

# Bilingual experiences induce dynamic structural changes to basal ganglia and the thalamus

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## Article

### Keywords:

**Posted Date:** December 13th, 2021

**DOI:** <https://doi.org/10.21203/rs.3.rs-1017465/v1>

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# Abstract

Bilingualism has been linked to structural adaptations of subcortical brain regions that are important nodes in controlling of multiple languages. However, research on the location and extent of these adaptations has yielded variable patterns. Existing literature on bilingualism-induced brain adaptations has so far largely overseen evidence from other domains that experience-based structural neuroplasticity often triggers non-linear adaptations which follow expansion-renormalisation trajectories. Here we use generalised additive mixed models (GAMMs) to investigate the non-linear effects of quantified bilingual experiences on the basal ganglia and thalamus in a sample of bilinguals with wide range of bilingual experiences. Our results revealed that volumes of bilateral caudate nuclei and accumbens were positively related to bilingual experiences in a non-linear pattern, with increases followed by decreases, in the most experienced bilinguals, suggesting a return to baseline volume at higher levels of bilingual experience. Moreover, volumes of putamen and thalamus were positively linearly predicted by bilingual experiences. The results offer the first direct evidence that bilingualism, similarly to other cognitively demanding skills, leads to dynamic subcortical structural adaptations which can be nonlinear, in line with expansion-renormalisation models of experience-dependent neuroplasticity.

## 1. Introduction

Mounting evidence in the past two decades has shown that the cognitively demanding experience of bilingualism affects brain structure<sup>1</sup>. Given that the majority of the world's population is bilingual<sup>2</sup>, bilingualism-induced neuroplasticity constitutes an appealing candidate for investigating how long-lasting demanding cognitive skills and experiences affect brain morphology<sup>3</sup>. However, using knowledge about bilingualism-induced neuroplasticity to draw conclusions about experience-dependent brain adaptations has been hampered by inconsistent results from studies in the field. Namely, existing research often reports structural changes in different regions and effects in different directions, including both volumetric increases and decreases<sup>4</sup>. While the field of bilingualism-induced neuroplasticity has generally embraced the basic assumption that demanding experiences can lead to neural adaptations, it has not examined the inconsistencies through the prism of general principles of experience-dependent neuroplasticity. In fact, experience-induced structural brain changes are often not linear, but rather dynamic, and they depend on the quality, quantity, and time course of experiences that trigger them<sup>5,6</sup>. Consequently, the exact dynamic nature of the effects of bilingualism on the brain might have remained overlooked. To address this issue, bilingualism needs to be approached as a continuous cognitively demanding experience, which can trigger dynamic structural adaptations.

The general brain mechanisms behind the acquisition of a new skill, such as learning a new language, resemble an audition<sup>7</sup>. When facing a new cognitive challenge which cannot be met by the existing neural resources, brain expands to explore new candidates for efficient neural circuits to perform the newly emerged task. Upon selection of the most promising neural circuit resulting in required performance efficiency, the brain eliminates the superfluous neural resources. With respect to volumetric

brain changes, the prominent theories argue for expansion-renormalisation model<sup>5,7,8</sup>. According to it, initial volumetric increases related to skill acquisition are followed by decreases once the skill has been acquired and exercised efficiently. From this follows that cognitively demanding experiences often trigger brain adaptations that are not linear, but rather following an expansion-renormalisation trajectory.

Experience-dependent neural adaptations are typically observed in brain regions which functionally support managing of the task at hand<sup>9</sup>. In the case of second language learning (L2) and bilingual language use the critical regions are those subserving switching, cognitive and articulatory control, and language selection. Perhaps the most important of these regions are the basal ganglia (including structures such as caudate, putamen, globus pallidus and accumbens) and the thalamus<sup>10,11</sup>. In general, these structures subserve integration of information from multiple cortical areas to select purposeful action in response to external stimuli or internal cues<sup>12</sup>. It has been shown that language switching and selection of appropriate language systems allowing bilinguals to achieve fluent communication draws upon the cognitive-general functionality of basal ganglia and thalamus<sup>10</sup>. Specifically, several studies reported recruitment of bilateral caudate during language-switching, and vocabulary learning<sup>13–16</sup>. The globus pallidus and putamen have both been reported to engage in phonological monitoring and selection<sup>17</sup>, while the putamen has also been implicated in the employment of motoric control schemata linked to language-specific articulatory demands<sup>18</sup>. Activation of the nucleus accumbens has been explained by its role in maintaining the motivation to learn the second language<sup>19</sup>. The thalamus, a region extensively connected with basal ganglia, has been implicated in language selection and, together with the globus pallidus, it subserves the coordination of motor routines related to language-specific articulatory motor programmes<sup>20–22</sup>.

