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Neuroplasticity and cognitive reserve effects in the Caudate Nucleus of young bilingual adults

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Abstract

This study investigates bilingualism-induced neuroplastic and cognitive-reserve effects in the Caudate Nucleus (CN), a structure believed to support both bilingual language control and domain-general executive functioning. We computed a generalized bilingualism index incorporating several dimensions of bilingual experience in a sample of bilingual young adults and tested whether this index would predict behavioral executive performance (measured using a Flanker task) and volumetric differences in the CN. Moreover, we investigated whether bilingualism mitigates the relationship between CN volume and executive performance, a sign of cognitive reserve. Our results indicate that bilingualism facilitates executive performance and induces an inverted U-shaped neuroplastic trajectory in bilateral CN, consistently with the view that structural increases are replaced by functional improvements as bilingual experience progresses. The emergence of bilingualism-induced cognitive reserve effects in CN further supports the view that bilinguals rely progressively less on the availability of structural resources in the face of increased functional efficiency.

1. Introduction

Widespread evidence indicates that, in a bilingual brain, both languages are constantly active, resulting in crosslinguistic interference during language processing (e.g., Kaushanskaya & Marian, 2007; Kroll et al., 2014). As a result, bilingual speakers must persistently resolve cross-linguistic conflict to achieve successful communication. This task is performed by a cognitive device termed LANGUAGE CONTROL (Abutalebi & Green, 2007; Green & Abutalebi, 2013), whose neural underpinnings overlap with the domain-general executive network (Abutalebi & Green, 2016). As a result of extensive training of these cognitive abilities and of the respective neural resources related to executive functioning, bilinguals are posited to experience neurocognitive executive benefits (e.g., Kroll et al., 2015). This hypothesis is confirmed by investigations reporting bilingualism-induced advantages in executive performance, as well as neuroplastic changes in the brain's executive network (for a review, see Bialystok et al., 2012).

The socio-economic potential offered by these findings is of particular importance. Bilingualism-induced neurocognitive changes have been shown to support the development of a capacity that has been termed (COGNITIVE) RESERVE, whose most widespread definition is that of a lifestyle-induced buffer against cognitive aging (Stern, 2009). Nevertheless, since its introduction, further developments in the understanding of the reserve concept have led to a more general definition of it as A DISCREPANCY BETWEEN EXPECTED AND OBSERVED COGNITIVE PERFORMANCE IN THE FACE OF A CERTAIN OBSERVED NEUROSTRUCTURAL STATUS (e.g., Gallo et al., 2021a; Reed et al., 2010; Zahodne et al., 2013). As a consequence of this more general view, it has become progressively clearer that reserve accrual originates during early life stages as a result of various practices, and that already young adults also display individual differences in reserve levels (Tucker & Stern, 2011). Accordingly, bilingualism is no exception among the lifestyle factors promoting reserve accrual in regards to the age when its effect begins to influence the neurocognitive system. Indeed, the neuroprotective effects, which reveal their full potential during later life stages, have been documented in bilinguals as early as at 18 years of age (Gallo et al., 2021b).

Identifying practices that might potentially help mitigate detrimental effects of cognitive aging is an important issue for the modern days' rapidly aging society (Kontis et al., 2017), which allocates disproportionate amounts of public health funds to senior citizens' healthcare (Prince et al., 2016; Wimo et al., 2017) whilst conventional healthcare solutions to the aging problem as such are not available (Dyer et al., 2018).

1.1 Bilingual experience and the Caudate Nucleus

Several studies indicate that the CAUDATE NUCLEUS (CN) is one of the brain structures involved in bilingual language control. The Adaptive Control hypothesis (Green & Abutalebi, 2013), arguably the most popular account of neural mechanism of bilingual language control, attributes a specific role in language control ability to the left CN. Supporting this claim, several studies have reported left CN engagement in various aspects of language control including translation (e.g., Lehtonen et al., 2005), language selection (e.g., Branzi et al., 2016), and language switching (e.g., Abutalebi et al., 2013). Although the evidence is more scarce for right CN, its activity has also been linked to language switching (Ma et al., 2014) and simultaneous interpretation (Hervais-Adelman et al., 2015). Moreover, bilingualism-induced neuroplastic changes have been shown for the CN bilaterally (e.g,, Burgaleta et al., 2016; DeLuca et al., 2019b; Pliatsikas et al., 2017; Zou et al., 2012). These findings are in line with the notion that the CN, among other cognitive functions, plays an important role in executive functioning in general. Specifically, the CN has been shown to contribute to tasks that span from working memory (Cools & D'Esposito, 2011) to regulation of goal-directed behavior through the selection of appropriate action schemas and sub-goals following the evaluation of the action-outcome relationship (Grahn et al., 2008). Moreover, CN atrophy has been related to the so-called dysexecutive syndrome, i.e., an impairment of attentional and mnemonic executive abilities, supporting the argument of its key role in the frontostriatal executive circuit (Macfarlane et al., 2013).

