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3   **Title**: A neural mechanism of cognitive reserve: The case of bilingualism
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5
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17

18   Abstract

19

20   Cognitive Reserve (CR) refers to the preservation of cognitive function in the face of age- or

21   disease-related neuroanatomical decline. While bilingualism is known to contribute to CR, the

22   extent to which, and what particular aspect of, second language experience contributes to CR are

23   debated, and the underlying neural mechanism(s) unknown. Intrinsic functional connectivity

24   reflects experience-dependent neuroplasticity that occurs across timescales ranging from minutes

25   to decades, and may be a neural mechanism underlying CR. To test this hypothesis, we used

26   voxel-based morphometry and resting-state functional connectivity analyses of MRI data to

27   compare structural and functional brain integrity between bilingual and monolingual older adults,

28   matched on cognitive performance using a rigorous propensity score matching technique, and

29   across levels of second language proficiency measured as a continuous variable. Bilingualism,

30   and degree of second language proficiency in particular, were associated with lower grey matter

31   integrity in a hub of the default mode network – a region that is particularly vulnerable to decline

32   in aging and dementia – but preserved functional network organization that resembled the young

33   adult brain. Our findings confirm that lifelong bilingualism contributes to CR through

34   experience-dependent maintenance of optimal functional network structure of the domain-

35   general attentional control network across the lifespan.

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36   Multiple factors contribute to Cognitive Reserve (CR) across the lifespan, such as education,

37   occupation, and intellectual and social engagement (Cabeza et al., 2018; Song et al., 2022; Stern,

38   2021). There is compelling evidence that lifelong bilingualism also contributes to CR (Anderson

39   et al., 2020; Bialystok, 2021). Relative to their monolingual peers, bilingual older adults 1) have

40   better cognitive function, given similar levels of neuroanatomical decline, 2) demonstrate signs

41   of dementia later in life, 3) show more significant neuroanatomical pathology, given similar

42   levels of dementia, and 4) show more rapid rates of cognitive decline in later stages of dementia

43   (Bialystok, 2021). Bilingual individuals must continuously exert cognitive control to

44   appropriately direct their attention towards one situationally relevant language of two that are

45   simultaneously active in mind and competing for attention (Kroll et al., 2014; van Heuven et al.,

46   2008). Evidence suggests that this ongoing need for selection leads to an adaptation in domain-

47   general attentional control that enhances multiple subordinate cognitive control process across a

48   range of tasks and mitigates typical age-related cognitive decline (Bialystok, 2015; Bialystok and

49   Craik, 2022). This adaptation is the foundation for CR in bilingualism (Bialystok, 2021). Thus,

50   bilingualism serves as a useful proxy for investigating neural mechanisms underlying CR. Given

51   the evidence that lifelong bilingualism is a CR factor, two predictions are that 1) given equal

52   neuroanatomical health, bilinguals will have better cognitive performance than monolinguals and

53   2) given equal cognitive performance, bilinguals will have poorer neuroanatomical health than

54   monolinguals. Both relationships have been confirmed in recent work (Anderson et al., 2021;

55   Berkes et al., 2021; Brian T. Gold et al., 2013; Perani et al., 2017; Schweizer et al., 2012).

56

57   The neural mechanism underlying CR in bilingualism is unknown. Studies investigating

58   differences in brain structure associated with bilingualism have produced mixed, often

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59   contradictory results. For example, while some studies have shown better structural integrity in

60   bilingual than monolingual individuals (John A.E. Anderson et al., 2018; Luk et al., 2011;

61   Marin-Marin et al., 2020; Olsen et al., 2015), others have shown the opposite (Anderson et al.,

62   2021; Brian T. Gold et al., 2013; Schweizer et al., 2012), or dissociable patterns of grey vs. white

63   matter integrity (Macbeth et al., 2021). While the underlying neural mechanisms by which

64   augmented cognitive engagement across the lifespan leads to preservation of cognitive faculties

65   in later life are undetermined, there might be multiple pathways to CR (Oh et al., 2018). Another

66   possibility is that CR might result from adaptive shifts in cognitive strategy or more efficient

67   task-related engagement of brain regions or circuits (Abutalebi et al., 2012; Anderson et al.,

68   2021; B. T. Gold et al., 2013). A third possibility is that experience-dependent maintenance or

69   enhancement of the brain's long-term intrinsic functional network integrity could be a neural

70   mechanism underlying CR (Chan et al., 2021, 2018; N. Franzmeier et al., 2017; Nicolai

71   Franzmeier et al., 2017b; Weiler et al., 2018; Wig, 2017).

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73   RSFC, which can be quantified by analyzing spontaneous fluctuations of the blood-oxygen-

74   level-dependent (BOLD) signal in resting-state functional MRI (fMRI) data, reflects the brain's

75   intrinsic large-scale functional network architecture [for example, see refs. (Biswal et al., 1995;

76   Fox and Raichle, 2007)]. RSFC plays a central role in human cognition through a Hebbian-like

77   mechanism, whereby repeated experience-driven coupling or decoupling of task-related activity

78   among brain regions over time lead to enduring increases or decreases in RSFC among these

79   regions, respectively (Stevens and Spreng, 2014). This, in turn, facilitates or inhibits future

80   coupling (Kelly and Castellanos, 2014), thus enhancing or optimizing cognitive performance

81   with experience over time. Thus, RSFC reflects a previously unappreciated mechanism of long-

82   term neurocognitive plasticity that allows past experiences to mold sustained functional network

83   architecture to facilitate future cognitive performance. Research on RSFC has demonstrated that

84   1) it can be modulated by ongoing or recent experience across functionally relevant brain

85   regions/circuits/networks on relatively short timescales ranging from minutes to days (Martin et

86   al., 2021); 2) the degree of sustained experience-dependent change predicts learning, memory

87   consolidation, and future performance (Lewis et al., 2009; Stevens et al., 2010; Tambini et al.,

88   2010); 3) patterns of RSFC are correlated with individual differences in personality, behavior,

89   and cognition (Adelstein et al., 2011; Nostro et al., 2018); and 4) differential patterns of RSFC

90   are associated with neurodevelopmental and neurodegenerative disorders, and the extent of

91   neurocognitive decline/preservation in old age (Stevens and Spreng, 2014; Wig, 2017). Thus,

92   RSFC reflects a critical process underlying long-term neurocognitive plasticity that facilitates the

93   development, specialization, stabilization, and preservation of large-scale functional brain

94   networks across the lifespan. While there may be multiple pathways to CR, we propose that

95   experience-dependent maintenance of intrinsic functional networks is a fundamental neural

96   mechanism that could underly the phenomenon of CR in lifelong bilingualism.

97

98   Various RSFC analytic techniques can be used to parcellate the brain into multiple functionally

99   dissociable regions that are organized into large-scale functional sub-networks with varying

100   degrees of spatial resolution (Power et al., 2011; Schaefer et al., 2018; Wig et al., 2014; Yeo et

101   al., 2011). Previous work has focussed on three specific sub-networks that play foundational

102   roles in higher cognitive functioning (Grady et al., 2016; Setton et al., 2022; Spreng et al., 2013;

103   Spreng and Schacter, 2012): 1) the dorsal attention network (DAN), involved in externally

104   focussed cognition; 2) the default mode network (DMN), involved in internally focussed

105   cognition; and 3) the frontoparietal control network (FPCN), which facilitates volitional control

106   over the locus of attention by flexibly alternating its coupling between the DAN vs. DMN during

107   externally vs. internally focussed cognition, respectively (Spreng et al., 2010). Critically,

108   different nodes within these networks play specialized roles in facilitating within-network

109   communication and cross-network interactions among these networks, a set of dynamics that can

110   be characterized and quantified using graph theory analyses (Rubinov and Sporns, 2010; Wig et

111   al., 2011). Previous work has identified two discrete nodes of the FPCN within the left middle

112   frontal gyrus (MFG) that play opposite but complementary roles – an anterior region (aMFG;

113   Brodmann area (BA) 9) that has dense within-network connections but little cross-network

114   connectivity with other networks (i.e., a "provincial hub node"), and a posterior region (pMFG;

115   BA 6), which has high betweenness centrality, a measure of the extent to which a node

116   contributes to communication across networks (i.e., a "connector node") (Spreng et al., 2013).