Evidence from structural studies confirms that the basal ganglia and the thalamus adapt structurally following bilingual practices. However, existing studies presented seemingly scattered patterns of these adaptations, often reporting effects in different regions, in different directions, or even absence of some effects altogether<sup>1</sup>. For example, compared to monolinguals, bilinguals have generally been reported to have larger caudate nuclei, putamen, globus pallidus, and thalamus<sup>23–25</sup> but these effects tend to disappear in bilinguals immersed in bilingual context<sup>26</sup>. Perhaps more confusingly, *smaller* caudate volumes have been reported in long-standing interpreters, that is exceptional bilinguals using both languages professionally, when compared to individuals with less cumulative interpreting experiences<sup>27</sup>. These contrasting patterns have posed a challenge to the field in understanding the mechanisms that lead to bilingualism-induced adaptations.

Recall that a lot of this variability may be because of lack of understanding or systematic study of the dynamic nature of these adaptations. With respect to bilingualism, the Dynamic Restructuring Model (DRM)<sup>4</sup> builds on the expansion-renormalisation model<sup>6</sup> to conceptualise the bilingualism-induced brain changes. The DRM argues that in the case of bilingualism, structural brain adaptations are triggered by environmental changes in language control demands, which are determined by practices in bilingual

language use and the amount of bilingual experiences. As such, the DRM offers a unifying theory explaining the divergent findings on brain changes brought about by bilingualism mentioned earlier.

We now turn to the specific predictions by the DRM on the regions of interest of the present paper, namely the basal ganglia and the thalamus. Individuals who start to learn a vocabulary of the second language face a new need to control between lexical alternatives for the same concepts. This assumedly triggers volumetric expansion of the caudate which subserves acquisition of new words in the second language<sup>16</sup> and lexical selection and control<sup>10</sup>. Once bilinguals become proficient in both languages and start to engage with both languages more often, the most efficient networks get selected among the newly built neural resources. In turn, the volumetric expansion of caudate will reverse over time. This explains the variability in results in the studies mentioned above; volumes of caudate increase in less experienced bilinguals when compared to monolinguals, but these effects are absent in highly proficient bilinguals<sup>26</sup>. Highly proficient bilinguals face new cognitive challenges linked to increased language production and control, which poses greater demands on language monitoring and motor control related to articulation. This explains the findings of increases in regions implicated in articulatory control and phonological selection in more experienced bilinguals, such as the left putamen<sup>23,25</sup> and globus pallidus<sup>24</sup>. Similarly, more experienced bilinguals have a likely richer vocabulary, which leads to the growing need for lexical selection during production. This can explain the expansion of thalamic volumes, which is assumed to enable a more efficient selection mechanism<sup>20</sup>.

In light of the above, acquisition and use of two or more languages resembles other complex skills in that it requires lifelong reconfiguration of the behavioural repertoire to address the altering cognitive demands. The DRM posits that such a longstanding dynamic process such as bilingualism brings about dynamic, non-linear effects on brain structure and that specific bilingual experiences can predict these effects. These experiences have been suggested to include onset of the second language (L2) acquisition<sup>28</sup>, proportional usage of first (L1) and L2<sup>29</sup>, duration of L2 use<sup>30</sup>, L2 proficiency<sup>31</sup>, linguistic differences between L1 and L2<sup>32</sup>, and intensity of switching between the languages<sup>33</sup>. Nevertheless, the DRM predictions remain formulated based on the synthesis of results from single studies which largely used between-groups comparisons (e.g. bilinguals vs. monolinguals). Such an approach cannot account for the variability in the aforementioned individual bilingual experiences. Instead, treating bilingualism as a continuous rather than categorical variable and looking at the variability within a bilingual sample has been called upon as an alternative approach with a potential to contribute new insights in the effects of bilingualism on the mind and brain<sup>34,35</sup>.

Following from these suggestions, a recent study applied an experienced-based approach in revealing dynamic changes of neural adaptations in bilinguals<sup>19</sup>. To quantify bilingual experiences, the *Language and Social Background Questionnaire (LSBQ)*<sup>36</sup> was used, which provides continuous measures of bilingual use in different contexts. The study revealed expansions of left accumbens, caudate and right thalamus to be predicted by social language use, whereas age of language acquisition predicted both expansions and contractions in parts of right caudate and putamen and contractions in bilateral

accumbens and thalamus. These results support the notion that bilingual experiences assessed on a continuum can reveal complex patterns of brain adaptations. Critically however, these analyses assumed *linear* structural adaptations. Treating effects of bilingualism linearly disallows for testing of predictions rooted in evidence that demanding experiences can have *non-linear* effects on brain structure. Therefore, it is crucial to allow for non-linearity of these effects in order to examine the evidence-based DRM predictions that changes brought about by bilingualism are dynamic.