Coming back to bilingual language control, the CN seems to play a peculiar role among areas of the language control network, lying at the intersection of cortical and subcortical areas, as we detail below. The CN is implicated in two main theoretical accounts modeling the underlying mechanisms of bilingualism-induced neuroplastic trajectories and consequent cognitive benefits – namely, the BILINGUAL ANTERIOR-TO-POSTERIOR AND SUBCORTICAL SHIFT (BAPSS; Grundy et al., 2017) and the DYNAMIC RESTRUCTURING MODEL (DRM; Pliatsikas, 2020). The BAPSS model posits that increasing bilingual experience leads to improvements in the efficiency and automatization of language control and thus of executive functioning. This in turn results in a shift of the site of bilinguals' executive-related neural activation from frontal to posterior cortical and to subcortical brain regions. In the BAPSS, the CN is argued to behave similarly to all other subcortical structures involved, which are increasingly relied on by bilinguals to perform executive tasks. In turn, the DRM models the trajectory of neurostructural changes associated with increasing bilingual experience. Interestingly, for all subcortical structures involved in bilingual language control, except the CN, the DRM posits a steady volumetric increase associated with increasing bilingual experience.

Similarly to BAPSS, this feature reflects the brain's augmented reliance on these structures for language/executive control. For the CN, however, the structural neuroplastic trajectory predicted by the DRM is different from those of other subcortical structures. The CN would increase in volume at INITIAL stages of second language (L2) acquisition in order to cope with cognitive demands associated with the novel task of language control. This novel cognitive demand would induce the CN to undergo structural changes via the formation of new synaptic connections. Subsequently, increasing bilingual experience would lead to an increase of CN's functional efficiency. This increased functional efficiency, in turn, renders the previously accumulated "extra" structural resources no longer necessary for optimized language control. At this stage, surplus connections would thus be eliminated via SYNAPTIC PRUNING. In line with theories of synaptic reorganization (see e.g., Lövdén et al., 2013), only the most efficient synaptic connections are maintained during the pruning phase. This process would cause CN's structural substrate to return to pre-bilingualism levels in gross volumetric terms, while its enhanced synaptic connectivity has been reorganized towards higher efficiency. The DRM bases this claim on existing evidence of expansion-renormalization of CN volume (Burgaleta et al., 2016; DeLuca et al., 2019b; Pliatsikas et al., 2017; Zou et al., 2012). The increased efficiency resulting from this structural and functional reorganization (in the CN as well as in other cortical and subcortical structures of the language control network) is argued by the DRM to underlie the neuroprotective effects observed in senior bilinguals.

The DRM predicts a similar structural renormalization trajectory for all the CORTICAL language control areas, but not for other subcortical structures except the CN. The reason behind these different predictions would be that other subcortical structures (i.e., putamen, globus pallidus, thalamus) are involved in more motor-related aspects of language control, i.e., articulation and learning of motor programs related to foreign language production. They would thus follow a somewhat different learning (and thus neuroplastic) trajectory, with these latter abilities becoming more relevant at a later stage of L2 mastery. Thus, the CN's role in bilingual language control seems to lie in-between that of cortical (DRM) and subcortical (BAPSS) regions. This view of the CN as a sort of interface between cortical and subcortical language control areas well reflects its role in domain-general executive control, which is exerted via regulating dopamine release towards prefrontal areas (e.g., Badgaiyan & Wack, 2011). As such, the CN can in principle be viewed as a relay structure between the subcortical and the cortical architecture of the executive network.

To our knowledge, only two studies have previously investigated both neuroplastic and cognitive reserve effects of bilingualism on the CN at once. The first was by Del Maschio et al. (2018), who found no differences in bilateral gray matter volumes (GMVs) of the CN between bilinguals and monolinguals across young (aged 18-35 years) and senior (aged 60 years and above) age groups while, at the same time, registering a bilingualism-related cognitive reserve effect in the left CN. Specifically, senior bilinguals' executive performance on a Flanker task was optimized irrespectively of volumetric variations in the left CN, while the performance of senior monolinguals was related to GMV variations in the region. According to the cognitive reserve theory (Stern et al., 2020), this effect is supported by an increase in functional efficiency enabling the individual to cope with neural atrophy in a given brain network or area, in this case the left CN. This results in an observed mitigation of the relationship between brain structure and the corresponding cognitive performance. Similarly, the second such study found no relationship between bilingual experience and neuroplastic changes in the bilateral CN, while an effect of bilingualism on cognitive reserve development in the left CN emerged, this time in a sample of young adults aged 18-35 years (Gallo et al., 2021b). Thus, the available evidence from studies involving both young and senior bilinguals appears to suggest that the structural and functional modifications posited by the DRM may constitute the underlying mechanism for bilingualism-related cognitive reserve accrual.

1.2 The present study

The present study is motivated by the theoretically-driven need to test the DRM and BAPSS predictions for the CN by combining neuroimaging investigations with behavioral data analyses. By doing this, we also aim to further explore the mechanisms behind the emergence of cognitive reserve effects in bilinguals' CN in the apparent absence of bilingualism-induced volumetric changes, as reported in Del Maschio et al. (2018) and Gallo et al. (2021b) studies mentioned above. Following the DRM logic, for the former study we hypothesize that renormalization to pre-bilingualism volumes of the CN may have already taken place in the sample of lifelong bilinguals, thus explaining the absence of differences between linguistic groups. As per the latter study, we believe the reason for not observing a relationship between bilingual experience and volumetric variations in the CN might be that the authors did not directly test a polynomial relationship, namely the inverted U-shaped trajectory posited by the DRM. Rather, they focused on linear interactions between different sub-aspects of bilingual experience.

