, $p < 0.001$) is shown in Figure 1a and identified regions having robust functional connectivity with the DMN (cool colors) and those functionally connected to the SLN (warm colors). Table 1 shows the brain regions contributing to the DMN and SLN, consistent with the areas thought to be major nodes of these networks. The graphs in Figure 1c show the mean strength of the functional connectivity in the networks, averaged across the entire resting run (i.e., the correlations between seed activity and the brain scores, averaged across the “blocks” in the resting run). Both language groups had reliable functional connectivity within each of the networks ($p < 0.005$, one-sample t-tests per group testing whether the correlation values differed from zero), but the connectivity within the DMN was significantly stronger for bilinguals than for monolinguals, $t(62) = 3.2$, $p = 0.002$. There were no group differences in the strength of the functional correlations within the SLN, $t(62) < 1$.

A second LV, orthogonal to the first LV, was extracted from this analysis (explaining 3.9% of the covariance, $p < 0.001$). This LV identified a set of regions with functional connectivity to the aIFO (Figure 2), consistent with major nodes of the FPC (Table 1). Network functional connectivity was significantly greater than zero in the bilingual group, $p < 0.001$, but not in the monolingual group ($p = 0.17$). In addition, bilinguals also had stronger connectivity than monolinguals, $t(62) = 3.7$, $p = 0.001$. Activity in this network was not reliably correlated with PCC activity in either group (p’s > 0.10), and there was no group difference in PCC connectivity, $t(62) < 1$. Thus, these two LVs show patterns of connectivity that are consistent with the first prediction, indicating that bilinguals showed stronger functional connectivity in both the DMN and FPC than the monolinguals; however, there was equivalent functional connectivity in the SLN in the two groups.

3.2 Comparison Analyses

Figure 3a shows the results of the analysis involving the MTL seed. If the effect of bilingualism is primarily in regions involved in EC, then a network of functional connectivity based on the MTL should not show differences between monolinguals and bilinguals in functional connectivity. This analysis identified a set of regions with strong correlations to the left MTL seed (warm colors in Figure 3a), including posterior occipitotemporal regions, basal ganglia and medial parietal cortex. There was no group difference in the functional connectivity of this network, $t(62) = 1.6$, $p = 0.11$.

An additional analysis involving the lingual gyrus seed is shown in Figure 3b. Regions with strong functional connections to this extrastriate region included homologous visual cortex in the left hemisphere, temporal cortex (mostly in the right hemisphere) and medial parietal cortex. The strength of these functional connections did not differ between groups, $t(62) = 1.2$, $p = 0.23$. Thus, both of these analyses suggest that differences in functional connectivity due to bilingualism are specific to the FPC and DMN.

3.3 Dynamic Range of Network Activity during Task and Fixation

The behavioral data for the two groups are shown in Figure 4. Reaction times during the task runs were significantly slower for incongruent than congruent trials, as expected ($F(1,24) = 11.9$, $p = 0.002$; congruent RT $M = 845 \pm 118$ msec; incongruent RT $M = 886 \pm 119$ msec), but did not differ between language groups ($F < 1$; Monolingual $M = 876 \pm 122$, Bilingual $M = 854 \pm 118$ msec). In addition, the group x condition interaction was not significant ($F < 1$). Both groups attained a high level of accuracy (Monolingual $M = 0.92 \pm 0.04$, Bilingual $M = 0.96 \pm 0.02$), and none of the effects were significant (Fs < 1).

The analysis comparing brain activity across the tasks and fixation are shown in Figure 5. The DMN (cool colors) is clearly distinguished from a distributed set of task-active regions (warm colors) and overlaps substantially with the DMN regions identified in the functional connectivity analysis (Figure S1). The regions active during the task include nodes from both the FPC and SLN, which also show considerable overlap with the SLN and FPC areas found to correlate with the aIFO (Figure S1). To assess the range of activity modulation between the DMN and task-related areas, the brain scores obtained for each participant were contrasted between the fixation and task conditions. For this contrast we predicted that the bilingual group would have higher brain scores in both task and fixation, consistent with the idea of an increased dynamic range of activity. However, there were no group differences in the brain scores from either the fixation, $t(26) < 1$, or task conditions, $t(26) = 1.2$, $p = 0.22$, or in a difference score, $t(26) = 1.1$, $p = 0.26$, calculated as the difference between the task brain score and the score from the fixation condition (see Figure 5).