117   These two nodes are thought to play critical roles in attentional control through mediating

118   within-network communication of the FPCN, and dynamic flexibility of cross-network coupling

119   with the DAN and DMN, respectively (Spreng et al., 2013). There is evidence that age-related

120   cognitive decline is related to functional connectivity changes most prominently within the

121   FPCN (Campbell et al., 2012), and of the MFG in particular (Spreng et al., 2018).

122

123   While some aspects of cognition decline in old age, such as working memory, episodic memory,

124   and processing speed, others remain stable or improve across the lifespan, such as semantic

125   memory and verbal knowledge (Park et al., 2002). This pattern of age-related change has been

126   characterized as a shift from fluid to crystalized cognition in later life (Craik and Bialystok,

127   2006), and it is correlated with increased RSFC of the left middle frontal gyrus, a core node of

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128   the FPCN, with the DMN – a phenomenon characterized by the "default-executive coupling

129   hypothesis of aging" (DECHA) (Spreng and Turner, 2019). The DECHA is consistent with prior

130   work demonstrating that 1) unlike young adults, older adults "fail to deactivate" the DMN during

131   externally focussed cognition (Grady et al., 2006; Lustig et al., 2003; Miller et al., 2008) and 2)

132   age-related differences in how the FPCN connects with other networks impacts both the function

133   of these other networks and cognitive ability in older adults (Grady et al., 2016).

134

135   Here, we investigated the hypothesis that lifelong bilingualism contributes to CR by mitigating

136   the typical age-related changes in functional connectivity of the FPCN described above (e.g.,

137   DECHA (Spreng et al., 2018)), specifically, by bolstering functional integration within the

138   FPCN and maintaining the dynamic flexibility of its cross-network coupling with the DMN and

139   DAN (Spreng et al., 2010). To isolate the extent to which lifelong bilingualism contributes to

140   CR, one must either compare cognitive performance between monolingual and bilingual groups

141   equated for neuroanatomical health (Berkes et al., 2021), with the expectation that bilinguals will

142   outperform monolinguals; or alternatively, compare differences in brain structure and function

143   between groups equated for cognitive performance (John A.E. Anderson et al., 2018), with the

144   expectation that bilinguals will show more prominent signs of neuroanatomical aging. Here, we

145   took the latter approach, and compared brain structure and intrinsic functional network integrity

146   in groups of monolingual vs. bilingual older adults equated on multiple measures of cognitive

147   performance and demographic variables using a rigorous propensity score matching (PSM)

148   technique. Recent research has also supported the view that bilingualism is better characterized

149   and investigated as a multidimensional set of continuous variables on which individuals vary

150   based on language experience, rather than a dichotomous variable separating individuals into

151   ostensibly homogenous groups (Dash et al., 2022; DeLuca et al., 2019; Gullifer and Titone,

152   2020; Macbeth et al., 2021; Sulpizio et al., 2020). Moreover, previous behavioural research has

153   implicated the active use and proficiency of a second language as the critical factor that might

154   contribute most to CR in bilingual older adults (Calabria et al., 2020). Thus, we also assessed the

155   degree to which these measures of structural and functional brain integrity are associated with

156   second language proficiency, measured as a continuous variable across all older adults in our

157   sample. We predicted that bilingual older adults would show more prominent signs of

158   neuroanatomical aging (i.e., "older looking" brain structure), but preserved integrity of intrinsic

159   functional network connectivity (i.e., "younger looking" brain functional organization) relative

160   to cognitively matched monolinguals, who would show typical patterns of degraded functional

161   network connectivity associated with aging. Specifically, we hypothesized that 1) bilingual older

162   adults will show lower grey matter integrity in brain regions that are particularly susceptible to

163   age-related decline (e.g., DMN regions); 2) bilinguals will show less default-executive coupling,

164   i.e., RSFC between the MFG and the DMN, a hallmark characteristic of neurocognitive aging

165   (Spreng and Turner, 2019); 3) bilinguals will show preserved flexibility of cross-network RSFC

166   of the MFG with the DAN and DMN; and 4) these measures of structural and functional integrity

167   will be associated with second language proficiency specifically, across all older adults.

168

169   **Results**

170   Ninety-three right-handed older adult participants (age: mean ± SD = 74.04 ± 3.86, range = 68-

171   85; 63 female) with no history of heart disease, neurological or psychological disorders, or

172   traumatic brain injuries, were recruited from the local area surrounding York University,

173   Toronto, Canada (Note: An additional 3 participants were recruited but not included in this

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174 study, due to excessive head motion in the MRI scanner). Behavioral and structural MRI data

175 from a subset of these participants have been analyzed in previous reports (Anderson et al., 2021,

176 2017; John A.E. Anderson et al., 2018). The Language and Social Background Questionnaire

177 [LSBQ (John A. E. Anderson et al., 2018)] was used to categorize participants as monolingual or

178 bilingual (LSBQ composite score) and to assign a score on second language proficiency (LSBQ

179 factor), a continuous variable. Participants were interviewed via telephone to validate language

180 status, and those who could not be reliably identified as monolingual or bilingual were not

181 included in the study. Forty-seven participants (29 female) were identified as bilingual and 46

182 (34 female) were identified as monolingual. All participants completed the D-KEFS battery

183 (Delis et al., 2001), comprising multiple neuropsychological tests of executive function, and the

184 Mini-Mental State Examination [MMSE (Folstein et al., 1975)]. We used a PSM technique to

185 equate the groups across performance on multiple cognitive measures (MMSE, Trail Making

186 Task (letter-number-switching score), Shipley-2 verbal score, Shipley-2 block patterns score), as

187 well as demographic variables (age, education, gender), similar to previous work (John A.E.

188 Anderson et al., 2018). We used voxel-based morphometry (VBM) analysis of structural MRI

189 data, and RSFC analyses of resting-state fMRI data, to compare neuroanatomical and intrinsic

190 functional network integrity, respectively, between the groups and across second language

191 proficiency.

192

193 **Propensity score matching on cognitive measures and demographic variables**

194 Previous research has used sequential bivariate matching; however, this fails to account for

195 potential multivariate interactions between the matching variables and may introduce bias into

196 participant selection when using a high dimensional set of matching criteria (John A.E. Anderson

197   et al., 2018; Ho et al., 2007; Rosenbaum and Rubin, 1983). With PSM, a propensity score for

198   each individual is obtained by using logistic regression to predict group membership, given a set

199   of observed covariates. Participants from one group are then individually matched to those in the

200   second group based on propensity scores (Rosenbaum and Rubin, 1983). PSM can account for

201   multivariate interactions, minimizes selection error when using a large number of matching

202   variables, and is better suited for smaller sample sizes, as is often the case in neuroimaging

203   studies (Austin and Steyerberg, 2015; Ho et al., 2007; Rosenbaum and Rubin, 1983). To

204   prioritize matching the monolingual and bilingual groups on cognitive performance, PSM was

205   done using the MatchIt R package (Ho et al., 2011) in a 2-stage hierarchical manner. The first

206   stage matched the groups on 4 neuropsychological measures: MMSE, Trail Making Task (letter-

207   number-switching score), Shipley-2 verbal score, and Shipley-2 block patterns score. Using the

208   propensity scores, each bilingual participant was matched to a monolingual; bilinguals that could

209   not be matched, and any remaining monolinguals, were removed from the matched-group

210   analyses. The distribution of propensity scores for the matched monolingual and bilingual

211   groups, as well as for the excluded participants from each of the unmatched groups, are shown in

212   Supplementary Figure 1a. Once the groups were matched on cognitive performance, they were

213   then matched on 3 demographic variables (age, education, and sex) using the same procedure.

214   The distribution of propensity scores for the two matched groups following the second stage are

215   shown in Supplementary Figure 1b. The absolute standardized mean difference between

216   monolinguals and bilinguals on each of the matching variables for the matched vs. unmatched

217   groups are show in Supplementary Figure 1c. Following the PSM procedure, the final group

218   sizes were 39 monolinguals (age: mean ± SD = 73.51 ± 3.25, range = 68-79; 30 female) and 39

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219   bilinguals (age: mean ± SD = 73.87 ± 4.00, range = 69-83; 23 female). The matched groups did

220   not differ significantly on any of the cognitive or demographic variables (Table 1).