To tackle these issues and answer our research questions, here we used structural equation modeling to compute a comprehensive index incorporating several dimensions of bilingual experience. Deriving a single, individual and continuous measure enabled us to test curvilinear relationships between bilingual experience and volumetric changes in the CN. Showing a neuroplastic trajectory that increases, peaks, and renormalizes with increasing bilingual experience would provide direct support to the DRM's assumptions, although in a cross-sectional design (see the Discussion section for more details). We also attempted to replicate findings suggesting that (i) increasing bilingual experience benefits executive performance as measured by the Flanker task (Fan et al., 2002) and (ii) bilingualism supports the development of cognitive reserve in young adults, namely by mitigating the relationship between variations in CN volume and executive performance.

2. Materials and methods

2.1 Participants

Forty bilingual participants (L1: Russian, L2: English; mean age = 21.93, SD ± 2.75; 10 males) were recruited from the population of the HSE University students. All participants were right-handed, as confirmed by the Edinburgh Handedness Inventory scale (Oldfield, 1971), and had no psychiatric or neurological impairments. Individual socio-demographic profiles for age, educational attainment, and socio-economic status (SES) were assessed with the MacArthur Scale of Subjective Social Status (MacArthur Foundation, 2007). Annual household income bands used as a proxy of SES were adapted to local standards based on the European Social Survey 2020 (ESS Round 10: European Social Survey Round 10 Data, 2020). We also assessed participants' general intelligence via a subset of the Raven's Standard Progressive Matrices for adults (Court & Raven, 1992). Demographics and language background characteristics of the study sample are presented in Table 1. The study was approved by the local research ethics committee, and all participants gave their written informed consent.

2.2 Individual profiles of bilingual experience

We used the Russian version of the Language Experience and Proficiency Questionnaire (LEAP-Q; Marian et al., 2007) to assess several dimensions of individual bilingual experience including self-rated L2 proficiency and L2 exposure in various modalities (i.e., writing, reading, speaking, listening) and L2 age of acquisition (AoA). Moreover, we collected objective measures of L2 proficiency via the Cambridge test for adult learners (http://www.cambridgeenglish.org/test-your-english/general-english/) and a custom-made translation task including 42 Russian-to-English entries and 42 English-to-Russian entries. In the translation task, participants were presented with words of three frequency levels (low, medium, high), calculated using the Russian National Corpus (https://ruscorpora.ru/en/) and the Subtlex-UK corpus (van Heuven et al., 2014), respectively, and had to provide what they considered to be the best translation for each entry.

Table 1. Demographic and language background characteristics of the study sample

	Mean	SD	Range
Age	21.93	2.75	18-29
Education Years	14.88	1.96	11-18
SES	5.90	1.41	3-9
Raven's Matrices Score	14.68	0.53	13-15
L2 Age of Acquisition	7.98	3.03	4-16
L2 Speaking Subjective Proficiency	6.53	1.48	3-10
L2 Writing Subjective Proficiency	6.60	1.41	3-9
L2 Reading Subjective Proficiency	7.58	1.47	4-10
L2 Speaking Exposure	8.30	7.35	0-30
L2 Writing Exposure	10.88	11.38	0-50
L2 Listening Exposure	42.25	28.24	0-99
L2 Reading Exposure	32.25	22.56	0-90
Cambridge Test Score	18.30	4.12	11-25
L2-L1 Translation Score	24.30	6.51	14-38
L1-L2 Translation Score	18.10	4.28	11-26

2.3 Executive performance assessment

To measure their executive performance, participants underwent the Flanker task within the standard ANT set-up (Fan et al., 2002). In this task, a fixation cross appeared for 400 ms at the center of the screen, followed by an array of five arrows pointing to the left or to the right for a maximum duration of 1700 ms. Participants had to detect the direction of the central target arrow as accurately and as fast as possible by pressing the designated arrow key on the PC keyboard. The task included three conditions: congruent, where the target arrow is flanked by arrows pointing to the same direction (→→→→→); incongruent, where target and flankers point to opposite directions (←←→←←); and neutral, where the target is flanked by uninformative dashes rather than arrows (– – → – –). Incongruent trials require interference suppression to override prepotent incorrect responses, which typically entails lower accuracy and longer RT in responses. Prior to the task, participants underwent a practice run of 24 pseudo-randomized trials. Subsequently, two pseudo-randomized runs of 96 trials each (32 per each condition) were presented.

The Flanker Task is a benchmark in executive functioning assessment. The reason for selecting this task is two-fold. First, as mentioned above, one of our aims was to further expand previous findings from studies with a similar design (Del Maschio et al., 2018; Gallo et al., 2021b). Since issues with cross-task correlations have been previously raised in the field (Paap & Sawi, 2014), we kept the executive task constant with the previous investigations in question, for replicability purposes. Second, and more important, the Flanker task is one of the few tasks whereby the structural brain-behavior (SBB) relationship has proven to be valid, especially in young populations (Boekel et al., 2015). Given that our cognitive reserve analysis (detailed below) consisted in testing the potential modulation of the expected SBB relationship between CN and executive performance by bilingualism it was of crucial importance to choose a task that is known to follow this relationship in the first place.