3.4 Correlations among brain measures

Although we did not find group differences in the expression of network activity during the task and fixation conditions, it is possible that there would be group differences in how these measures of dynamic network activity were related to strength of functional connectivity in these networks. To test the idea that bilingualism would strengthen the correlations among these measures, we calculated correlations within each group among measures of functional connectivity in the FPC, SLN and DMN (i.e., between-network correlations), and correlations between connectivity and the difference between task-related and fixation-related brain scores (for a total of six correlations per group). Only one of these correlations was significant for monolinguals: the between-network correlation involving the FPC and DMN (Table 2). Four of these correlations were significant for bilinguals. First, functional connectivity within the FPC and the SLN in bilinguals was significantly correlated with the task-fixation difference scores ($p < 0.01$). That is, stronger functional correlations within these two cognitive control networks at rest were associated with a greater ability to modulate activity in these networks and the DMN in an anti-correlated fashion during the task runs in bilinguals. In addition, using the Fisher r-to-Z transformation we found that the correlation between the FPC and the task-fixation difference, $Z = 2.95$, $p < 0.01$ (see Figure 6), and the correlation between the SLN and the difference score, $Z = 2.36$, $p < 0.05$, were both significantly larger in bilinguals than monolinguals. In bilinguals, there were also significant correlations between functional connectivity in the SLN and connectivity in the DMN and FPC (Table 2), suggesting strong between-network connectivity in this group. These results indicate that despite the lack of group differences in some brain measures, bilinguals showed stronger correlations among these measures, in line with the idea that bilingualism enhances the links among measures of network dynamic range in older adults.

Because the strength of functional connectivity in the FPC differed between groups, and this connectivity was related to modulation of activity during the task runs only in the bilinguals, we conducted a final analysis to determine the brain regions that expressed the latter effect. To do this we entered the participants' mean functional connectivity measure for the FPC into a PLS analysis (this is the same procedure as that used for assessing seed connectivity, but with the external variable being mean FPC connectivity). Since resting functional connectivity in the FPC is related to the ability to modulate overall activity during task vs fixation in bilinguals, as indicated by the correlation seen in Figure 6, then stronger resting coupling in the FPC should be associated with more activity in at least some task-positive regions during task and/or more activity in task-negative regions during fixation in the bilinguals, but not in the monolinguals. This is indeed what we found. The PLS analysis identified a single significant LV ($p < 0.001$, explaining 51% of the covariance) showing a set of regions with the expected effect in bilinguals (Figure 7). Those bilingual individuals with stronger functional connectivity in the FPC at rest had more activity in a distributed set of regions during the task (positive correlation) and less activity in these regions during fixation (negative correlation). These regions are a subset of those areas that were active in both groups during the task vs. fixation (compare with Figure 5 and see Figure S2), and include bilateral aIFO, dorsolateral PFC, and regions of occipitotemporal and parietal cortex (Table 3). In contrast, those monolingual individuals with stronger resting functional connectivity in the FPC showed less activity in these areas during the task (negative correlation), and no relation between FPC functional connectivity and activity during fixation. This analysis thus supports the relations seen in Figure 6, and further shows that only in the bilinguals is up-regulation of activity in task-positive regions during the task associated with how strongly the FPC is coupled at rest.

4. Discussion

In this study, we examined different measures of dynamic activity in the brains of older adults to test the hypothesis that lifelong bilingualism is associated with stronger functional connectivity in specific networks and a greater range of task-fixation modulation of activity in these networks. In terms of functional connectivity in the three networks of interest, we found that bilinguals had stronger connections in both the DMN and FPC, consistent with our predictions. Modulation of activity between rest and task did not show the hypothesized differences between the language groups. However, bilinguals did show stronger correlations among these brain measures, specifically in correlations between EC network functional connectivity and the ability to modulate network activity between task and rest periods.

These results complement studies showing that bilingualism in older adults provides some advantage for EC of behavior (Bialystok & Craik, 2010) by showing differences between bilinguals and monolinguals in the functional properties of the brain networks underlying this control. In addition, these results extend our earlier findings of greater anterior-posterior functional connectivity in bilinguals (Luk et al., 2011) by showing increased functional connectivity within defined networks, with demonstrated involvement in EC tasks.

The focus of this study was on several measures of brain activity that have been related to EC, as this is the cognitive function that is enhanced in bilinguals. The finding of stronger functional connectivity within the FPC of bilinguals is consistent with prior reports of differences in activation of prefrontal regions in bilinguals vs. monolinguals (Bialystok et al., 2005; Gold, Kim, et al., 2013; Luk et al., 2010). Stronger functional connectivity in the DMN and FPC is in line with the better maintained white matter connections that we previously reported in these bilingual participants (Luk et al., 2011) both between hemispheres and between anterior and posterior brain areas. These are precisely the kind of long-range connections that would support functional connections within the DMN and FPC (Greicius, Supekar, Menon & Dougherty, 2009), both of which are distributed across the brain and involve frontal and parietal regions. However, we did not find group differences in SLN functional connectivity although the SLN also is distributed across the brain. The lack of a group difference in this functional network may not be related to any group differences in white matter connections. Instead, the lack of a group difference in SLN functional connectivity may lie in the fact that the SLN involves limbic and subcortical regions more than the other two networks, including areas such as the amygdala and ventral striatum that are involved in emotional processing and reward (Seeley et al., 2007). Thus, the SLN's contribution to EC is likely to involve emotional processing, which may be less amenable to influence from language experience than other control processes.