221

222   Table 1. Participant information, demographics, and test scores.

	Matched Groups					Unmatched Group						
	ML (n = 39)		BL (n = 39)			ML (n = 46)		BL (n = 47)			ALL (n = 93)	
	M	SD	M	SD	p	M	SD	M	SD	p	M	SD
Demographics												
Age	73.51	3.25	73.87	4.00	0.665	74.04	3.89	74.04	4.00	0.999	74.04	3.86
Education	3.82	0.88	3.92	0.90	0.613	3.82	0.95	3.27	0.93	0.842	3.80	0.94
Sex (female/male)	30/9		23/16			34/12		29/18			63/30	
MMSE	29.28	1.10	29.31	0.92	0.911	29.28	1.09	29.21	1.16	0.765	29.24	0.89
Shipley												
Verbal	108.56	7.55	106.61	8.93	0.301	109.74	7.52	101.55	17.03	0.003*	105.60	13.77
Blocks	107.40	10.05	104.02	11.80	0.180	110.33	12.47	101.85	12.64	0.001*	106.21	13.20
Trail Making Task												
Letter Number Switching	11.92	2.30	10.87	2.97	0.085	12.26	2.41	10.34	3.27	0.002*	11.29	3.02

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224   ML, monolingual; BL bilingual; * $p < 0.01$.
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226
227   **Second language proficiency as a continuous variable across all older adults**

228   The quantity and quality of exposure to multiple languages is extremely variable across

229   individuals, and most have at least some experience with a second language. A recent study

230   reported that more than 80% of nearly 1,000 respondents in the United Kingdom who claimed to

231   be monolingual English-speakers had learned other languages at some point in their lives,

232   sometimes to high degrees of fluency (Castro et al., 2022). Previous behavioural research has

233   implicated the active use and proficiency of a second language as the critical factor that might

234   contribute most to CR in bilingual older adults (Calabria et al., 2020). In addition to the

235   composite score, the LSBQ quantifies second language proficiency based on a factor analysis,

236   which produced a latent variable comprising clustered items that were identified as representing

237   second language proficiency. The eigenvalue from this latent variable is used as the quantitative

238   measure of second language proficiency (for details, see ref. 59). Thus, an important subscale of

239   the LSBQ is second language proficiency, on which individual participants vary along a

240   continuum (John A. E. Anderson et al., 2018). To test the hypothesis that second language

241   proficiency is a key factor that contributes to CR in bilingualism, we correlated normalized

242   scores on this factor with normalized measures of neuroanatomical and intrinsic functional

243   network integrity across our entire sample of 93 older adults included in the study.

244

245   **Monolingual adults have higher grey matter density in a core hub of the DMN**

246   To test the hypothesis that monolingual older adults will have higher neuroanatomical

247   integrity than bilinguals when the groups are equated on cognitive performance, we quantified

248   grey matter density across the brain using VBM analysis (FSL-VBM software suite) of T1-

249   weighted structural MRI images. This analysis identified a large cluster in the posterior cingulate

250   cortex (pCC), a core hub of the DMN (Buckner et al., 2009; Hagmann et al., 2008; van Oort et

251   al., 2014), that showed higher grey matter density in monolingual older adults relative to the

252   bilinguals [$p < 0.05$, cluster corrected for multiple comparisons using ETAC (Cox, 2019)] (Fig.

253   1a-b). Morever, grey matter density in the pCC was negatively correlated with second language

254   proficiency across the entire sampe of older adults ($r = -0.30$; $p = 0.002$, 2-tailed; Fig. 1c).
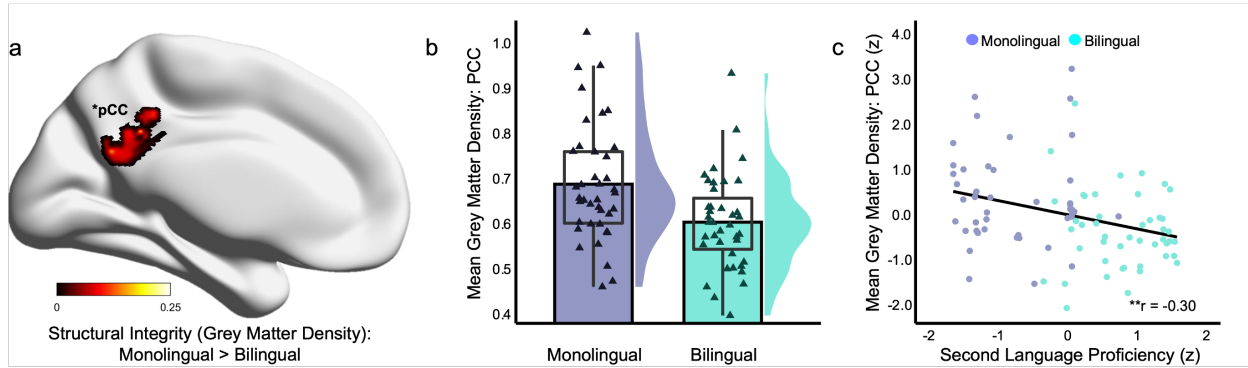
Figure 1. Differences in structural integrity estimated using VBM. (a) Comparing groups matched on cognitive performance using PSM, monolinguals have higher grey matter density than bilinguals in the posterior cingulate cortex, a hub of the DMN (p < 0.05, ETAC corrected; cluster centre of mass: x = -3, y = -50, z = 30, mni_152 coordinates). (b) Mean grey matter density in the pCC cluster showing a significant difference between the matched groups (solid bars); distribution of values for all participants (triangles) overlaid with the first and third quartiles (box), interquartile range (whiskers), and density curve for each group. (c) Across all older adults (n = 93), second language proficiency is negatively correlated with grey matter density in the pCC (r = -0.30; p = 0.002, 2-tailed). pCC, posterior cingulate cortex; DMN, default mode network; z, standardized scores; * p < 0.05; ** p < 0.01.

Monolingual older adults show greater default-executive coupling, with stronger RSFC

between a FPCN hub node and the DMN

To test the hypothesis that bilingual older adults will show preserved intrinsic functional network

integrity, despite lower neuroanatomical integrity, we used RSFC analysis to investigate within-

and between-network connectivity among the nodes of three foundational large-scale networks –

the FPCN, DMN, and DAN. The locations of 43 network nodes across these 3 networks were

based on previous work that identified and characterized these networks based on both task-

related and resting-state fMRI data (Spreng et al., 2013). The full matrices of the group means

for all pairwise correlations between nodes for the monolingual and bilingual groups were

calculated, and the latter subtracted from the former to produce the group difference matrix

(Supplementary Fig. 2). The upper half of the matrix shows the group difference in mean

pairwise correlation values; the lower half of the matrix is thresholded to show only the

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279 statistically significant differences (permutation test: q < 0.05, FDR-corrected for multiple

280 comparisons across the entire matrix). Significant differences in RSFC between the monolingual

281 and bilingual groups were highly specific and consistent with our hypotheses, with the

282 monolinguals showing stronger RSFC between the aMFG in the left prefrontal cortex (PFC) and

283 multiple nodes of the DMN only, including dorsomedial PFC, pCC, left posterior inferior

284 parietal cortex, left superior frontal gyrus, left superior temporal sulcus, and ventromedial PFC

285 (Fig. 2a,b). Mean RSFC between the aMFG and each of the 6 DMN nodes was also negatively

286 correlated with second language proficiency across the entire sample of older adults (r = -0.29; p

287 = 0.005, 2-tailed; Fig. 2c).
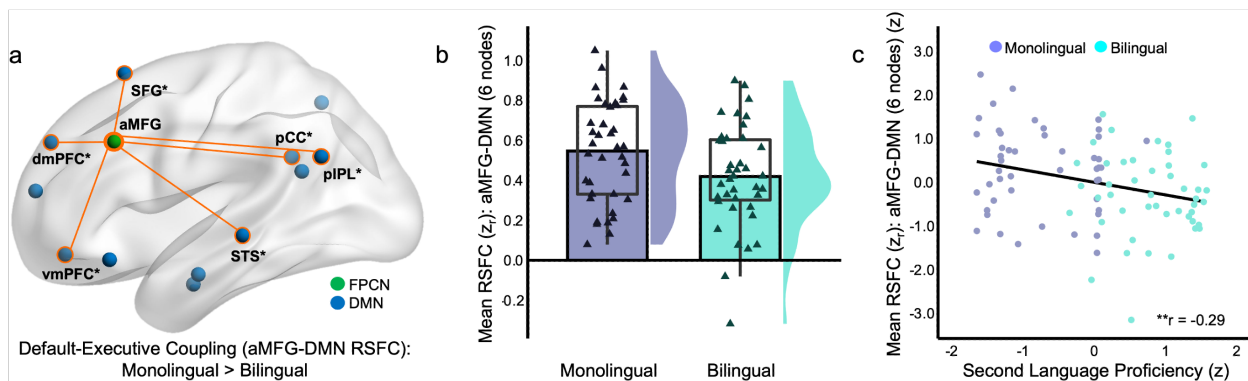
288

289 **Figure 2.** Differences in functional integrity estimated using RSFC. (a) Monolingual older adults
290 show stronger RSFC of the left aMFG with multiple nodes of the DMN only (i.e., default-
291 executive coupling), relative to bilinguals, including the dmPFC, pCC, left IPL, left SFG, left
292 STS, and vmPFC ($p < 0.05$ FDR corrected for all pairwise correlations among all 43 nodes of the
293 FPCN, DMN, and DAN) displayed on a glass brain representation of left hemisphere (see also
294 Supplementary Fig. 2); orange lines/circles indicate significantly stronger pairwise RSFC in the
295 monolingual older adults. (b) Mean RSFC between the aMFG and each of the 6 DMN nodes
296 showing a significant difference between the matched groups (solid bars); distribution of values
297 for all participants (triangles) overlaid with the first and third quartiles (box), interquartile range
298 (whiskers), and density curve for each group. (c) Across all older adults (n=93), second language
299 proficiency is negatively correlated with mean RSFC between the aMFG and the 6 nodes of the
300 DMN ($r = -0.29$; $p = 0.005$, 2-tailed). FPCN, frontoparietal control network; DMN, default mode
301 network; RSFC, resting-state functional connectivity; z_r, Fisher z-transformed correlation; z,
302 standardized score; for full list of all node label definitions, see Supplementary Table 1. * $p <$
303 0.05; ** $p < 0.01$.
304

305   Note that this pattern of increased functional connectivity between the MFG and DMN (i.e.,

306   default-executive coupling) is a hallmark characteristic of neurocognitive aging; it is associated

307   with an inability to disengage the DMN during externally focussed tasks [task-related fMRI

308   (Spreng and Schacter, 2012; Turner and Spreng, 2015)] and an increased reliance on semantic

309   memory in the context of episodic memory decline (Spreng and Turner, 2019).