2.4 MRI data acquisition and preprocessing

A Philips Intera 1.5T MRI scanner was used to acquire T1-weighted images with the following parameters: TR = 25 ms, TE = 4.6 ms; flip angle = 30, FOV = 240 × 240, resolution = 1 × 1×1 mm, matrix = 256, TA = 5.35 min, mode = 3DFFE, number of slices = 191. We used region-based morphometry in CAT12 (Computational Anatomy Toolbox, https://neuro-jena.github.io/cat/) within SPM12 (Statistical Parametric Mapping, https://www.fil.ion.ucl.ac.uk/spm/) to extrapolate the total amount of GMV in atlas-based regions of interest (ROIs) for the bilateral CN. First, we visually inspected images to check for gross field distortions and movement artifacts; no participants were discarded for this reason. We then manually set the origin for each image to correspond to the anterior commissure – posterior commissure (AC-PC) line. Subsequently, we followed a two-step procedure for GMV extraction:

i) Raw structural images were segmented into different tissue classes – gray matter (GM), white matter (WM), and cerebrospinal fluid (CSF) – via CAT12 segmentation routine. This routine utilizes an adaptive Maximum A Posterior (aMAP) technique that reduces the need for a priori information about tissue probabilities (Rajapakse et al., 1997) and accounts for local variations and inhomogeneities of GM intensity (Dahnke et al., 2012). After the aMAP segmentation, CAT12 also performs a Partial Volume Estimation (PVE) of mixed tissue-classes (GM-WM and GM-CSF; Tohka et al., 2004) resulting in a higher segmentation accuracy via estimations of the percentage of pure tissue of each type within each voxel. Segmentation was further improved via a spatial-adaptive non-local means (SANLM) denoising filter in a pre-segmentation step (Manjón et al., 2010). After segmentation, each brain was co-registered to the ICBM (International Consortium for Brain Mapping) European brain space template via the affine regularization option.

ii) GMV values were extracted from bilateral ROIs in the CN via an in-built CAT12 function that allows for GMV estimation in non-normalized native space using maximum tissue probability labels derived from the Neuromorphometrics Atlas (http://www.neuromorphometrics.com/). Participants' total intracranial volume (TIV) was extracted by summing native space global volumes of GM, WM and CSF to control for individual differences in brain size.

2.5 Procedure

Participants were tested at the experimental facilities of the Institute for Cognitive Neuroscience, HSE University. The testing procedure was as follows. Participants were first instructed on the experimental procedure, and they signed an informed consent. They then were seated in an electrically shielded and acoustically dampened chamber. All questionnaires and tasks were presented on a 75 cm-diagonal computer screen. First, participants underwent Raven's Standard Progressive Matrices and filled out the LEAP-Q, which were presented using Google Forms. Subsequently, they performed the Flanker task, which was presented via OpenSesame (v. 3.3.7). Finally, the Cambridge test for adult learners and the translation task were presented to participants also via Google Forms. All tasks were performed in the same experimental session, which lasted around 60 minutes. MRI acquisition was performed on a separate day in a specialized MRI center in Moscow using a clinical-grade Philips Intera scanner (see above).

2.6 Statistical analyses

We used structural equation modeling in order to combine information from different sub-dimensions of bilingual experience and obtain a single, continuous, and individual index of bilingualism. The model included a 2-level hierarchical structure with first-level latent variables computed for L2 exposure, subjective and objective L2 proficiency. In turn, these latent variables, together with L2 AoA, informed a higher-level latent factor, the comprehensive bilingual index. The reason behind the choice of a hierarchical SEM structure is the following: the L2 AoA variable is informed by a single score (i.e., the answer to the question "How old were you when you began understanding/speaking English?") rather than multiple scores or answers as in the case of L2 exposure and subjective/objective L2 proficiency. Thus, had we not grouped observables informing the other bilingual experience factors and adopted a hierarchical structure, the contribution of AoA to the BI could have been obscured among the contributions of the multiple lower-level observables that inform exposure, objective and subjective proficiency. By selecting this hierarchical structure, we constrained the model to consider the weight of AoA on the latent Bilingual Index as comparable to those of the other three bilingual experience factors.

Maximum likelihood estimation was used to estimate the model. Model fit was assessed using conventional criteria and omitted paths were explored using modification indices. The final model fit to the data was acceptable (CFI = 0.946; TLI = 0.922; RMSEA = 0.09). The model is presented in Figure 1. Individual predicted values of the latent bilingual index were extracted. The resulting variable was normally distributed with a mean of 0 (range: -1.64, 1.53).

As for the Flanker data, neutral, incorrect and false start (RT < 100 ms) trials were removed, as well as outlier trials displaying RTs beyond 3 SDs from individual mean RT values (Baayen & Milin, 2010). This data pre-processing procedure resulted in discarding 1.13% of the total data.

All statistical analyses were conducted using Stata 17 (StataCorp, 2021).

The contribution of bilingual experience to executive performance

To assess whether bilingual experience affects executive performance, we used linear mixed regressions with a trial-by-trial approach, which enabled us to increase the number of the data points per participant from 2 (one average for incongruent trials, one for congruent trials) to 128 (one per each trial). At the same time, it entails the impossibility to calculate a Flanker effect in the traditional way (i.e., the difference between average incongruent RTs and congruent RTs). To overcome this issue, we inserted