We also found that enhanced functional connectivity in bilinguals was specific to the networks that impact EC, as no group differences were seen in networks that would be closely tied to other processes such as memory (MTL) or visual processing (lingual gyrus). This is precisely the pattern that would be expected if the bilingual advantage in EC were the result of resolving interference from competing languages, requiring extended practice with EC over time. It is interesting that there were no group differences in MTL connectivity, despite the MTL being considered a node of the DMN (Fox et al., 2005), and we found group differences in functional coupling of the DMN. However, the MTL also is functionally connected with a set of regions that has been described as an MTL subsystem within the DMN (Andrews-Hanna et al., 2010; Campbell et al., 2013), and the regions shown in Figure 3 are consistent with this subsystem (Andrews-Hanna et al., 2010; Campbell et al., 2013). This MTL subsystem is thought to play a major role in the construction of mental scenes in which past and future events are embedded (Andrews-Hanna et al., 2010), a role that would involve the MTL with the DMN under some types of internal thought, but not others. Our results suggest that bilingualism influences the "core" DMN regions (PCC, ventromedial prefrontal cortex, angular gyri) that are consistently found to be part of this network and may primarily contribute to the task-related deactivation that influences EC performance (Dang et al., 2013). In contrast, regions that play subsidiary roles within the DMN and/or primarily represent cognitive processes other than EC would not be influenced by bilingualism.

Some researchers have reported that older adults show less differentiation between rest and task-related brain activity than younger adults (Lustig et al., 2003; Sperling et al., 2009). We were not able to compare our groups to young adults, but nevertheless found robust modulation of task-positive and task-negative activity in both of our older language groups, with no differences between them in the degree of overall modulation within these distributed patterns of activity. Although this does not support our hypothesis of greater modulation in bilinguals, it may be due to the fact that our sample of bilinguals and monolinguals did not show any group differences on behavioral tests of EC (Luk et al., 2011). Thus, the brain response to switching between task and fixation may not differ between groups in the present study because the cognitive demand involved in our particular task was equivalent in these samples, unlike the more typical situation of better EC in bilinguals. It should also be noted that some studies have found less task-related activity with better white matter connectivity (Burzynska et al., 2013), or less task-related activity in specific EC-related regions in bilingual older adults relative to monolinguals (Gold, Kim, et al., 2013), situations that would suggest more efficient use of cognitive resources in bilinguals. However, we found no evidence for this alternative in the task-related brain patterns identified by PLS.

Nevertheless, the modulation of activity between task and fixation was more strongly related to FPC and SLN functional connectivity in bilinguals than in monolinguals, indicating a stronger link in bilinguals between functional connectivity in these EC networks and the ability to modulate activity in the networks during tasks. In particular, stronger FPC connectivity at rest was associated with larger task-related increases in a number of task-positive regions, including frontal and parietal cortices, in bilinguals but not monolinguals. This finding of a relation between FPC functional connectivity and up-regulation of task-positive activity in prefrontal and parietal cortex, but not down-modulation of task-negative activity, is consistent with our earlier work showing that bilinguals recruit EC regions for resolving interference to a greater extent than do monolinguals, even when the task does not involve language per se (Luk et al., 2010). Initially, we also expected to find a correlation between DMN connectivity and task-fixation modulation, given the findings in young adults of a relation between functional connectivity and deactivation of the DMN during tasks (Dang et al., 2013). However, we did not find a significant correlation in either group, although there was a trend for such a relation in the bilinguals. Given the particular vulnerability of the DMN to aging relative to other brain networks (Damoiseaux et al., 2008; Grady et al., 2010; Tomasi & Volkow, 2012), it may be that links between DMN functional connectivity and modulation of activity during tasks are vulnerable to aging in general despite the bilingual advantage seen in DMN functional connectivity per se.

The bilingual advantage in EC for cognitive processing in older adults can be considered as a type of cognitive reserve in older age (Luk et al., 2011; Schweizer, Ware, Fischer, Craik & Bialystok, 2012). Overall our findings showing strengthened network functional connectivity and enhanced links among various aspects of dynamic range in bilinguals support the idea that this reserve is facilitated by differences in the way that brain dynamics impact the networks involved in cognitive control. However, although it seems clear that lifelong bilingualism influences these aspects of brain function, the precise nature or timing of this influence, and its impact on EC performance, await future research. One possible scenario (see Figure 8) is that over many years, resolving the interference between two languages helps to maintain stronger functional connectivity within the brain networks that can influence EC. Stronger connectivity results in greater ability to modulate activity in task-positive regions during tasks (as we found here for older bilinguals, and as shown in young adults by Dang et al., 2013). Both functional connectivity and task-related modulation could be influenced by other factors important in aging, such as better maintained white matter connections (as shown in Luk et al., 2011) and the variability/complexity of brain activity during cognitive tasks (Garrett, Kovacevic, McIntosh & Grady, 2011, 2013; McIntosh et al., 2014). This cascade of effects might then act to support the bilingual advantage in EC performance seen in older age, although we cannot show this relation to behavior in the current study. Future research clearly will be needed to examine all these hypothesized links directly.