310   To further explore the extent of increased RSFC of the aMFG with the DMN, we used graph

311   theory analysis to quantify the clustering coefficient of the aMFG with all nodes of DMN across

312   the entire brain (see Fig. 3a for illustration of clustering calclulation, displayed in the left

313   hemisphere). The monolingual group showed significantly higher clustering of the aMFG with

314   the whole DMN than the bilingual group (mean difference = 0.20; permutation test: $p = 0.04$, 2-

315   tailed) (Fig. 3b). Furthermore, clustering of the aMFG with the DMN was negatively correlated

316   with second language proficiency across the entire sample of older adults ($r = -0.22$; $p = 0.03$, 2-

317   tailed; Fig. 3c).

318

15
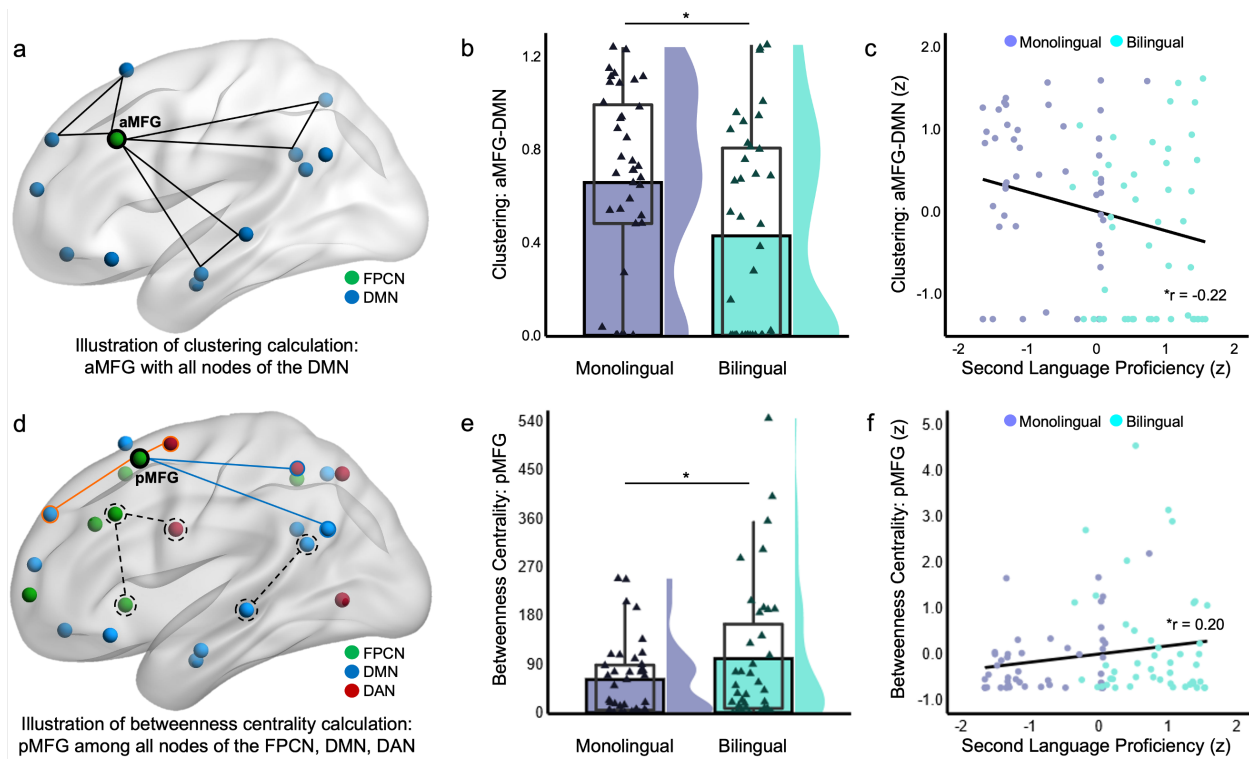
Figure 3. Differences in functional integrity estimated using graph theory analyses of RSCF. (a) Illustration of clustering coefficient calculation: number of complete triangles between the aMFG, a provincial hub of the FPCN, and every unique pair of nodes in the DMN, where triangle-sides (black lines) indicate statistically significant RSFC between nodes at a given density threshold. Illustration shows hypothetical clustering at a given threshold, displayed on a glass brain representation of the left hemisphere. (b) Monolingual older adults had higher clustering of the left aMFG with the DMN than bilinguals (mean clustering coefficient difference = 0.20; permutation test: $p = 0.04$, 2-tailed). Plot shows mean clustering coefficient (area under the curve) for each of the matched groups (solid bars); distribution of values for all participants (triangles) overlaid with the first and third quartiles (box), interquartile range (whiskers), and density curve for each group. (c) Across all older adults (n = 93), second language proficiency is negatively correlated with clustering of the aMFG with the DMN ($r = -0.22$; $p = 0.03$, 2-tailed). (d) Illustration of betweenness centrality calculation: number of shortest pairwise paths for all possible node-pairs among the 43 nodes of the FPCN, DMN, and DAN that pass through the left pMFG, a connector node of the FPCN. Illustration shows two shortest pairwise paths (solid lines) for 2 node-pairs (circled in orange and blue) that pass through the pMFG, and two shortest pairwise paths that do not (dashed black lines/circles). (e) Monolingual older adults had lower betweenness centrality of the left pMFG than monolinguals (mean difference = -45.06; permutation test: $p = 0.04$, 2-tailed). Plot shows mean betweenness centrality for each of the matched groups (solid bars); distribution of values for all participants (triangles) overlaid with the first and third quartiles (box), interquartile range (whiskers), and density curve for each group. (c) Across all older adults (n = 93), second language proficiency is positively correlated with betweenness centrality of the pMFG ($r = 0.20$; $p = 0.04$, 2-tailed). aMFG, anterior middle frontal gyrus; pMFG, posterior middle frontal gyrus; FPCN, frontoparietal control network;

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344 DMN, default mode network; DAN, dorsal attention network; RSFC, resting-state functional
345 connectivity; *z*, standardized score. * *p* < 0.05.

346

347 **Bilingual older adults have higher betweenness centrality of a connector node of the FPCN**

348 The FPCN facilitates control over one's locus of attention by flexibly alternating its coupling

349 between the DMN and DAN during internally vs. externally focussed cognition, respectively

350 (Spreng et al., 2010). Previous work identified a key connector node of the FPCN in the pMFG

351 with very high betweenness centrality, a graph theory analysis metric that quantifies the extent to

352 which a node contributes to cross-network communication; thus, this node is thought to play a

353 critical role in cognitive flexibility (Spreng et al., 2013). To assess potential differences in the

354 flexibility of cross-network communication in monolingual vs. bilingual older adults, we

355 compared the betweenness centrality of the pMFG (see Fig. 3d for illustration of betweenness

356 centrality calculation, displayed in the left hemishpere) between the two groups. Bilingual older

357 adults showed higher betweenness centrality of the pMFG than the monolinguals (mean

358 difference = -45.06; permutation test: p = 0.04, 2-tailed; Fig. 3e). Finally, betweenness centrality

359 of the pMFG was positively correlated with second language proficiency across the entire

360 sample of older adults (r = 0.20; p = 0.04, 2-tailed; Fig. 3f).