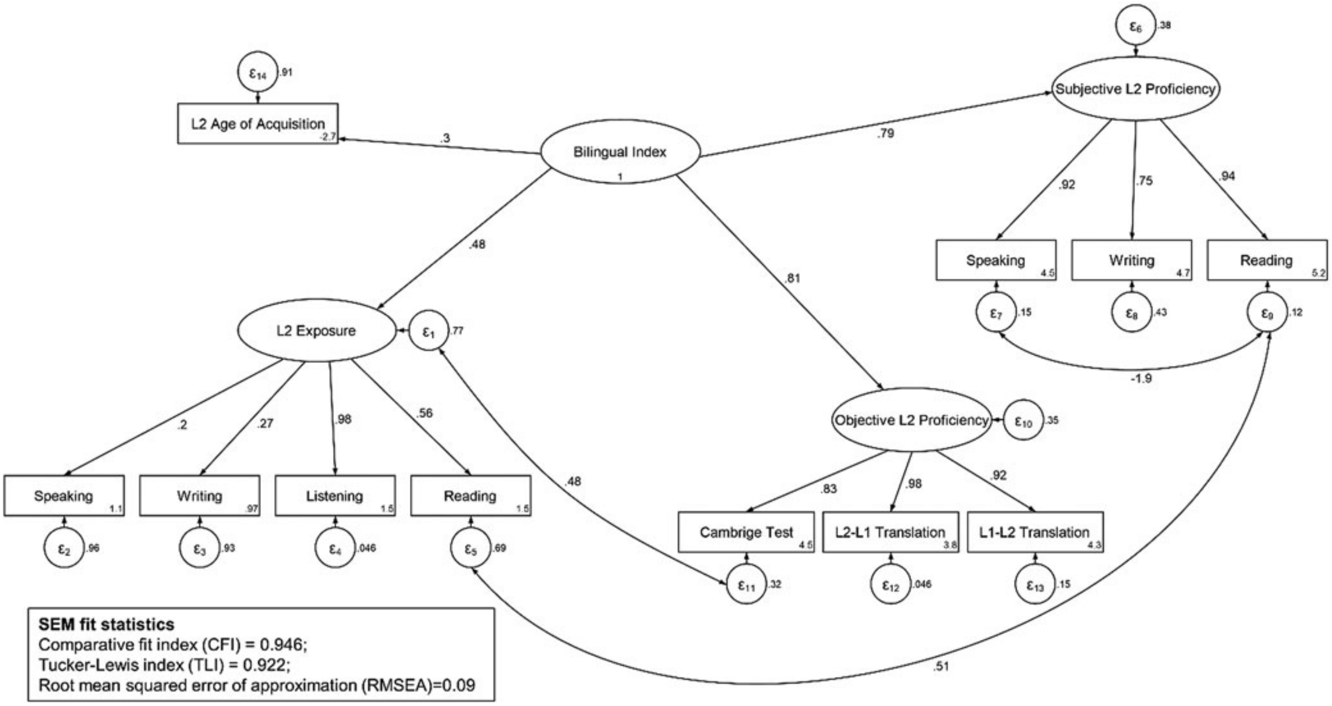

Figure 1. Standardized estimates from the best-fitting structural equation model for the bilingual index latent variable.

an interaction term for trial type (congruent vs. incongruent) in all our models including Flanker data. Hence, our model included: (1) Flanker RTs as the dependent variable, (2) main effects of task condition (congruent vs. incongruent) and bilingual index, as well as their interaction, as predictors, and (3) covariates for age, sex, general intelligence, SES and maximal educational attainment, all factors known to affect executive performance. The model also included random intercepts for participants and random slopes for trials. Accuracy was not analyzed since it was at near-ceiling levels (average score = 97.3%), which is typical for the Flanker task performance in young adults (Hooper et al., 2022; McMorris & Hale, 2012).

The inverted U-shaped relationship between bilingual experience and the Caudate Nuclei

To test the relationship between variations in bilingual experience and neuroplastic changes in the bilateral CN, we ran two linear regressions (one per hemisphere) with GMV of the left or right CN as the dependent variables, bilingual index as the main predictor and covariates for TIV, age, sex, general intelligence, SES and maximal educational attainment. To investigate the presence of curvilinear relationships between bilingual experience and GMV of the CN, we inserted an interaction of bilingual index with itself, forcing the model to consider bilingual index also as a quadratic term.

Bilingualism-induced cognitive reserve effects in the Caudate Nuclei

To test whether bilingualism fosters cognitive reserve effects, we examined whether increasing levels of bilingual experience progressively mitigated the structural brain-behavior relationship between the CN and Flanker performance. To this end, we fitted two linear-mixed regressions with Flanker RTs as the dependent variable, a full-factorial structure (i.e., all main effects + all interactions) including task condition, bilingual index and left and right CN, respectively, as predictors, covariates for age, sex, general intelligence, SES and maximal educational attainment, random intercepts for participants and random slopes for trials.

3. Results

3.1 The contribution of bilingual experience to executive performance

The linear mixed regression model revealed a significant interaction between task condition and bilingual index (β=4.294; p = 0.036), indicating that bilingual experience differentially affected Flanker RTs in the two conditions. The interaction plot revealed a beneficial effect of bilingual index on Flanker performance in both conditions, with the facilitation being slightly stronger for congruent trials (see Figure 2).

3.2 The inverted U-shaped relationship between bilingual experience and the Caudate Nuclei

Both linear regression models revealed a significant effect of the quadratic term for bilingual index on CN GMVs bilaterally (left CN: β= -0.35; p = 0.002; right CN: β= -0.253; p = 0.043), but no effect of the linear term, confirming our prediction regarding a curvilinear pattern of the relationship between bilingual experience and neuroplastic changes in the CN. Regression plots confirmed that the relationship followed an inverted-U shape (see Figure 3), in line with predictions by the DRM account.