5. Conclusion

Older bilinguals show enhanced network activity relative to their monolingual peers. This enhancement is seen primarily in stronger functional connectivity within networks that influence cognitive control and stronger links between this connectivity and other measures of brain dynamic range. This strengthening of functional network activity, along with better maintained white matter connections in these bilingual individuals, provides evidence that language experience begun in childhood and continued throughout adulthood influences brain networks in ways that might provide benefits in later life, as has been shown for education (Bennett et al., 2003; Stern, Alexander, Prohovnik & Mayeux, 1992). Since a bilingual advantage on EC tasks can be found in children, this influence on the brain must begin very early, although neuroimaging studies of EC in bilingual children have not been done. We found that bilingual young adults showed increased engagement of areas consistent with the FPC (and similar to those seen in Figure 2) during incongruent trials on a flanker task, relative to monolinguals (Luk et al., 2010), indicating that such differences in EC regions are evident by young adulthood. An interesting area for future research would be to study bilinguals across the lifespan to determine when the influence of bilingualism on the brain emerges and whether this influence evolves as people mature or remains relatively stable.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Highlights

- Functional connectivity (FC) in the frontoparietal control network is stronger in bilinguals.
- FC in the FPC is correlated in bilinguals with greater modulation of task-positive activity.
- Language experience influences brain networks in ways that may provide benefits in later life.

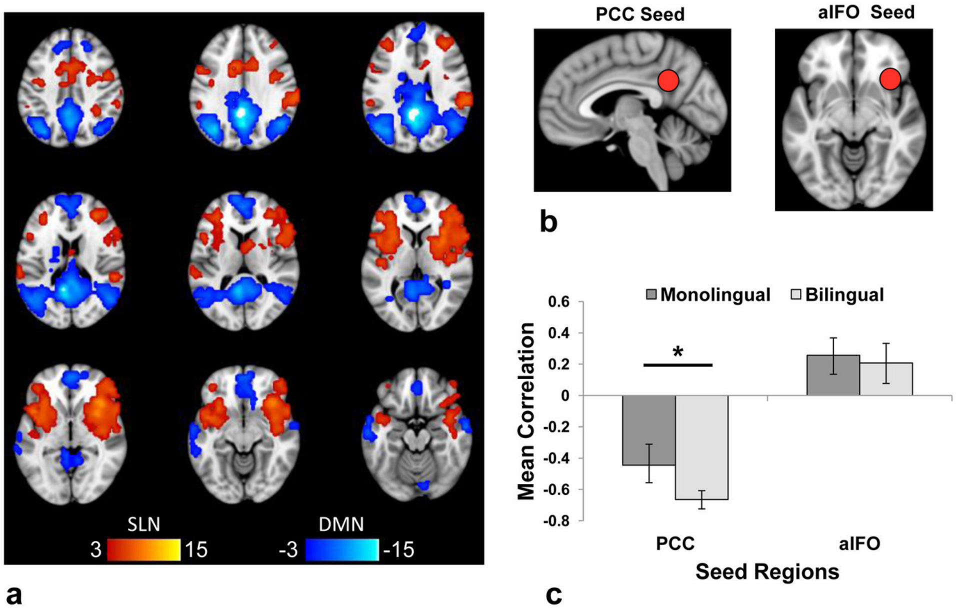

Figure 1.

Functional connectivity of the DMN and SLN (First LV). Warm colors in (a) indicate regions functionally connected with the aIFO (SLN) and cool colors indicate regions functionally connected to the PCC (DMN). The approximate location of the two seeds is shown in (b). Note that the regions seen here are enlarged for illustrative purposes (the data for the analyses were extracted from a single 4mm isotropic voxel). The graph in (c) shows the mean correlations over the resting-state run for the two groups. Positive bars indicate that the mean resting correlation was positive between the aIFO and warm colored regions and negative bars indicate that the mean correlation was positive between the PCC and cool colored regions. Bilinguals showed stronger functional connections within the DMN than monolinguals (indicated by "*"). Error bars are the bootstrapped 95% confidence intervals (1000 bootstraps). The color scales indicate the range of BSRs shown in the brain images.