361

362 **Discussion**

363 Here, we demonstrate that when equated on cognitive performance using a rigorous matching

364 procedure, bilingual older adults had lower grey matter density than their monolingual peers in

365 the pCC, a hub of the DMN, which is particularly susceptible to structural and functional decline

366 in aging and neurodegenerative disease (e.g., Alzheimer's disease) (Buckner, 2005; Grady et al.,

367 2006; Lustig et al., 2003). This finding confirms that lifelong bilingualism is a CR factor, as it

368   demonstrates that bilingual older adults perform just as well as their monolingual peers on tasks

369   of executive function despite showing signs of more advanced neuroanatomical aging. In

370   contrast, the bilingual older adults had preserved intrinsic functional network structure, related to

371   executive function and cognitive flexibility specifically, more consistent with that of younger

372   brains (Spreng et al., 2013) than their monolinguals peers. While the monolingual older adults

373   showed more prominent coupling of a hub node (aMFG) of the FPCN with the DMN, a hallmark

374   characteristic of advanced age associated with a shift from fluid to crystalized cognition (Spreng

375   et al., 2018), the bilinguals showed higher betweenness centrality of a connector node of the

376   FPCN (pMFG), thought to underly cognitive flexibility (Spreng et al., 2013). Moreover, across

377   all older adults, second language proficiency was negatively correlated with structural integrity,

378   but positively correlated with multiple measures of intrinsic functional network integrity. These

379   findings confirm that lifelong bilingualism, and second language proficiency in particular,

380   contribute to CR, and support our hypotheses that this occurs through a process of bolstering the

381   functional integrity, and maintaining neurocognitive flexibility, of the FPCN. Thus, a neural

382   mechanism underlying CR in bilingualism is the experience-dependent maintenance of optimal

383   intrinsic functional network structure in the face of neuroanatomical changes across the lifespan.

384

385   Several studies have investigated the possibility that lifelong bilingualism could lead to the

386   preservation of, and/or compensatory increases in, the brain's neuroanatomical structure by

387   investigating white matter integrity using diffusion tensor imaging MRI. While some studies

388   reported higher white matter integrity associated with bilingualism in older adults (John A.E.

389   Anderson et al., 2018; Luk et al., 2011; Marin-Marin et al., 2020; Olsen et al., 2015), others

390   reported prominent widespread declines in white matter integrity (Anderson et al., 2021; Brian T.

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391   Gold et al., 2013; Schweizer et al., 2012). A lack of consensus on the potential role of

392   experience-dependent plasticity of brain structure in CR underscores the need for more research

393   in this area using rigorous matching techniques to compare monolingual vs. bilingual groups –

394   i.e., to delineate neuroanatomical differences associated with bilingualism per se, groups must be

395   equated on cognitive performance (Anderson et al., 2021; John A. E. Anderson et al., 2018). One

396   study that did this provided evidence of a more nuanced relationship between lifelong

397   bilingualism and brain structural integrity in older adults. Cognitively healthy bilingual older

398   adults had lower structural integrity of both grey and white matter globally, relative to

399   monolinguals, but the bilinguals also had higher white and grey matter integrity within focal

400   regions putatively involved in executive cognitive function specifically (Anderson et al., 2021).

401

402   Research has also investigated the possibility that differences in the way brain regions are

403   engaged during task performance between monolingual and bilingual older adults could underlie

404   or be a consequence of CR. Monolingual older adults show increased engagement of frontal

405   brain regions or circuits reflective of increased cognitive effort at lower levels of task difficulty

406   than bilingual adults, akin to differences between older and younger adults, respectively (Grundy

407   et al., 2017). For example, monolingual older adults, despite having higher overall grey and

408   white matter integrity than bilinguals, performed worse on a 2-back working memory task, and

409   showed increased engagement of a frontostriatal circuit, including the left MFG in particular,

410   during task performance (Anderson et al., 2021). Decreased task-related activation of frontal

411   brain regions in bilingual older adults has been interpreted as increased efficiency (Grundy et al.,

412   2017). However, the underlying structural or functional properties that could facilitate this more

413   efficient task-related processing under certain task conditions have not been determined. We

19

414   propose that intrinsic functional network connectivity – which is bolstered by task-related

415   activity over time, which in turn facilitates future task performance – underlies the more efficient

416   dynamic neurocognitive processing in bilingual older adults measured at the task-level.

417

418   Previous studies using fMRI to investigate potential differences in RSFC associated with

419   bilingualism (Berken et al., 2016; Dash et al., 2022; DeLuca et al., 2019; Grady et al., 2015;

420   Gullifer et al., 2018; Li et al., 2015; Luk et al., 2011; Marin-Marin et al., 2021; Thieba et al.,

421   2019) have typically focussed on younger adults only, had small sample sizes, and/or failed to

422   explicitly or adequately account for cognitive performance or neuroanatomical differences across

423   groups of older individuals, complicating interpretations and limiting inferences about how

424   observed changes are associated with CR per se. Nevertheless, our results are broadly consistent

425   with previous work reporting increased RSFC primarily among regions involved in cognitive

426   control (Grady et al., 2015) and attention networks specifically (Dash et al., 2022), in older

427   bilingual adults. Previous work has also investigated differences in RSFC associated with

428   various other CR factors across the lifespan (Anthony and Lin, 2018; Benson et al., 2018; Chan

429   et al., 2021, 2018; N. Franzmeier et al., 2017; Nicolai Franzmeier et al., 2017a; Pietzuch et al.,

430   2019; Stern et al., 2021; Weiler et al., 2018). One study demonstrated that level of education, as

431   a proxy for CR, was positively correlated with increased RSFC between a left PFC region of the

432   FPCN and the DAN, and negatively correlated with RSFC of this region with the DMN, in older

433   adults with mild cognitive impairment (Nicolai Franzmeier et al., 2017b). The latter result

434   parallels our findings of a negative correlation between second language proficiency and RSFC

435   of the FPCN (aMFG) with the DMN, and increased RSFC between these regions in monolingual

436   older adults, relative to bilinguals. This suggests that our discovery of the critical role of left

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437　MFG connectivity with other networks in CR associated with bilingualism might generalize to

438　other CR factors as well, a hypothesis that should be investigated in future work using the

439　analyses described here.

440

441　How could bilingualism have a long-term influence on RSFC of intrinsic functional networks?

442　Managing multiple simultaneously active languages (Kroll et al., 2012; van Heuven et al., 2008)

443　requires dynamically alternating the locus of one's attention between the external environment,

444　to monitor the situationally relevant language, and the content of one's internal mental

445　environment. Age-related memory declines are due, in part, to distraction resulting from a

446　reduced ability to ignore task-irrelevant information (Healey et al., 2008; Stevens et al., 2008).

447　Task-related modulation of functional connectivity of lateral PFC is critical for suppressing task-

448　irrelevant processing in the brain (Zanto et al., 2011), which is reduced in older adults compared

449　to young adults (Gazzaley et al., 2005). Moreover, task-related functional connectivity of the left

450　lateral PFC with DMN regions specifically has been associated with memory failure in older

451　adults due to an inability to ignore distraction (Stevens et al., 2008). The latter is consistent with

452　research demonstrating that, unlike young adults, older adults "fail to deactivate" the DMN

453　during externally focussed cognition (Grady et al., 2006; Lustig et al., 2003; Miller et al., 2008),

454　and that this failure is associated with persistent functional connectivity of the DMN with the

455　FPCN (Spreng and Schacter, 2012; Spreng and Turner, 2019; Turner and Spreng, 2015). Taken

456　together, these results suggest that lateral PFC regions involved in cognitive control play a role in

457　age-related differences in selective attention due to 1) reduced dynamic flexibility of functional

458　connectivity with other brain regions/networks generally, and 2) persistent functional

459　connectivity with the DMN, specifically. These task-related differences in older adults mirror

21

460   age-related differences in intrinsic RSFC (Grady et al., 2016; Spreng et al., 2018), demonstrated

461   most prominently by the monolingual older adults in this study, who showed lower cross-

462   network RSFC of a connector node of the FPCN, and stronger RSFC of a hub node of the FPCN

463   with the DMN. Previous work demonstrated that age-related differences in functional

464   connectivity of the FPCN with other networks during both task and rest predicted cognitive

465   performance (Grady et al., 2016). Thus, the differences reported here between monolingual and

466   bilingual older adults in cross-network RSFC of two key nodes of the FPCN (aMFG and pMFG)

467   could account for the preservation of cognitive function in bilinguals in the face of more

468   advanced neuroanatomical aging, relative to monolinguals.

469

470   Younger looking patterns of RSFC in the bilingual older adults could be the consequence of a

471   long history of increased demand on the FPCN to facilitate attentional control. Metaphorically,

472   just as targeted physical exercise builds specific muscles of the body needed to optimize physical

473   performance over time, "mental exercise" may strengthen RSFC among specific brain regions

474   needed to optimize cognitive performance. Experience-dependent changes in RSFC are highly

475   specific to the brain regions engaged during task performance (Albert et al., 2009; Lewis et al.,

476   2009; Stevens et al., 2010; Tambini et al., 2010). Further, the magnitude of experience-

477   dependent changes in RSFC predicts the degree of improvement in future task performance

478   (Lewis et al., 2009; Stevens et al., 2010; Tambini et al., 2010). Thus, the pattern of preserved

479   RSFC of the FPCN hub and connector nodes in the brains of bilingual older adults is highly

480   consistent with the pattern of task-evoked activity that facilitates domain-general attentional

481   control, needed to cognitively manage multiple languages simultaneously.