3.3 Bilingualism-induced cognitive reserve effects in the Caudate Nuclei

The model for the right CN revealed no significant three-way interaction between task condition, bilingual index and GMV

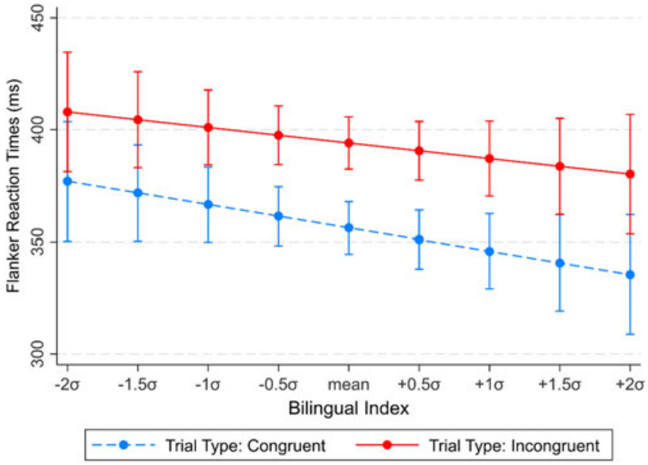

Figure 2. Interaction plot for the bilingual index*task condition interaction predicting Flanker RTs (in ms). Increasing levels of bilingual index predict lower RTs, i.e., better performance, in both congruent and incongruent trials.

on Flanker RTs. A significant three-way interaction emerged, however, for the left CN model (β= -10.85; $p = 0.023$). The interaction plot revealed that increasing bilingual index levels progressively mitigated the structural brain-behavior relationship between the left CN and Flanker performance in incongruent trials. Combined with previous results (see Introduction) and the present sample age, this indicates that bilingualism-induced cognitive reserve-like effects might develop already in young adulthood (see Figure 4).

4. Discussion

This study investigated bilingualism-related neuroplastic and cognitive reserve effects in the CN, a structure responsible for both bilingual language control and domain-general executive functioning. The CN lies at the crossroads of two important theoretical models of the neurocognitive consequences of bilingualism – the DRM (Pliatsikas, 2020) and the BAPSS (Grundy et al., 2017). On the one hand, we directly tested the DRM's

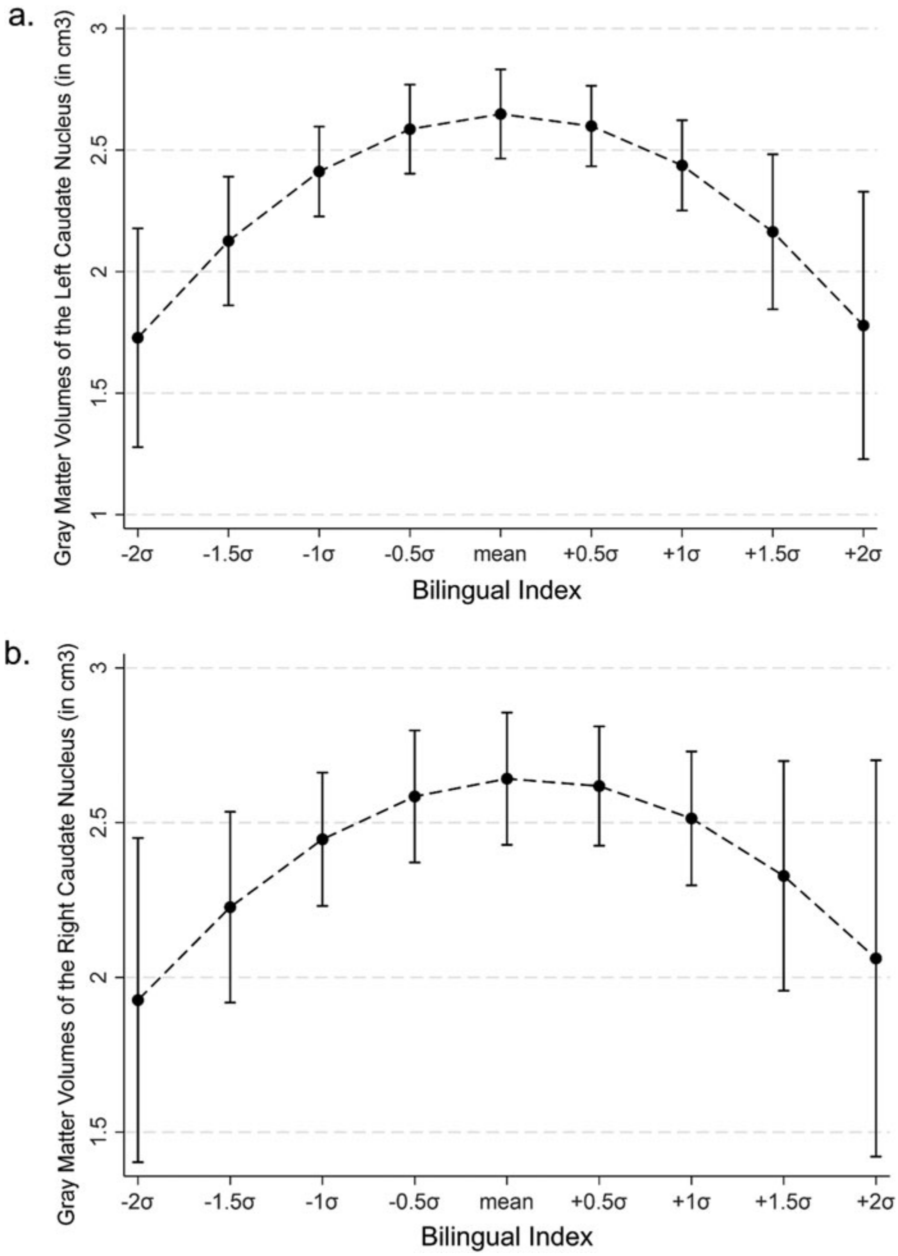

Figure 3. Gray matter volumes (GMVs; in cm3) of the left (3a) and right (3b) Caudate Nuclei predicted by variations in bilingual experience. The relationship between bilingual experience and Caudate GMVs follows an inverted U-shaped curve.