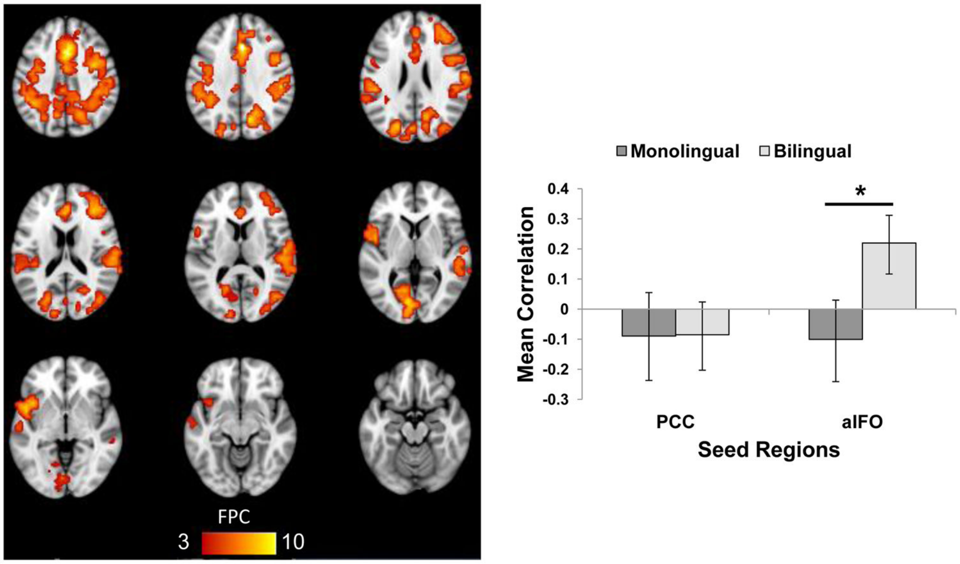

Figure 2.

Functional connectivity of the FPC (Second LV). Warm colors indicate regions functionally connected with the aIFO. The graph shows the mean correlations over the resting-state run for the two groups. Positive bars indicate that the mean resting correlation was positive between the aIFO and warm colored regions, negative bars indicate that seed activity was negatively correlated with activity in these regions. Bilinguals showed stronger functional connections within the FPC than monolinguals (indicated by “*”). Error bars are the bootstrapped 95% confidence intervals (1000 bootstraps). The color scale indicates the range of BSRs shown in the brain images.

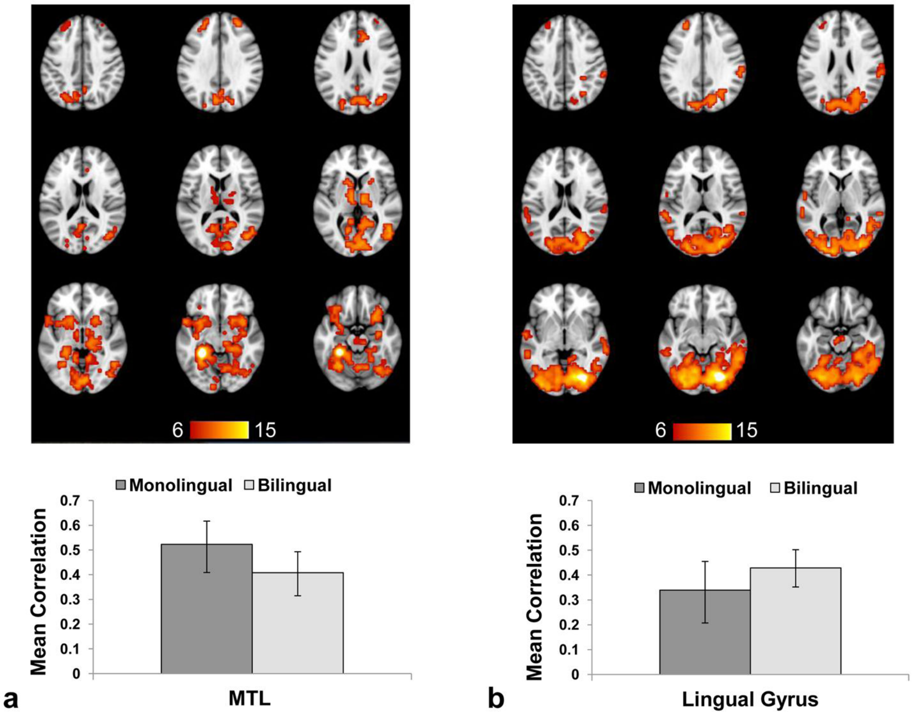

Figure 3.

Functional connectivity patterns for the MTL (a) and lingual gyrus (b). Warm colors indicate regions functionally connected with the seeds. The graph shows the mean correlations over the resting-state run for the two groups. Positive bars indicate that the mean resting correlation was positive between the seed and warm colored regions. There were no group differences in the strength of connectivity for either seed. Error bars are the bootstrapped 95% confidence intervals (1000 bootstraps). The color scales indicate the range of BSRs shown in the brain images.