In point of fact, prominent theories of experience-dependent neuroplasticity advocate *against* assuming linear brain volume growth during skill acquisition (for review, see Wenger et al., 2017), with some even calling assumed continual increase in brain volumes unfeasible<sup>37</sup>. With respect to bilingualism, Pliatsikas and colleagues (2021) used Generalised Additive Mixed Models (GAMMs), a statistical method that can reveal non-linear effects, to study concentrations of brain metabolites in the basal ganglia as a function of bilingual experiences. Among other markers, they investigated concentrations of myo-Inositol (INS) and N-acetyl aspartate (NAA), which have been treated as markers of the processes that underlie neuroplasticity, such as synaptic pruning and repurposing of neural substrates. They revealed that bilingual experiences predicted these concentrations in a non-linear fashion. The authors interpreted this as indirect evidence for microscopic experience-based restructuring of the basal ganglia, signifying increases in synaptic connections and also the elimination of the superfluous synapses depending on the amount of bilingual experiences. Such an interpretation is in accordance with the DRM. However, it remains to be determined whether such non-linear adaptations observed on the microscopic level occur also at the level of volumes of relevant brain structures.

Following up from this approach, in the present study we employ GAMMs to model non-linear effects of continuous measures of bilingual experiences on volumes of basal ganglia and thalamus across a rich sample of bilinguals with a wide range of bilingual experiences. Specifically, our sample ranges from bilinguals with limited opportunity for active bilingual languages use, to advanced bilinguals and translators, who engage with two languages daily, to exceptional bilinguals such as interpreters, who face extreme control demands in their jobs. The dynamicity of bilingualism is captured on the continuum using the LSBQ composite score (henceforth *Bilingual composite score; BCS*), which spans information about language proficiency, exposure, switching, and duration and proportionality of the use of both languages<sup>36</sup>.

Based on DRM, we predicted distinct trajectories of volumetric adaptations of basal ganglia and thalamus as a function of quantified bilingual experiences. Specifically, we expected an expansion-renormalisation pattern of the caudate, expressed as a trajectory suggesting increases in volume with limited bilingual experience, which will however plateau and eventually decrease as bilingual experience increases. A similar pattern was also predicted for the neighbouring nucleus accumbens, a region that is strongly interconnected with the caudate nucleus and has also been shown to contract in experienced bilinguals<sup>19</sup>. According to the DRM, adaptations of putamen and globus pallidus have been suggested to come after the onset of caudal changes. With respect to the putamen, we expect to observe a pattern consistent with onset of structural brain adaptations in bilinguals with larger amount of bilingual

experiences than for the caudate and the accumbens. If putamen will manifest renormalisation, we predict that this will occur only in individuals at the highest end of the spectrum of bilingual experiences. Globus pallidus has received less attention than the neighbouring putamen. However, we expect comparable patterns as in putamen due to the interrelatedness of both structures, and their shared functionality<sup>26</sup>. Expansions of thalamus have been reported in long-standing, regularly practicing bilinguals whose brain has reached efficiency in the mechanisms that undertake vocabulary learning and control<sup>19</sup>. It has been suggested to be involved together with globus pallidus in coordinating of motor programmes<sup>39</sup>, a function employed for successful articulation of different languages. Taken together, we expect to observe comparable adaptation patterns as in putamen and globus pallidus, i.e., later onset of thalamic volumes increases relative to caudate with possible renormalisation only in bilinguals with high level of bilingual experiences.

## 2 Results

### 2.1 Effects of bilingual experiences on volumetric changes in left and right hemisphere

In the first-level model using GAMMs, we examined whether bilingual composite scores had different effects on the volumes of the ROIs in the left and right hemisphere. To do so, we examined whether BCS x Hemisphere interaction is reliably significant when its effects are tested for both left and right hemisphere as reference levels. The results revealed that the BCS x Hemisphere was reliable significant with both reference levels of hemisphere for the globus pallidus (see *Supplementary Materials 3*). This suggested that effects of the BCS on each hemisphere of the globus pallidus may be significantly different. Therefore, in the subsequent second-level model (see next section), we split the globus pallidus data across hemispheres and examined effects of BCS in each hemisphere. For all other ROIs BCS x Hemisphere interaction did not emerge as a reliably significant predictor, so we collapsed the data across hemisphere for these structures at the second level analysis.

### 2.2 Effects of individual bilingual experiences on volumes of ROIs

The results from the second-level analysis are illustrated in Figure 1. BCS, the metric of interest, emerged as a non-linear predictor of caudate and accumbens volumes. Specifically, the results reveal a positive relationship between BCS and volumes in these two regions, but only to a certain level of bilingual experience after which the growth in volumes appears to reach a plateau for the accumbens, and start decreasing for the caudate (See Figure 1). BCS was also a significant linear predictor of putamen and thalamus volumes, in that the higher BCS, the larger volumes. Age emerged as a significant predictor for volumes of the caudate, the putamen, and the thalamus with smaller volumes as a function of age. The analysis also revealed a significant main effect of Hemisphere. The left accumbens and the putamen were larger than the right ones. Conversely for the caudate and the thalamus, the volumes of these

structures in the right hemisphere were larger than in the left hemisphere. The two second-level models for each hemisphere of the globus pallidus showed that the BCS is not a significant predictor of globus pallidus volumes, in neither of both hemispheres (illustrated in Figure 2). The results from the second second-level models for structures collapsed across hemispheres can be found in Table 1.