482

483   Recent work sought to identify a RSFC connectome associated with cognitive reserve using a

484   data-driven approach, which could be useful as a direct measure of cognitive reserve and a

485   potential outcome measure for interventions aimed at improving CR (Stern et al., 2021). The

486   pattern of RSFC identified was correlated with IQ, and notably, included primarily frontal brain

487   regions. Indeed, understanding the factors that give rise to CR and its underlying neural

488   mechanism(s) is an important endeavour, with broad implications ranging from the level of the

489   individual to society. For example, a recent large-scale longitudinal study demonstrated

490   relationships between educational attainment, RSFC of the brain's functional networks, and

491   neurocognitive health in older age (Chan et al., 2021). In general, older adults show reduced

492   within-network RSFC and increased between-network RSFC relative to young adults, reflecting

493   a widespread pattern of dedifferentiation [also referred to as reduced segregation (Wig, 2017)] of

494   functional network organization broadly (Chan et al., 2014; Geerligs et al., 2015; Grady et al.,

495   2016; Setton et al., 2022; Spreng et al., 2016). This effect of aging is more prominent in older

496   adults without a college degree than their college-educated peers, and predicts impending

497   progression of dementia up to a decade later (Chan et al., 2021).

498

499   Our results are generally consistent with previous work described above reporting large-scale

500   network dedifferentiation in aging and widespread, somewhat non-specific differences in

501   patterns of RSFC associated with CR (e.g., education and IQ). Importantly, however, our results

502   further delineate the specific processes that lead to network-wide changes at the level of

503   individual network nodes, revealing their dissociable roles in maintaining within- and between-

504   network communication in the context of a well-established CR factor – bilingualism. Notably,

505   the pattern of cross-network functional connectivity of MFG regions that was more prominent in

23

506   bilingual older adults and correlated with second language proficiency in the current study is the

507   reverse of the pattern associated with the well-established shift from fluid to crystalized

508   cognition in typical aging (Spreng and Turner, 2019). Therefore, our findings highlight the

509   critical roles of specific brain regions – i.e., discrete nodes of the FPCN within the MFG – in

510   maintaining domain-general attentional control in aging, and suggest the intriguing possibility

511   that the pattern of RSFC of these regions associated with bilingualism could be a neural

512   mechanism underlying multiple CR factors. Understanding these factors is critical for informing

513   personal lifestyle choices and policy decisions in an increasingly older global population.

514

515   **Materials and Methods**

516   **Participants**

517   Ninety-three participants (age: mean ± SD = 74.04 ± 3.86, range = 68-85; 63 female) were

518   recruited from the local area surrounding Toronto, Ontario, Canada; each participant was a

519   resident of Canada at the time of testing. All participants were right-handed and had no history of

520   heart disease, neurological or psychological disorders, or traumatic brain injuries. Data from a

521   subset of these participants were analyzed in previous work (Anderson et al., 2021; John A.E.

522   Anderson et al., 2018). An additional 3 participants were recruited but to ensure data quality,

523   these participants were excluded from analyses due to head motion in the MRI scanner

524   exceeding 3mm in one or both of the resting-state fMRI runs.

525

526   The Language and Social Background Questionnaire [LSBQ (John A. E. Anderson et al., 2018)]

527   was used to categorize participants as monolingual or bilingual. Participants were interviewed

528   via telephone to validate bilingual status, and those who could not be reliably identified as either

24

529   monolingual or bilingual were not included in the study. Of the 93 participants analyzed, 47

530   participants (29 female) were identified as bilingual and 46 (34 female) were identified as

531   monolinguals. All participants completed the Mini-Mental State Examination [MMSE (Folstein

532   et al., 1975)] and D-KEFS battery (Delis et al., 2001). The D-KEFS is a well-established battery

533   that assesses a comprehensive variety of cognitive processes related to executive control.

534

535   **Propensity Score Matching**

536   Interpreting group differences in brain structure and function related to cognitive reserve requires

537   that monolingual and bilingual groups have an equivalent level of cognitive functioning.

538   Therefore, in the current study, monolinguals and bilinguals were matched on multiple

539   neuropsychological and demographic variables using propensity-score matching (PSM). A

540   propensity score for each individual was obtained by using logistic regression to predict group

541   membership given a set of observed covariates. Participants from one group were then matched

542   to those in the second group based on the propensity scores (Rosenbaum and Rubin, 1983).

543   Nearest neighbour matching was used to match the propensity scores of individuals between

544   groups. PSM accounts for multivariate interaction, minimizes selection error when using a large

545   number of matching variables, and is well-suited for smaller sample sizes that are usually found

546   in neuroimaging studies (Austin and Steyerberg, 2015; Ho et al., 2007; Rosenbaum and Rubin,

547   1983).

548

549   To prioritize matching the monolingual and bilingual groups on cognitive performance, PSM

550   was done using the MatchIt R package (Ho et al., 2011) in a 2-stage hierarchical manner. The

551   first level matched the groups on 4 neuropsychological measures: MMSE, Trail Making Task

25

552   (letter-number-switching score), Shipley-2 verbal score, and Shipley-2 block patterns score

553   Using the propensity scores, each bilingual participant was matched to a monolingual; bilinguals

554   that could not be matched, and any remaining monolinguals, were removed from the matched-

555   group analyses. Once the groups were matched on cognitive performance, they were then

556   matched on 3 demographic variables using the same procedure: age, education, and sex. The

557   final group sizes were 39 monolinguals (age: mean ± SD = 73.51 ± 3.25, range = 68-79; 30

558   female) and 39 bilinguals (age: mean ± SD = 73.87 ± 4.00, range = 69-83; 23 female).

559

560   **MRI Data Acquisition**

561   MRI data were collected in Toronto, Ontario, Canada at York University using a Siemens Trio

562   3T scanner with a 32-channel head coil. For each participant, a high-resolution T1-weighted

563   anatomical scan was acquired (TR = 1.9 s, TE = 2.52 ms, 192 axial slices, slice thickness = 1

564   mm, field of view (FOV) = 256 mm, 256 x 256 acquisition matrix). After the anatomical scan,

565   participants completed two six-minute, multi-echo "resting-state" functional scans, wherein

566   participants were instructed to remain still in the scanner while visual maintaining fixation on a

567   cross (TR = 3 s, TE= 14 ms, 30 ms, 46 ms, flip angle = 83°, 43 axial slices, FOV = 216 mm,

568   voxel size = 3 mm isotropic).

569

570   **Voxel-Based Morphometry**

571   To assess differences in grey matter integrity, voxel-based morphometry (VBM) was conducted

572   using the FSL-VBM software suite (Douaud et al., 2007; Smith et al., 2004). T1-weighted

573   structural images were brain-extracted (BET) to remove skull. Next, tissue-type segmentation

574   was conducted (FAST4) to quantify grey matter density at the voxel-wise level across the whole

575   brain for each participant. Grey matter images were normalized to a study-specific grey matter

576   template through a two-step process. First, all grey matter volume images were non-linearly

577   aligned to the MNI_152 grey matter template and averaged to create a study specific grey matter

578   template; second, the native-space grey matter image for each participant was non-linearly

579   aligned to the study specific template (FNIRT). The registered grey matter images were

580   corrected for local expansion or contraction (caused by the non-linear component of the spatial

581   transformation) by dividing by the Jacobian of the warp field. The modulated images were then

582   smoothed with an isotropic Gaussian kernel of 3 mm full width at half maximum (FWHM).

583   Group differences in grey matter density were determined using voxel-wise t-tests (3dttest++) in

584   Analysis of Functional Neuroimages [AFNI (Cox, 1996)] with alpha < 0.05; correction for

585   multiple comparisons was done using the AFNI non-parametric equitable thresholding and

586   clustering (ETAC) method (Cox, 2019), with 10 voxel-wise p-thresholds ranging from $p = 0.01$

587   to $p = 0.001$. To calculate the correlation between second language proficiency and grey matter

588   density in the pCC across all participants (n = 93), a single significant cluster from the group

589   analysis was used as a ROI; mean grey matter probability across all voxels within this ROI was

590   calculated for each participant.