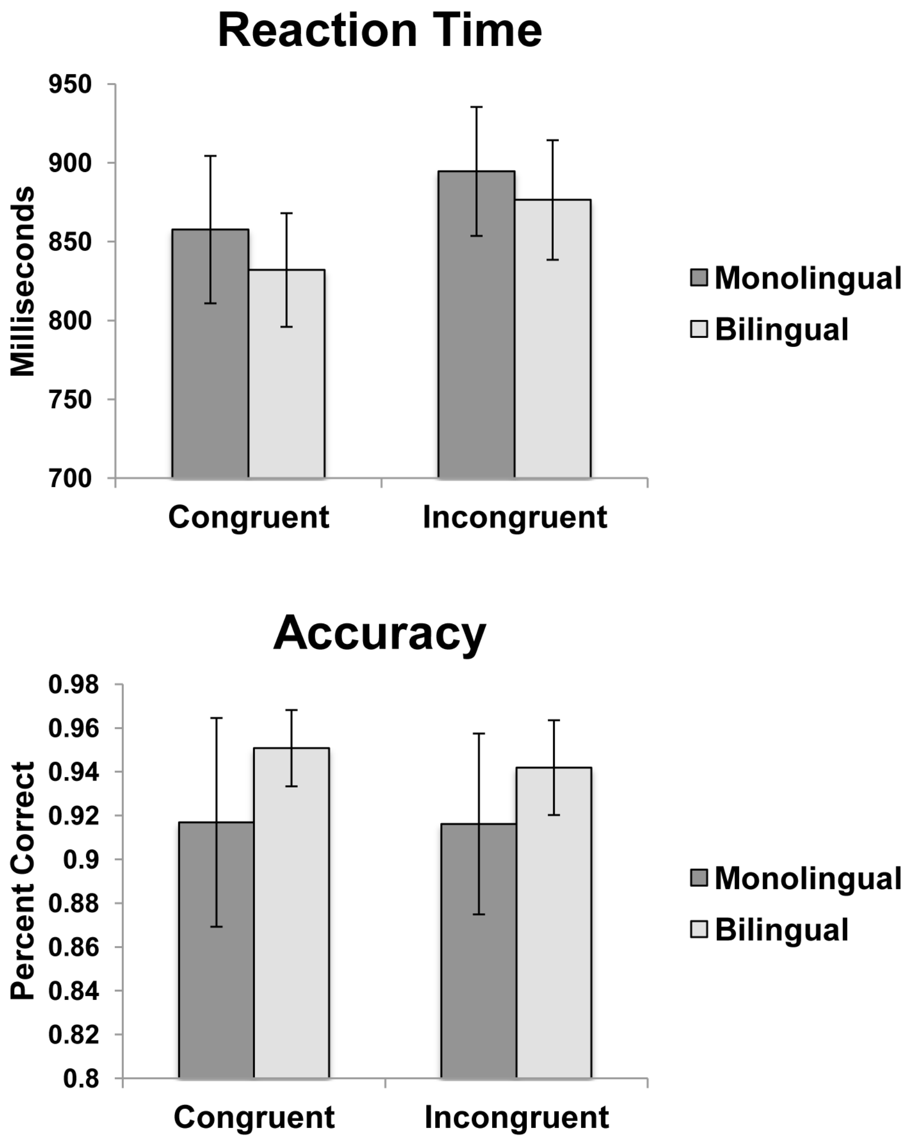

Figure 4.
Behavioral results for the Simon task carried out in the scanner. Values are mean ± S.E.