Table 1

Results from GAMMs, second-level model. GAMMs with main effects of bilingual experiences (BCS), age and hemisphere, and random effects of gender and subjects on subcortical volumes of caudate, putamen, accumbens, and thalamus. Two separate models for each hemisphere for globus pallidus with BCS and age as main effects and gender as random effect.

	<b>caudate</b>	<b>putamen</b>	<b>accumbens</b>	<b>thalamus</b>	<b>globus pallidus</b>	
						<b>left</b>
<b>BCS</b>	<0.001****	0.028*	0.027*^	0.014*	0.693	0.236
<b>Age</b>	0.003**	0.022*	0.271	0.047*^	0.469	0.508
<b>Hemisphere</b>	0.009**	<0.001***	<0.001***	<0.001***	-	-

For significant effects all Fs > 4.03

Note: ^: edf>1.0, denoting a non-linear effect.

### 3. Discussion

In this paper we show that quantified bilingualism has dynamic effects on the volumetric adaptations of the basal ganglia and the thalamus in a sample of bilinguals with varied bilingual experiences. More specifically, GAMMs analysis revealed volumetric trajectories indicating that the amount of engagement with bilingualism is linked to larger volumes of the caudate and the accumbens in less experienced bilinguals, followed by structural renormalisation in individuals who reached higher levels of bilingual experiences. Furthermore, our results revealed that the amount of bilingual experiences was a positive linear predictor of volumes of bilateral putamen and thalamus. These findings suggest that bilingualism, similarly to other cognitively demanding skills, follows an expansion-renormalisation trajectory that is similar to what has been proposed for experience-based neuroplasticity in general<sup>6</sup>. The observed brain adaptations will be discussed against relevant theories and findings from previous studies below.

The positive relationship of caudal volumes with bilingual experiences that we observed in relatively less experienced bilinguals are consistent with previous studies. Indeed, caudate nucleus has been reported to increase in volume mostly in bilinguals who have not been fully immersed in a bilingual environment<sup>26</sup>. Also, the observed decrease of caudal volumes after a certain level of bilingual experiences maps indirectly onto the lack of such findings from studies looking at experienced bilinguals: if the volumes of caudate in experienced bilinguals have already renormalised they may not significantly differ to those of monolinguals<sup>27</sup>. Overall, this supports the view that caudate subserves cognitive processes needed during the earlier stages of L2 acquisition, which triggers the increases of this structure, such as early

lexical control and selection<sup>40</sup>. The relatively smaller caudal volumes observed here in more experienced bilinguals signifies optimisation of the neural resources in handling the cognitive demands posed on bilinguals in the early stages of L2 acquisition.

We also observed a volumetric trajectory of the bilateral nucleus accumbens suggesting that this structure increases as a function of growing bilingual experiences and plateau in highly experienced bilinguals, a pattern that partly matches the one for the neighbouring caudate nucleus. This pattern expands on previous findings showing that length of language acquisition predicted contractions in bilateral accumbens, and social language use predicted expansion of the left accumbens<sup>19</sup>. The nucleus accumbens likely subserves the reinforcement of learning strategies<sup>10</sup>. Also, larger accumbens volumes have been reported in individuals with more extensive social networks<sup>41</sup>. In the context of the current findings, the nucleus accumbens can be responsible for reward in seeking social interactions in the earlier stages of L2 acquisition to encourage bilingual practice. The plateauing pattern reported here might reflect that when bilinguals reach the necessary language use efficiency the intrinsic motivation to seek social interaction in their L2 stabilises. This might be particularly true for participants in the present study who stayed in their home country. In such context, their communicative skills in the L2 do not necessarily determine their social well-being as they have enough chances to build their social interactions using their L1. In turn, such behaviour becomes superfluous, leading to the stabilisation of their neural resources. However, given that the role of accumbens is less well understood in bilingualism, we remain cautious of this interpretation.

Unlike for caudate and accumbens nuclei, the effect of bilingual experiences on the volumes of the neighbouring putamen was linear, which is consistent with previous studies and our predictions. The putamen is assumed to subserve articulatory control in selecting the appropriate motor schemata in speech production<sup>18</sup>. Therefore, we assume that the current results indicate structural changes toward increased efficiency in the production of L2. Larger putamen volumes have been also reported in previous studies. Specifically, bilinguals with longer or more intensive experience had larger putamen volumes than monolinguals<sup>24</sup>, or their less experienced bilingual counterparts<sup>19,25</sup>. However, the laterality of these effects varied, with increases reported in the right<sup>19</sup>, left<sup>25</sup>, and bilateral putamen<sup>24</sup>. Part of the differences with respect to the laterality of the observed effects might stem from variability in phonological transparency of languages the bilingual used, which has been shown to play a role in a previous study<sup>42</sup>. Phonological skills in Hindi, a phonologically transparent language, have been predicted by larger volumes of the right putamen, whereas performance on the same task in English, a relatively phonologically non-transparent language, was linked to larger volumes of the bilateral putamen<sup>42</sup>. These results were interpreted as indication that phonological skills in a non-transparent language require support from both hemispheric parts of this structure. However, this is an empirical question which could be answered in studies where bilingual samples are ensembled based on careful consideration of the language pairs involved.