591

592   **fMRI Data Preprocessing**

593   Echo-planar images were preprocessed using the AFNI multi-echo independent component

594   analysis (ME-ICA) processing pipeline (DuPre et al., 2021; Kundu et al., 2013, 2012). For each

595   echo of both resting-state runs, any large transient spikes of activity were identified and removed

596   via interpolation (3dDespike). Data were then slice-time corrected (3dTshift) and aligned to the

597   initial volume (3dVolreg). ME-ICA (tedana) was conducted to further remove noise components

598   related to motion and physiological artifacts (Kundu et al., 2013, 2012). The combination of

599   multi-echo fMRI and ME-ICA has been shown to be more effective at removing spurious noise

600   sources than conventional methods (Power et al., 2018). This denoising technique leverages the

601   TE-dependence of the transverse relaxation rate, R_2^*; almost all fMRI signal, regardless of

602   origin, can be expressed as some combination of R_2^*, and initial signal intensity, S_0 (Wu and Li,

603   2005). All echoes are combined and analyzed using ICA to determine the degree to which

604   independent components were associated with R_2^* changes. Components highly associated with

605   R_2^* mechanisms were identified as BOLD signal components, whereas weakly associated

606   components were identified as noise and removed (Kundu et al., 2013, 2012) . The effectiveness

607   of ME-ICA denoising obviates the need for global signal regression (Spreng et al., 2019). Data

608   for each run were then smoothed with an isotropic Gaussian kernel of 6 mm FWHM

609   (3dBlurInMask) and mean-scaled. Finally, the 2 scaled runs were concatenated and transformed

610   into a study specific MNI_152-template space (@auto_tlrc).

611

612   **Resting-State Functional Connectivity**

613   Coordinates for all nodes of the DMN, FPC, and DAN were obtained from a previous study that

614   identified and characterized these network-nodes based on both task-related and resting-state

615   fMRI data; nodes were assigned network labels corresponding to their "rest network affiliation"

616   (Spreng et al., 2013). For each participant, nodes were defined by spherical regions of interest

617   (ROIs) with a radius of 6 mm centered on the *a priori* coordinates. To quantify resting-state

618   functional connectivity (RSFC), the mean BOLD signal time-series across all voxels within each

619   node was extracted and pairwise Pearson correlation coefficients were calculated for all node-

620   pairs and transformed to z-values using Fisher's r-to-z transformation. This yielded a 43 by 43

28

621 node-wise correlation matrix for each participant. Significant differences in RSFC between the

622 monolingual and bilingual groups were determined using permutation tests (1000 permutations)

623 for every node-pair and false discovery rate correction (threshold: $q < 0.05$, FDR corrected) for

624 multiple comparisons across the entire matrix.

625

626 **Graph Theoretic Analysis**

627 For each participant, a graph was constructed from the node-wise correlation matrix using the

628 GraphVar software suite (Kruschwitz et al., 2015). To account for potential threshold effects, we

629 calculated graph metrics across a series of network densities (density range = 0.22-0.4). Two

630 graph metrics were calculated and reported here: weighted local clustering coefficient and

631 betweenness centrality. The weighted clustering coefficient of a node quantifies how tightly

632 clustered a given node is with its immediate neighbours, while considering the weight of the

633 connections; it is calculated as the sum of the weights of all closed triplets centered on a node at

634 a given density, normalized by the sum of the weights of all possible triplets centered around that

635 node. The betweenness centrality of a node is the number of shortest paths between all possible

636 node-pairs that pass through the given node at a given density; betweenness centrality is a

637 measure of the extent to which a node contributes to communication across networks, and thus

638 can be used to identify main interconnector nodes (Rubinov and Sporns, 2010). Both metrics

639 were normalized by calculating the mean area under the curve across the range of densities.

640 Significant group differences were determined using permutation tests (1000 permutations).

641

642 **Brain-Behaviour Correlations**

29

643   Previous behavioural research has implicated the active use and proficiency of a second language

644   as the critical factor having a positive effect on cognitive reserve (Calabria et al., 2020). Second

645   language proficiency was previously quantified from the LSBQ. A factor analysis on all the

646   LSBQ items identified a latent variable with clustered items representing second language

647   proficiency. The eigenvalue from this factor was used as a subscale of the LSBQ to quantify the

648   active use and proficiency of a second language (John A. E. Anderson et al., 2018). To determine

649   if second language proficiency is related to structural and functional brain properties, we used

650   Pearson correlation to quantify the relationship between second language proficiency and each of

651   our brain measures across the entire group of 93 participants (age: mean $\pm$ SD $= 74.21 \pm 4.09$,

652   range $= 68\text{-}85$; 65 female). Second language proficiency was correlated with each of the

653   following brain measures: PCC grey matter density, mean RSFC between the aMFG and the 6

654   DMN nodes identified in the group comparison of the full correlation matrix (dmPFC, pCC, left

655   IPL, left SFG, left STS, and vmPFC), clustering coefficient of the aMFG with the entire DMN,

656   and betweenness centrality of the pMFG. The significance of the Pearson correlation was

657   determined using two-tailed tests at alpha < 0.05.