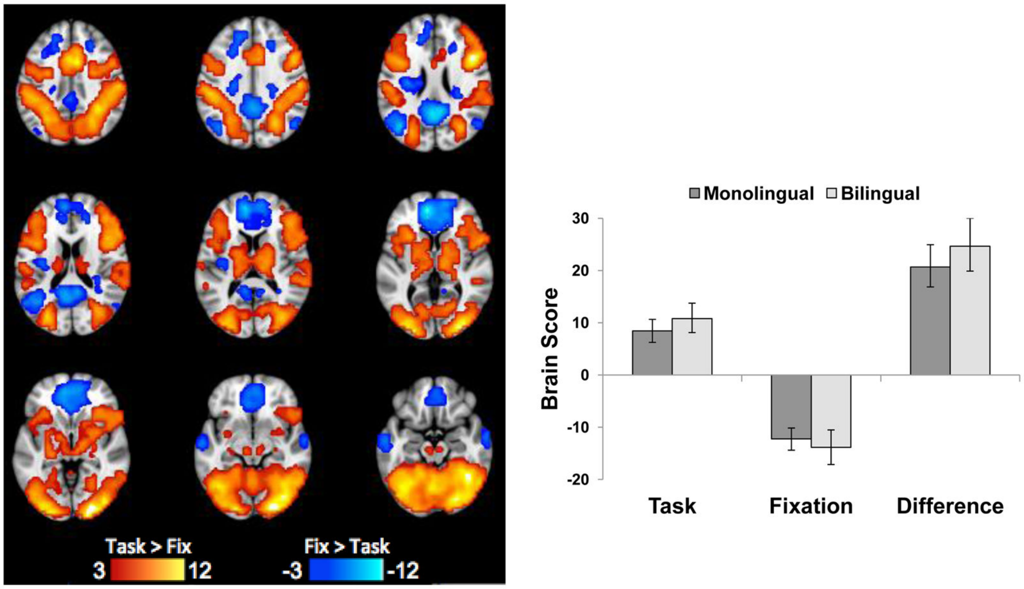

Figure 5.

Brain activity during fixation and task. Warm colored regions showed more activity during the task and cool colored regions showed more activity during fixation. The graph shows the mean brain score for each condition, as well as a difference score (task brain score minus fixation brain score). There were no group differences. Error bars are S.E. The color scales indicate the range of BSRs shown in the brain images.

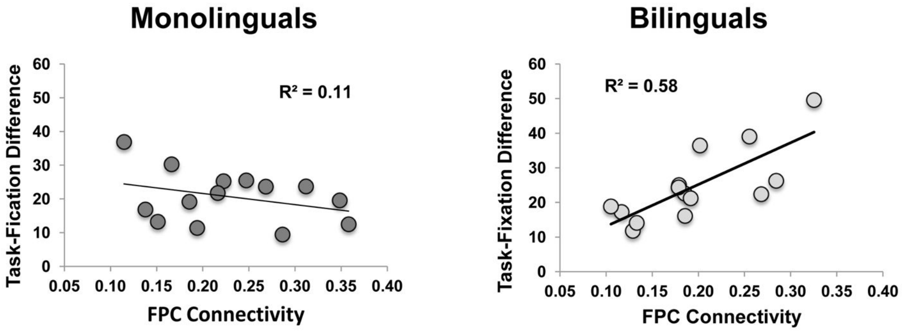

Figure 6.

Scatterplots of task-fixation difference score vs. FPC connectivity in the two groups. Correlations were significant only in the bilinguals and were larger in bilinguals than in monolinguals.

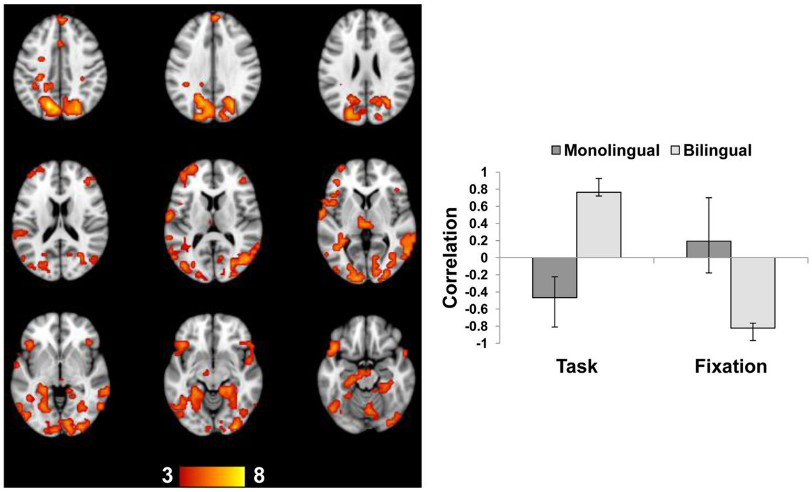

Figure 7.

Regions showing robust correlations between resting FPC functional connectivity and activity during the task run. The graph shows the correlations between FPC coupling and activity in the task and fixation conditions for both groups. The positive correlation seen in bilinguals during the task indicates that stronger resting functional connectivity in the FPC was associated with increased activity in these task-positive regions (also see Figure S2), whereas the negative correlation in the bilinguals indicates that stronger connectivity was associated with larger reductions of task-positive activity during fixation. This pattern of effects was not seen in the monolinguals. Error bars indicate the 95% confidence intervals for the correlations. The color scale indicates the range of BSRs shown in the brain image.