The observed positive correlation of bilateral thalamus volumes with bilingual experiences might reflect the longstanding necessity for language selection among participants in the current sample. Thalamus is extensively connected to the basal ganglia and the medial prefrontal cortex subserving language and domain-general cognitive control<sup>20,43</sup>. Furthermore, emergent views highlight the thalamus' role in shaping mental representations involved in learning and memory<sup>44</sup>. Accordingly, the present findings may reflect the need for bilinguals to constantly update mental representations. Experienced bilinguals in our study, including professional interpreters and translators, need to permanently monitor extent to which boundaries between concepts are similar across both languages. For example, the English word *chair* can refer to conceptually very distinct objects, such as a *desk chair*, *an armchair* or a *deck chair*. In contrast, the Czech translation of *chair* (*židle*) cannot refer to a *deck chair*, as this object falls within a category of *beds*. Thus, a translator needs to constantly be aware of the fact that conceptual distinctions are mapped onto words in each language in very different ways<sup>45,46</sup>.

In accordance to some recent findings<sup>19</sup>, we did not observe any effects of bilingualism on the volumes of globus pallidus, which has been shown to expand in experienced bilinguals in other studies<sup>24,26</sup>. A possible explanation relates to the fact that participants in our study were predominantly Czech natives who lived in Czechia. In a such monolingual context, bilinguals usually do not take part in code-switching<sup>47</sup>. Code-switching is a bilingual linguistic act of alternating between two languages within one sentence or paragraph<sup>48</sup>. It poses higher demands on cognitive control processes, which are assumed to be subserved together with anterior cingulate cortex also by globus pallidus<sup>49</sup>. Furthermore, globus pallidus has been reported as sensitive to reward-signals<sup>50</sup>, including reinforcement of behaviour leading to cultural accommodation<sup>51,52</sup>. In this view, the absence of adaptations of globus pallidus volumes observed here may reflect the lack of need for acculturation expected in participants living in their home country. In contrast, the study that reported increases of globus pallidus<sup>26</sup> included a largely migrant population, with likely higher demands exerted not only on linguistic but also cultural assimilation. However, further research is necessary to tease apart the role of language, cultural acquisition and code-switching on brain structure.

We now turn to the interpretation of the observed patterns with respect to theoretical time course of the bilingualism-induced brain adaptations. Notably, the trajectories of subcortical structural changes observed here appear to be in accordance with the predictions by the DRM<sup>4</sup>. Specifically, the trajectory of caudate adaptations indicates that caudate undergoes structural changes first. The pronounced expansion-renormalisation trajectory of caudal volumes in relation to bilingual experiences can be a sign of an onset of adaptations early in the process of language acquisition. Namely, for a structure to renormalise, it should be provided with sufficient time and training in the given skill to do so. In this view, the caudate have renormalised because it was provided enough opportunity to finetune its architecture as it was intensely relied on from the beginning of bilingual language use.

We observed a similar pattern with respect to volumes of bilateral accumbens, the volumes of which were shown to increase as a function of growing bilingual experiences, and to plateau, but not decrease, in

highly experienced bilinguals. Also as predicted by the DRM, the observed volumetric increases in putamen and the thalamus started later and after some amount of bilingual experience and continued to increase even in the highly experienced bilinguals but without any evidence of plateauing or even renormalising, which may still be the case in bilinguals of more extended experience that were not part of our sample. The observed patterns of grey volume changes and the hypothesised time-course of the adaptations are schematically illustrated in Figure 3. Although these interpretations are in line with our a-priori predictions based on an evidence-based model, we note that further research with longitudinal design is necessary to provide more evidence on the time-course of subcortical adaptations.

The volumetric patterns observed here (especially those in the caudate and the accumbens) align with the general principles of experience-dependent neuroplasticity. Specifically, these patterns are consistent with the expansion-renormalisation trajectory of experience-dependent brain changes induced by cognitively demanding experiences. For example, Wenger et al. (2017) reported grey matter expansion in motor cortices during the first weeks of motor learning and partial renormalisation following continued practice and increasing task proficiency. If viewed through this lens, existing studies on bilingualism-induced neuroplasticity that focused on the amount of various bilingual experiences also point in the direction that bilingualism induces structural increases that are followed by renormalisation as bilingual language use continues. The caudate and the accumbens both expanded and contracted in bilinguals, dependent on the amount of bilingual experiences<sup>19</sup>. These bidirectional volumetric effects were suggested to reflect both adaptations to newly emerged cognitive demands and the subsequent optimisation of the language control network.

The interpretation that our findings reveal an expansion-renormalisation pattern is further supported by recent study showing that quantified bilingual experiences predicted concentrations of myo-Inositol (INS), a metabolic marker of structural brain adaptations, in a cluster covering the caudate nucleus and the putamen<sup>38</sup>. This finding was interpreted as indirect evidence of renormalisation of these structures on the microstructural level. Although the link between metabolic and the macrostructural brain changes remains poorly understood<sup>54</sup>, this evidence complements our current findings from a different sample, and therefore it constitutes a promising step forward in understanding the holistic orchestration of brain adaptations in bilinguals. Overall, the current findings corroborate the view that experiences are central to bilingualism-dependent brain adaptations and extend them to modelled non-linear effects as revealed by GAMMs. Therefore, our results provide firm support for theoretical suggestions that bilingualism encompasses a dynamic set of experiences that pose variable demands on brain structure<sup>4</sup>.