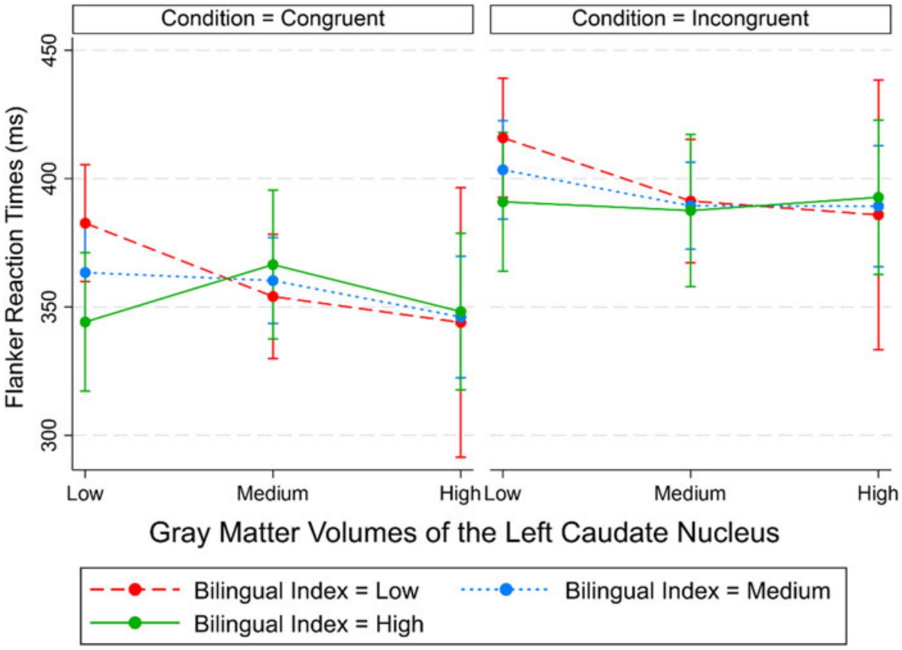

Figure 4. Interaction plot for the bilingual index*task condition*left CN GMV interaction predicting Flanker RTs (in ms). For increasing levels of bilingual experience, the impact of left Caudate volumes on executive performance is progressively mitigated. For plotting purposes, the three levels of left Caudate GMV, i.e., low, medium and high, represent the 33rd, 66th, and 99th percentile of the sample distribution, respectively; the three levels of bilingual index, i.e., low, medium and high, represent 1σ below the mean value, mean value, and 1σ above the mean value, respectively.

assumption that bilingual experience induces an inverted U-shaped neuroplastic trajectory in the CN. This trajectory is explained by an initial volumetric increase, which is believed to be necessary to cope with novel language control cognitive demands, but is later followed by a structural renormalization backed by steady functional enhancements and the consequential pruning of surplus structural resources in the CN. On the other hand, we tested the BAPSS's prediction, consequential to DRM's assumptions, that the hypothesized functional enhancements in the CN should trigger cognitive reserve effects. These effects would allow bilinguals to automatize executive control and shift its activation locus towards posterior and subcortical areas due to their increased functional efficiency. To test for the presence of bilingualism-related cognitive reserve effects in the CN, we investigated whether increasing levels of bilingual experience progressively modulated the relationship between CN volumes and cognitive performance, following from the definition of cognitive reserve as the discrepancy between *expected* and *observed* cognitive performance levels given the level of *observed* neural status (Stern et al., 2020).

Our first finding is that increasing bilingual experience is related to improved executive performance as measured by the Flanker task. Interestingly, we observed benefits both in the congruent and incongruent conditions, suggesting that bilingualism-induced effects on cognition might span beyond simple inhibitory control. If that were the case, the facilitation effects should have only emerged in incongruent trials, commonly linked to inhibition. In fact, evidence of a "generalized" beneficial effect of bilingualism on congruent and incongruent trials of executive tasks is widespread in the literature (see Hilchey & Klein, 2011). This observation has recently led Bialystok and colleagues (Bialystok, 2017; Bialystok & Craik, 2022) to reconsider the long-standing argument that the consequences of bilingualism for cognition would be mediated primarily by inhibitory control. Instead, based on the available evidence they suggested that a more accurate argument would be that bilingualism benefits a broader mechanism of ATTENTIONAL CONTROL by making the corresponding processes both more powerful and more flexible. In other words, enhancements in attentional control would result in a generalized improvement in the allocation of processing resources (Bialystok & Craik, 2022). Our findings lend support to this view.