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985 **Supplementary Material**
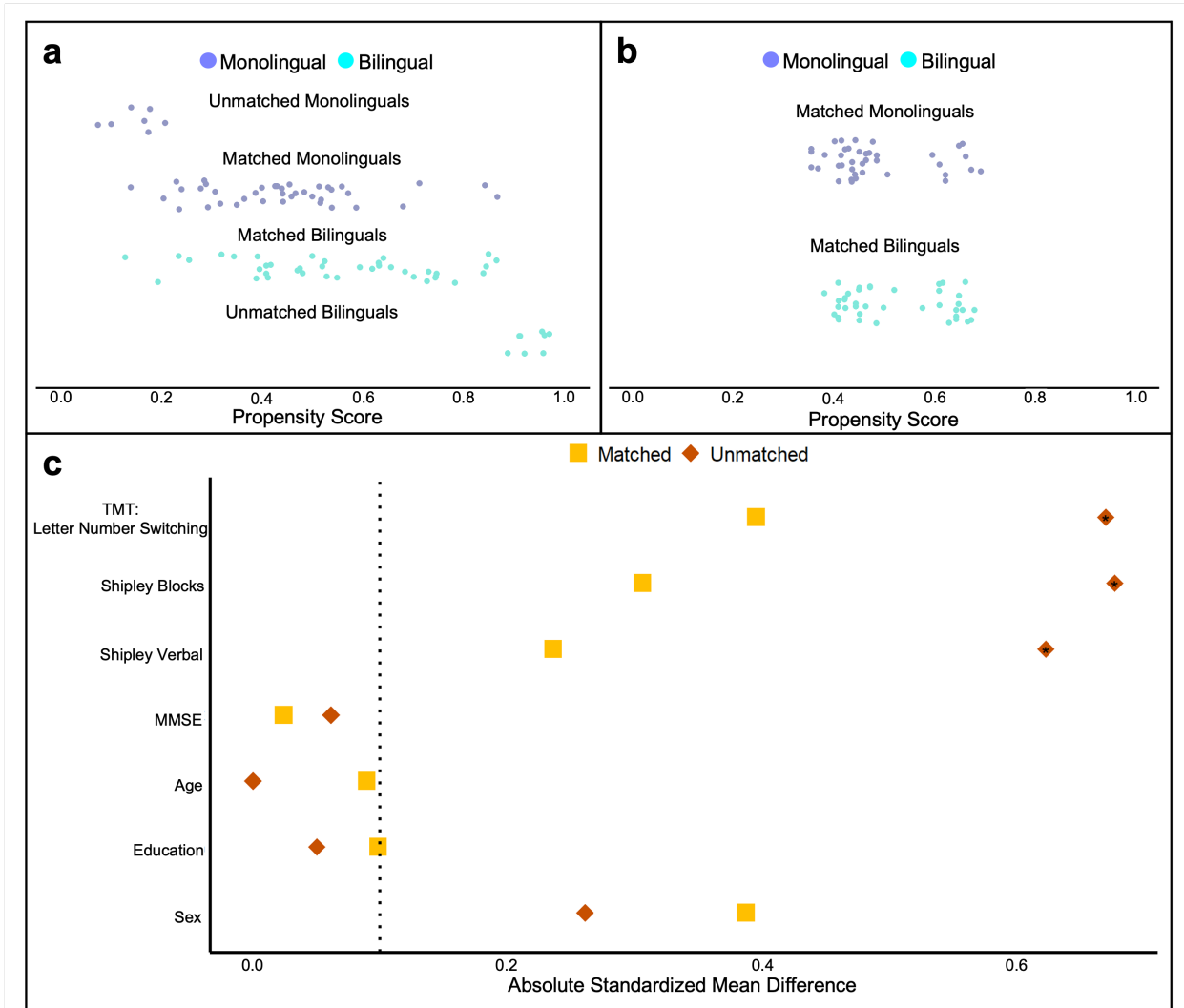
986
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988 **SupplementaryFigure 1:** Propensity score matching (PSM) of monolingual and bilingual
989 groups. (**a**) Distribution of propensity scores for the matched monolingual (n = 39) and bilingual
990 (n = 39) groups and excluded (unmatched) participants following PSM on cognitive measures.
991 (**b**) Distribution of propensity scores for the matched monolingual and bilingual groups
992 following PSM on demographic variables, which did not change group membership. (**c**)
993 Absolute standardized mean difference between monolinguals and bilinguals on each of the
994 cognitive and demographic variables for the matched and unmatched groups. Significant
995 differences (indicated by an asterisk) between the unmatched monolingual and bilingual groups
996 on three cognitive measures (TMT Letter Number Switching, Shipley Blocks, and Shipley
997 Verbal scores) were eliminated in the matched groups following PSM. TMT, Trail Making Task;
998 MMSE, Mini * p < 0.01
999
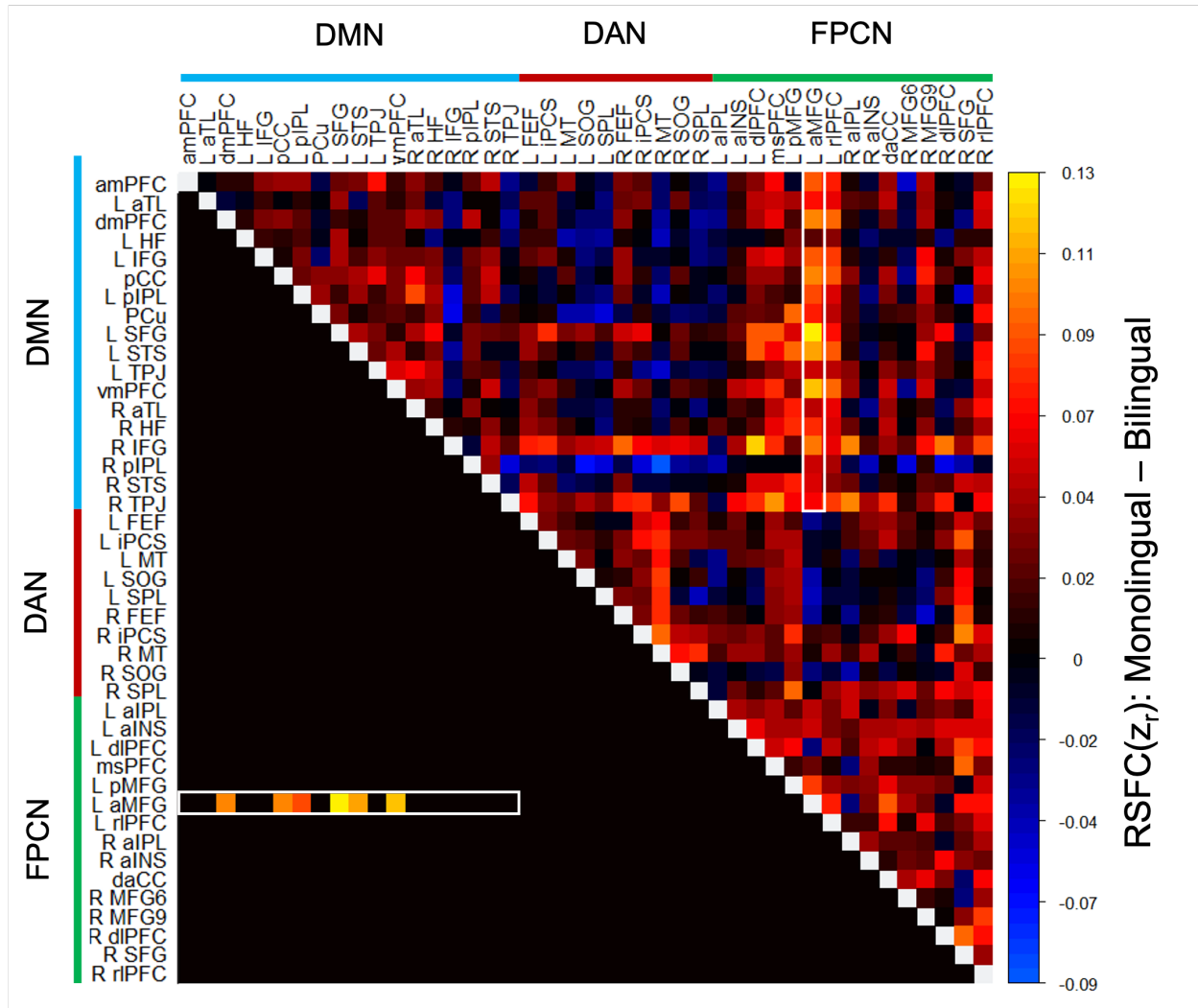
Supplementary Figure 2: Differences in RSFC within and between the DMN, DAN, and FPCN. Monolingual older adults show stronger RSFC of the left aMFG with multiple nodes of the DMN, relative to bilinguals. Full pairwise correlation matrix of all 43 nodes of the FPCN, DMN, and DAN: upper half of the matrix shows group differences (monolingual - bilingual) in mean RSFC for all pairwise correlations between nodes; lower half of the matrix shows only the statistically significant differences (permutation test: q < 0.05, FDR corrected). The left aMFG showed stronger RSFC with 6 nodes of the DMN: dmPFC*, pCC*, left IPL*, left SFG**, left STS*, and vmPFC*. RSFC, resting-state functional connectivity; z_r, Fisher z-transformed correlation; FPCN, frontoparietal control network; DMN, default mode network; DAN, dorsal attention network; for full list of all node label definitions, see Supplementary Table 1. * p < 0.002; ** p < 0.001

1013 Supplementary Table 1. List of all nodes of default mode network, dorsal attention network, and
1014 frontoparietal control network, and their abbreviations.

Region and Network Affiliation	Abbreviation	Coordinate (x y z)
Default Mode Network		
Left Hemisphere		
Anterior medial prefrontal cortex	amPFC	-8 56 14
Anterior temporal lobe	L aTL	-52 -10 -20
Dorsal medial prefrontal cortex	dmPFC	-8 50 34
Hippocampal formation	L HF	-26 -8 -24
Inferior frontal gyrus	L IFG	-42 26 -14
Posterior cingulate cortex	pCC	-2 -48 28
Posterior inferior parietal lobe	L pIPL	-50 -60 28
Precuneus	PCu	-2 -60 50
Superior frontal gyrus	L SFG	-8 20 62
Superior temporal sulcus	L STS	-60 -28 -4
Temporal parietal junction	L TPJ	-44 -52 22
Ventral medial prefrontal cortex	vmPFC	-2 44 -12
Right Hemisphere		
Anterior temporal lobe	R aTL	52 -4 -16
Hippocampal formation	R HF	24 -14 -22
Inferior frontal gyrus	R IFG	50 32 -6
Posterior inferior parietal lobe	R pIPL	58 -60 28
Superior temporal sulcus	R STS	50 -36 4
Temporal parietal junction	R TPJ	44 -58 18
Dorsal Attention Network		
Left Hemisphere		
Frontal Eye Fields	L FEF	-24 2 62
Inferior Precentral Sulcus	L iPCS	-36 0 28
Middle temporal motion complex	L MT	-44 -66 0
Superior occipital gyrus	L SOG	-18 -66 50
Superior parietal lobule	L SPL	-30 -48 52
Right Hemisphere		
Frontal Eye Fields	R FEF	24 -2 56
Inferior Precentral Sulcus	R iPCS	42 6 26
Middle temporal motion complex	R MT	54 -54 -6
Superior occipital gyrus	R SOG	26 -64 54
Superior parietal lobule	R SPL	38 -46 54
Frontoparietal Control Network		
Left Hemisphere		
Anterior inferior parietal lobule	L aIPL	-54 -48 48
Anterior insula	L aINS	-30 20 -2

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Dorsal lateral prefrontal cortex	L dlPFC	-38 32 30
Medial superior prefrontal cortex	msPFC	-2 20 50
Posterior middle frontal gyrus	L pMFG	-28 14 58
Anterior middle frontal gyrus	L aMFG	-40 24 34
Rostrolateral prefrontal cortex	L rlPFC	-32 58 2
Right Hemisphere		
Anterior inferior parietal lobule	R aIPL	50 -44 46
Anterior insula	R aINS	32 20 -4
Dorsal anterior cingulate cortex	daCC	6 30 40
Posterior middle frontal gyrus	R MFG6	26 16 48
Anterior middle frontal gyrus	R MFG9	44 26 42
Dorsal lateral prefrontal cortex	R dlPFC	44 42 26
Superior frontal gyrus	R SFG	12 18 62
Rostrolateral prefrontal cortex	R rlPFC	32 58 8

1015   R, right; L, left; Coordinate (x, y, z) are in MNI_152 space.