Findings from this study should be appreciated within the context of certain limitations. Although we maintain that our approach of treating bilingualism as a continuum of experiences constitutes a step in the right direction regarding the revelation of dynamic effects of bilingualism on the brain, we do acknowledge that such an approach is relatively novel within the field of bilingualism where a between-group design has been used predominantly. This restricts the comparability of our results to those from previous studies. We also acknowledge that our understanding of the relative contribution of concrete individual bilingual experiences (i.e., code-switching frequency, onset of language acquisition,

multicultural identities etc.) on the brain structures is still limited when composite scores like ours are used. A possible way forward in future studies is to combine the use of composite scores of bilingual experiences alongside other continuous measures of individual bilingual experiences and compare the results against each other. Such an approach would make it possible to establish which bilingual experiences or their combined effects have the most prominent effects on the brain structure. Also, the results demonstrated here use a measure of bilingual experiences at the time of data collection. Although such an approach remains valid as a level of current experience is indicative of the time necessary to reach that particular level of experience, individual differences and learning circumstances might compromise the results. A longitudinal study encompassing several measurements with a controlled training paradigm would advance our understanding of the structural adaptation processes brought about by bilingualism over specific periods of time.

In conclusion, this is the first study to prove that bilingualism, a cognitively demanding and complex skill, can trigger non-linear adaptations on the brain structure, expressed as initial expansion of brain volumes with limited bilingual experiences followed by renormalisation of some structures at higher levels of experience, indicating increased efficiency. Therefore, the data support the dynamic view of bilingualism-induced neuroplasticity proposed by Dynamic Restructuring Model <sup>4</sup>, which posits that the intensity of bilingual experiences predicts dynamic patterns of structural adaptations. Our approach also addressed inconsistent results in terms of location and direction of structural brain changes brought about by bilingualism reported in previous studies, which adopted assumptions of linearity of these effects. Thus, our findings constitute an intriguing methodological step toward a unifying explanation for previous work on bilingualism-induced neuroplasticity. On a broader level, the data also support the expansion-renormalisation model, which explains general principles of experience-dependent neuroplasticity <sup>8</sup>. Therefore, the current study puts bilingualism forward as a valuable candidate for studies investigating mechanisms of neural adaptations brought about by demanding, life-long experiences.

## 4 Methods

### 4.1 Participants

Data were acquired from native or native-like speakers of Czech ( $n = 114$ ; 43 males; 71 females; mean age = 32). All participants had upper intermediate to high command of English as measured by LexTale test for advanced learners of English <sup>55</sup>. While keeping our sample consistent in terms of high English proficiency, participants were sampled among bilingual groups with assumed variation in their relevant bilingual experiences. These included bilinguals with a relative short-term bilingual engagement, bilinguals who spent part of their lives abroad, or translators and interpreters. Hereby, we ensured to cover a wide range of relevant bilingual experiences such as onset of language acquisition, intensity of language contact, proportionality of language use, and practices of mixing of both languages. All participants were right-handed, with normal or corrected-to-normal vision and without history of neurological or language disorders. All participants reported holding a university degree or being students

enrolled in a university programme. This information was collected using the LSBQ (see Materials below). All participants were living in the Czech Republic at the time of testing and reported not to have visited any foreign speaking country two weeks prior testing. To minimize any effects caused by differences in typological proximity between the L1 and English<sup>56</sup>, all participants were native speakers of a Slavic language, with the following languages represented: Czech (n = 106), Russian (n = 4), Macedonian, Polish, Serbian, and Slovak (for each n = 1). The non-native Czech speakers were all court interpreters/translators in language combination Czech-English, which means they needed to fulfil the conditions stipulated by the Czech legal Act on Experts and Interpreters no. 36/1967 Coll.<sup>57</sup> including, native or native-like knowledge of Czech.

Four participants (native speakers of Czech) did not finish the whole scanning procedure, one participant did not complete the questionnaire, and their data were excluded from this study. The sample submitted for analyses consisted of 109 participants [39 males; 70 females; mean age (SD) = 32 (7.71); age range 18-53; mean LSBQ composite score (SD): 5.43 (3.96)].

All participants provided written consent prior the data collection. The study received a favourable opinion for conduct by the Ethics Committee of Masaryk University.