Our second finding relates to the hypothesis regarding the relationship between bilingual experience and neuroplastic changes in the CN. For a long time, the absence of brain volume differences between bilinguals and monolinguals has been interpreted as evidence against bilingualism-induced neuroplastic effects. The DRM account challenges this view based on the evidence of expansion-renormalization of CN volume (Burgaleta et al., 2016; DeLuca et al., 2019b; Pliatsikas et al., 2017; Zou et al., 2012). Importantly, reports providing such evidence also include a longitudinal study showing reductions in the left CN of immersed bilinguals over a three-year span (DeLuca et al., 2019b). Direct evidence for nonlinear neuroplastic trajectories in bilingual language control areas is still scarce. To the best of our knowledge, there are only two such studies. The first investigation is a report by Korenar et al. (2023), who observed nonlinear neuroplastic trajectories in the bilateral CN of bilingual young adults by employing generalized additive mixed models (GAMMs). This finding is in line with DRM's assumptions. The second investigation (Marin-Marin, et al., 2022) also used GAMMs, and it revealed nonlinear volumetric changes in the bilateral inferior frontal gyrus of bilingual young adults, providing further support to DRM's predictions. Importantly, our study offers direct empirical support to the argument of curvilinear bilingualism-induced neuroplastic trajectories (although only in a cross-sectional design – a limitation that should be addressed in future longitudinal studies, as discussed below). To the best of our knowledge, it is also the first investigation to test experimentally the relationship between such trajectories and behavioral outcomes.

In line with the DRM, we hypothesize the following sequence of events to underlie the inverted U-shaped neuroplastic trajectory emerging here:

(i) The novel cognitive burden imposed by language control demands during initial stages of L2 acquisition induces the brain to implement structural changes in the white and gray matter substrates via SYNAPTOGENESIS, i.e., the formation of new synaptic connections.

(ii) Progressive bilingual experience subsequently triggers increases in the functional efficiency of this rewired language control network.

(iii) As the functional efficiency is enhanced, the "additional" structural brain resources may no longer be necessary in the same amount for optimized language control, and surplus connections are eliminated via synaptic pruning, which, in turn, becomes manifest in measurable volumetric decreases. In alignment with existing theories of synaptic reorganization (see e.g., Lövdén et al., 2013), only the most efficient synaptic connections survive the pruning phase.

(iv) As a result of this process, bilinguals' executive network connectivity is reorganized towards higher efficiency levels with the total volume returning to near-original level.

This structural and functional reorganization is of great relevance as this increased efficiency is thought not only to enable better functioning of a bilingual's cognitive system as such, but also to underlie the neuroprotective effects observed later in life, in senior bilinguals. To reinforce this assumption, we tested the hypothesis that this neuroplastic trajectory would lead to cognitive reserve effects in bilingual speakers. We expected highly expert bilinguals, who stand at the more advanced end of the trajectory, to exhibit diminished reliance on structural resources in the CN for executive performance, based on the assumption that their functional efficiency in this region should be near its peak level. Our results confirmed this hypothesis by showing that increasing levels of bilingual experience progressively modulated the relationship between CN's GMVs and Flanker performance. Nonetheless, this result emerged only for the left CN. This is well aligned with the existing literature, where the role of the right CN for language control remains unclear. For instance, arguably the most influential model of neural underpinnings of bilingual language control, the adaptive control hypothesis (Green & Abutalebi, 2013), does not discuss any role of the right CN in language control. Our results are in line with the existing literature showing bilingualism-induced neuroplastic effects on the right CN (Burgaleta et al., 2016; DeLuca et al., 2019a; Pliatsikas et al., 2017), with no cognitive reserve effects registered for this area (Del Maschio et al., 2018).

One limitation of the present study that needs to be noted is its cross-sectional design. Future research will be required to use longitudinal designs to further confirm our findings, especially since the purported trajectories unfold over time. We also invite the reader to be aware, when interpreting our results, that the use of SEM with relatively small sample sizes should be treated with extreme caution (see e.g., Anderson & Gerbing, 1988). Nonetheless, recent accounts increasingly advocate a case-by-case evaluation of the required sample size for SEM estimation rather than a reliance on general rules of thumb (see e.g., Wang & Rhemtulla, 2021). Similarly, recent investigations deploying Monte Carlo simulations have shown satisfactory model fit for similar SEMs to the one estimated in the present study, with similar sample sizes (e.g., Sideridis et al., 2014). All in all, future studies on the issue should strive to acquire longitudinal structural, functional and behavioral data in large cohorts of participants.

A further future direction might be to incorporate a measure of language entropy in our index of bilingual experience. Language entropy describes the social diversity of language use within and across bilingual communicative contexts (Gullifer & Titone, 2020). Higher language entropy represents higher diversity in language use, namely the degree of predictability of each language being used in an individual's environment. In highly integrated contexts where two or more languages are used in relative balance, the executive network is expected to undergo further increased cognitive burden, which would result in further effects observable both at the behavioral and neural levels. Several recent studies have reported that greater language diversity enhances proactive control processes (e.g., Beatty-Martínez et al., 2020) and specialization and segregation of the default mode and executive control networks (Li et al., 2021).

5. Conclusions

The results reported in this study improve our understanding of the neurocognitive implications of bilingualism. They suggest neurophysiological mechanisms that underpin bilingualism-induced benefits for cognition, which may have a significant socio-economic potential in terms of promoting healthy cognitive aging. This investigation corroborates previously suggested prodromal cognitive reserve effects in young adult bilinguals, and it is among the few reports that have shown such effects in younger populations in general. The finding that benefits of bilingualism for cognitive aging are likely rooted in early life stages may inform interventions policies and, if confirmed by future investigations, hold valuable potential for both individuals and governments.

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