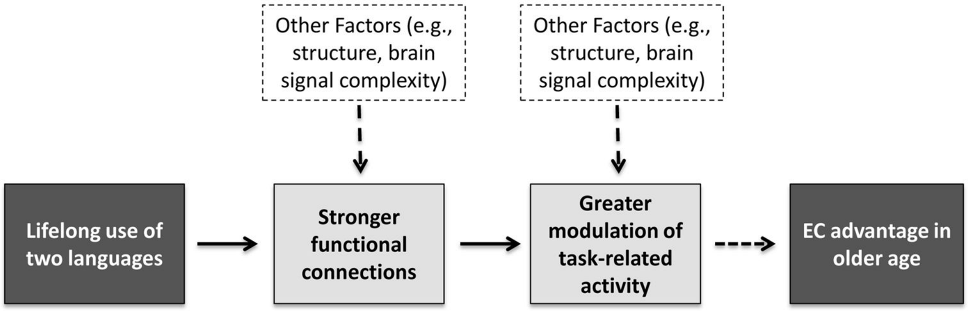

Figure 8.

A model of how bilingual language experience might lead to a cascade of brain effects resulting in cognitive reserve in older bilingual adults. The solid arrows indicate links supported by results in the current study (directions are hypothesized). Dashed arrows indicate effects that are plausible but not supported by the current study.

Table 1

Maxima of Clusters identified for each Network

Region	BA	X	Y	Z	BSR
Salience Network					
R aIFO	13/47	36	24	−8	seed
L aIFO	13/47	−32	16	−8	6.7
Supplementary motor area	6	4	−4	60	6.1
R supramarginal gyrus	40	60	−36	24	6.9
L supramarginal gyrus	40	−56	−36	28	4.9
R anterior cingulate gyrus	32	12	12	36	5.8
R middle frontal gyrus	9	36	40	20	7.1
Default Network					
PCC	31	−4	−48	28	seed
R angular gyrus	39	48	−60	28	−9.4
L angular gyrus	39	−36	−68	32	−13.1
R superior frontal gyrus	8	20	36	40	−4.7
L superior frontal gyrus	8	−12	36	40	−5.5
Ventromedial prefrontal	10	0	56	−4	−7.7
R middle temporal gyrus	21	64	−8	−16	−7.6
L middle temporal gyrus	21	−56	0	−24	−9.9
Frontoparietal Control Network					
R intraparietal sulcus	7	12	−64	44	10.5
L intraparietal sulcus	7	−12	−64	40	8.4
R intraparietal sulcus	7	28	−56	48	6.5
L intraparietal sulcus	7	−32	−48	52	7.5
Precuneus	7	16	−72	28	9
R anterior cingulate gyrus	32	4	20	32	11.6
R precentral gyrus	6	40	0	44	9.8
L middle frontal gyrus	6	−24	8	52	7.1
R middle frontal gyrus	9	36	36	16	7.9
L insula	13	−40	12	−4	8.1

R = right; L = left; BA = Brodmann area; X = right/left; Y = anterior/posterior; Z = superior/inferior; BSR = bootstrap ratio; PCC = posterior cingulate cortex; aIFO = anterior insula/frontal operculum.

Table 2

Correlations between brain measures

	Task-Fix	**DMN**	**FPN**
Monolinguals			
DMN	−0.17		
FPN	−0.13	0.69*	
SLN	−0.12	0.38	0.49
Bilinguals			
DMN	0.40		
FPN	0.81*[†]	0.48	
SLN	0.71*[§]	0.76*	0.69*

$p<0.05$ two tailed and bootstrap confidence intervals do not include zero;

[§] Bilinguals > Monolinguals $p<0.05$;

[†] Bilinguals > Monolinguals $p<0.01$.

Table 3

Task-Positive Regions where Increased Activity is Associated with Resting FPC Functional Connectivity in Bilinguals

Region	BA	X	Y	Z	BSR
R aIFO	47	44	28	−8	4.1
L aIFO	47	−40	28	0	4.7
R middle frontal gyrus	46	40	40	16	4.5
L middle frontal gyrus	46	−44	48	16	4.5
L middle frontal gyrus	6	−24	0	48	4.5
Medial frontal gyrus	8	0	56	36	6.3
R precuneus	7	24	−72	36	6.8
L precuneus	7	−16	−68	36	9.2
L inferior parietal lobe	40	−28	−28	40	6.1
R anterior intraparietal sulcus	40	40	−44	44	4.5
L middle temporal gyrus	37	−40	−52	0	5.7
L middle temporal gyrus	39	−56	−68	12	4.9
L superior temporal gyrus	42	−64	−8	8	5.3
R parahippocampal gyrus	36	24	−40	−12	5.3
L parahippocampal gyrus	35	−20	−24	−24	4.8
R inferior occipital gyrus	18	32	−92	−8	8.5
R lingual gyrus	18	12	−84	−4	5.1
L cuneus	18	−12	−100	4	5.4
L middle occipital gyrus	19	−40	−80	12	5.7
L thalamus		−4	−20	4	4.6
R cerebellum		32	−64	−28	5.3
L cerebellum		−44	−56	−36	4.9

R = right; L = left; BA = Brodmann area; X = right/left; Y = anterior/posterior; Z = superior/inferior; BSR = bootstrap ratio; aIFO = anterior insula/frontal operculum.