## 4.2 Materials

### 2.4.2.1 Language and Social Background Questionnaire

To assess the participants' level of bilingual language engagement, participants completed a Czech version of The Language and Social Background Questionnaire<sup>36</sup>. This questionnaire gathers information about the demographics, code-switching practices, language background, history, language use and proficiency. Answers to the questions marked on five-point or ten-point Likert scales are entered into an overall factor score calculator<sup>36</sup>, which creates LSBQ composite score of bilingual experiences, therefore assessing bilingualism as a continuous variable<sup>38</sup>. The Czech version was translated from English and back-translated to determine the quality and equivalence of the Czech version with the source version. This questionnaire is attached as *Supplementary Materials 5*.

## 4.3 MRI Data acquisition

MRI data were collected at the Central European Institute of Technology (Brno, Czechia) on a 3T Siemens MAGNETOM Prisma\_fit MRI scanner, with a 32-channel Head Matrix coil.

We carried out high-resolution anatomical scans for registration and structural analysis (sagittal orientation, 256 slices, 0.7 mm slice thickness, voxel size 0.7 x 0.7 x 0.7 mm, acquisition matrix 246 x 256 mm, in-plane resolution 250 x 250, TE = 2.41 ms, TR = 2400 ms, inversion time 1140 ms, flip angle 8°). The acquisition of anatomical scans took about 10 minutes.

## 4.4 Data analysis

## 4.4.1 MRI Data Preprocessing

We used the FSL\_anat software pipeline<sup>58</sup> to preprocess T1-weighted images. The subcortical structures were extracted using the FIRST software pipeline<sup>59</sup>. The following structures were automatically segmented for both hemispheres separately and were visually inspected for quality of extractions: accumbens, caudate nuclei, globus pallidus, putamen, and thalamus. To account for the impact of head size on the volume of subcortical regions, we divided the volumes of each region by the whole-brain volume. These proportional volumes were then submitted to the statistical analysis. The mean proportional volumes of the regions of interest are illustrated in the Table 2.

Table 2  
Mean and SDs of the proportional volumes of ROIs

Mean proportional volume (SD)		
	Left	Right
<b>accumbens</b>	0.379 (0.071)	0.317 (0.071)
<b>caudate</b>	2.661 (0.226)	2.71 (0.281)
<b>globus pallidus</b>	1.213 (0.09)	1.208 (0.082)
<b>putamen</b>	3.408 (0.243)	3.348 (0.252)
<b>thalamus</b>	5.844 (0.34)	5.712 (0.327)

Note: all values multiplied by 1000 for the purposes of illustration

## 4.4.2 Statistical data analysis

Data were analysed in R<sup>60</sup> with generalised additive mixed models (GAMMs) using the `gam()` function of the `mgcv` package<sup>61</sup>. The non-linear regression splines in GAMMs are computed as the sum of simpler non-linear functions for each of the fitted variables. However, the non-linear splines are only included when there is enough evidence in the data for a curved function, because the wiggliness penalizes the estimated model fit. GAMMs compute the estimated degrees of freedom (edf), which indicate whether the predictor is in a non-linear ( $\text{edf} > 1$ ) or a linear relationship ( $\text{edf} = 1$ ) with the dependent variable. We ran a series of GAMMs for volumes of each subcortical region.

In a first-level model, we fitted the regression splines for the main effect of bilingual experiences using BCS along with the main effect of Age, and Participant and Gender as random effects. The smooth term of Age was included to account for previously observed non-linear age-related developmental changes<sup>62</sup>. To estimate the effects of both main effects and interactions, we applied an analytical procedure in line with the “vibration of effects” approach<sup>63</sup>. We included BCS x Hemisphere interaction, where Hemisphere was an ordered factor with two levels (left and right). We examined effects of this interaction to account for previously reported cases when the observed effects of BCS on brain volumes were lateralized<sup>19</sup>. For

each ROI, we ran two GAMMs with both levels of ordered factors of Hemisphere as reference levels. The effects of the interactions Hemisphere x BCS were considered reliable only if they emerged significant in both relevant versions of the model with different reference levels.

In the second-level model, for the structure where interaction emerged as significant, we split the data for the left and right hemisphere and ran two models for each hemisphere with BCS and Age as main effects and Gender as random effect. For those regions where the BCS x Hemisphere interaction did not emerge as significant, we analysed the main effects of BCS and Hemisphere using data collapsed across hemispheres. These models further included Age as main effect and Gender and Participant as random effects.

### 4.4.3 The assessment of models fits

To assess the model fits of all the final models, we used the `gam.check()` function of the R package *mgcv*<sup>64</sup>. All the final models converged (convergence range: 7-10 iterations). The number of functions which gave rise to the regression splines exceeded in all cases the estimated degrees of freedom. For all continuous variables submitted to the analyses, there were no significant patterns in residuals as evaluated by the p-value above the 0.05 significance threshold. Also, the k-index was in all cases above 1 which supports the view that there were no missed patterns in residuals in our models<sup>65</sup>. The results of the model assessment analyses can be found in *Supplementary Materials 1*.

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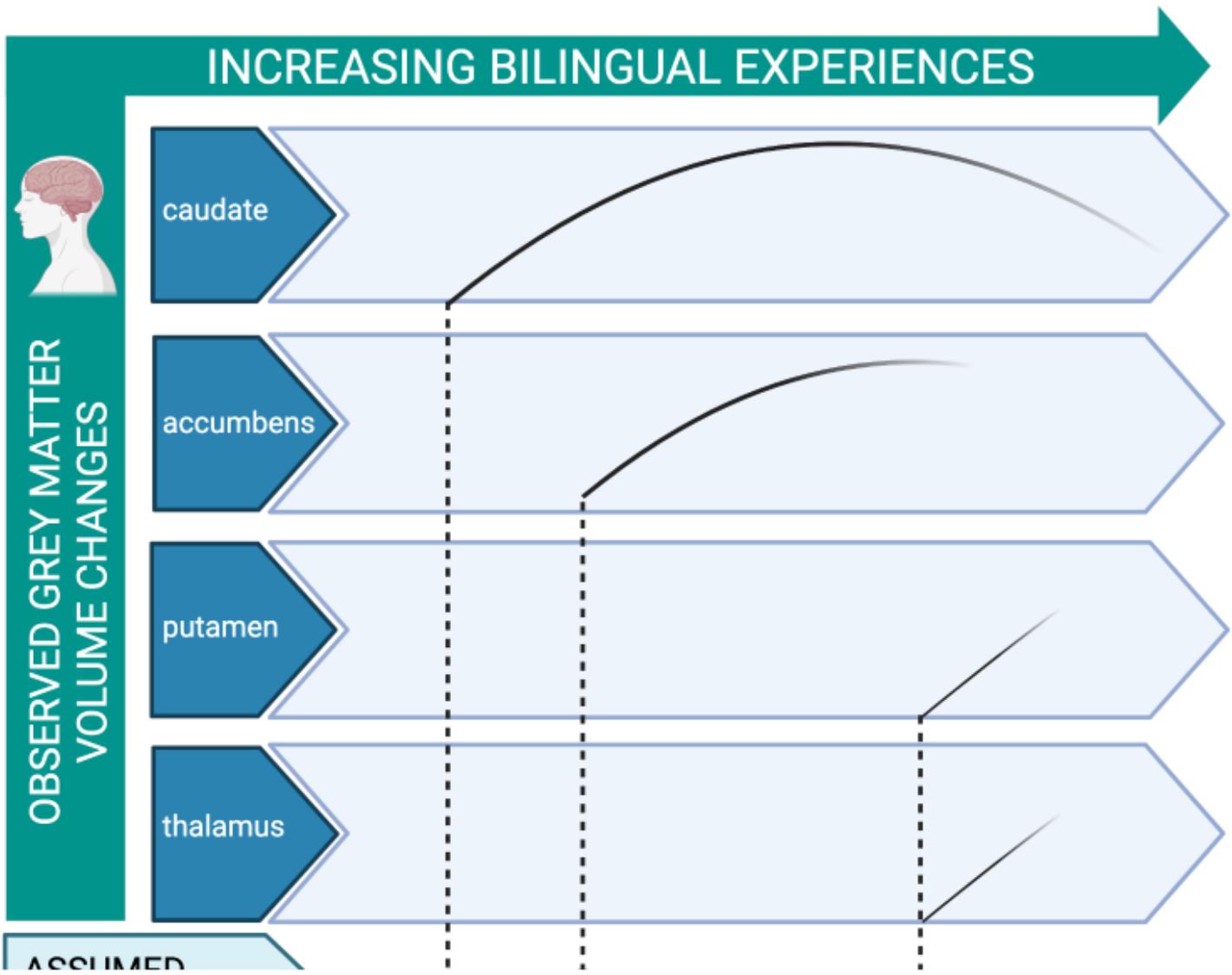
## Figures

### Figure 1

Effects of bilingual composite scores on the grey matter volumes of the ROIs. (a) GAMMs 3D plots illustrating the relationship between BCS (x-axes), age (z-axes) and normalised volumes of the regions of interest (rows) in cm<sup>3</sup> (y-axes). (b) GAMMs (black line) with 95% confidence interval (blue shade) depicting the effects of the BCS scores (x-axis) and the normalised volumes of the regions of interest in cm<sup>3</sup>. (c) Featured location of the regions of interest in the brain.

### Figure 2

Effects of bilingual composite scores on the grey matter volumes of the globus pallidus. (A) GAMMs 3D plots illustrating the relationship between BCS (x-axes), age (z-axes) and normalised volumes of the globus pallidus in the right (upper band) and left hemisphere (lower band) in cm<sup>3</sup> (y-axes). (B) GAMMs (black line) with 95% confidence interval (blue shade) depicting the effects of the BCS scores (x-axis) and the normalised volumes of the globus pallidus in cm<sup>3</sup> (y-axes). (C) Featured location of globus pallidus in the brain.



**Figure 3**

Schematic overview of the observed volumetric grey matter patterns for each of the regions of interest. The level of renormalisation suggests the time-course of the onset of the brain adaptations (depicted below). Regions for which renormalisation of volumes in highly experienced bilinguals was observed (i.e., caudate and accumbens) had likely earlier onset of structural adaptation.

## Supplementary Files

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