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DOI

[10.1016/j.cobeha.2024.101438](https://doi.org/10.1016/j.cobeha.2024.101438)

Publication date

2024

Document Version

Final published version

Published in

Current Opinion in Behavioral Sciences

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[Link to publication](#)

Citation for published version (APA):

Yee, J., Kořenář , M., Sheehan, A., & Pliatsikas, C. (2024). Subcortical malleability as a result of cognitively challenging experiences: the case of bi-/multilingualism. *Current Opinion in Behavioral Sciences*, 59, Article 101438. <https://doi.org/10.1016/j.cobeha.2024.101438>

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Review

Subcortical malleability as a result of cognitively challenging experiences: the case of bi-/multilingualism

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Experience-based neuroplasticity in the healthy brain is a well-documented finding, with functional and structural adaptations in cortical and subcortical structures reported as the brain's response to cognitively challenging experiences. These experiences include bi-/multilingualism: speaking more than one language entails increased cognitive demands related to language acquisition, processing and control, which affect subcortical structures subserving these processes, including the basal ganglia and the cerebellum. This paper reviews evidence on bilingualism-induced subcortical neuroplasticity at the level of brain structure, function, and metabolism and explores how it interacts with brain decline. As such, it highlights bi-/multilingualism as a test case for studying long-term neuroplastic effects in the brain.

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Current Opinion in Behavioral Sciences 2024, 59:101438

This review comes from a themed issue on **Subcortical Cognition**

Edited by **William Saban, Karolina Janacsek and Michael Ullman**

Available online xxxx

Received: 28 July 2023; Revised: 13 May 2024;

Accepted: 31 July 2024

<https://doi.org/10.1016/j.cobeha.2024.101438>

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Bilingualism as a plasticity-inducing long-term cognitive challenge

Experiences and skills acquired throughout life can lead to measurable changes in the brain at the cellular and synaptic level, demonstrating its ongoing plasticity. These include not only learning complex motor skills such as musical instrument training [1], practising writing with a nondominant hand [2] and juggling [3] but also cognitively challenging tasks such as road navigation [4] and acquiring and controlling between multiple languages (i.e. bilingualism) [5]. In several studies on experience-based neuroplasticity, the specific brain regions underlying the tasks exhibit structural adaptations that follow nonlinear patterns [6–9]. Specifically, upon acquiring the skill, or with consistent practice, previously expanded regions have been shown to contract (or ‘re-normalise’) [10]. Given their multifaceted roles in cognition, subcortical structures such as the basal ganglia and the cerebellum are key for our understanding of the processes of experience-dependent neuroplasticity, and the conditions that promote and guide it. Bi-/multilingualism is an appropriate experience to examine as a test case for the effects of cognitively demanding experiences on the brain. This experience not only encompasses the acquisition of multiple languages but also additional processing needs, which may differ amongst the acquired languages, but most crucially, additional control needs: it is well understood that all languages remain active in the bi-/multilingual mind and compete for production [11–13]; thus, more efficient control is needed in order for the target language to be produced. Given the central role that the basal ganglia and the cerebellum have in both language processing [14] and cognitive control [15], it only follows that these regions would be expected to be affected structurally and functionally in bi-/multilinguals.

Indeed, an increasing body of research has provided evidence for bilingualism-induced brain adaptations, which have been reported as cortical and subcortical differences between monolinguals and bi-/multilinguals, including in brain structure (in grey and white matter) and function (task-based and at rest) [16]. However, the

evidence has not been consistent in terms of the location or the direction of the effects [17]. This has recently led to suggestions that bilingualism should be viewed as a dynamic experience, causing different adaptations at different stages of bilingual acquisition and use. The Dynamic Restructuring Model (DRM) [5] proposed an expansion–renormalisation trajectory for bilingualism-induced structural adaptations, which is contingent on the increasing experience of being bilingual. Following up on this, the Unified Bilingual Experiences Trajectory (UBET) model [18] combined suggestions by various other models and proposed a unified account suggesting that adaptations are subject to a variety of factors pertaining to the bilingual experience, including its duration, the intensity and diversity of language use, the frequency of language switching and the respective proficiency in each language spoken.

In this paper, we review the available evidence on the dynamic adaptations (structural, metabolic and functional) that subcortical structures undergo as a direct result of the cognitively demanding experience of bilingualism. Recent findings, especially from studies treating bilingualism as a gradient of experiences, are emphasised and compared against the models explaining dynamic bilingualism-induced neuroplasticity. The paper will first highlight the subcortical regions implicated in managing the use and control of more than one language, followed by evidence for structural adaptations observed in individuals with increasing or different language control and processing demands, from bilinguals to multilinguals and interpreters. Thereafter, it will highlight metabolic changes in subcortical regions, which support the structural adaptations found. This is followed by a review on related adaptations in subcortical functional connectivity. Finally, the implications of these findings for the proposed neural and cognitive reserves in healthy ageing and progressive neurodegeneration are discussed before concluding with suggestions for future research directions.

Bilingualism-induced subcortical and cerebellar adaptations

Much of the available evidence on bilingualism-induced structural adaptations has been reported with respect to the cerebellum and subcortical areas that subserve language acquisition, processing and control, including the thalamus, caudate nucleus, globus pallidus and putamen. The relevant roles played by these subcortical structures include acquiring and processing grammatical rules, managing lexicosemantic operations, processing phonological repertoires, controlling speech articulation, and language switching. Crucially, language switching taps domain-general cognitive functions such as executive control, cognitive flexibility, and procedural learning, which all involve the caudate nucleus [14,19].

Correspondingly, expansions in the caudate nucleus have been observed in bilinguals when compared with monolinguals [20,21], reflecting the increased need of the former group for executive control. Similar effects have been reported in the globus pallidus and putamen, which have been implicated in fluency and speech articulatory processes [20,22], and the thalamus, which is involved in language selection, motor programming relating to articulatory processes and lexical access [19]. Since managing languages involves various language systems, a bilingual would also have to process additional sets of phonological and grammatical rules and perform more motor speech planning, which are functions related to the cerebellum [19,23]. Indeed, when compared to monolinguals, bilinguals have exhibited larger cerebellar volumes [22], which have also been linked to better performance in grammatical tasks [23]. Crucially, much of this evidence has been reported in experienced bilinguals, for example, lifelong bilinguals or sequential bilinguals who have been immersed in bilingual environments for long periods, suggesting that the acquisition and control needs that drive these adaptations only emerge as a result of substantial and sustained bilingual experience. Critically, these were the findings that inspired models such as the DRM and UBET. Newer studies that used continuous measures of the bilingual experience have produced evidence which corroborates the predictions of these models: for example, positive correlations have been reported between bilingual experience and the volumes of the putamen and cerebellum among individuals living in a highly immersive bilingual environment [24]. These findings line up with the predictions of the UBET, which posits that high intensity and diversity of language use are associated with neurocognitive adaptations. Moreover, nonlinear relationships have been reported between the volumes of the caudate nucleus and nucleus accumbens, with initial increases in less experienced bilinguals plateauing in bilinguals with the most experience, accompanied by a linear relationship between increasing bilingual experience and the volumes of the putamen and thalamus [7]. These patterns lend support to the DRM which predicts that, with increasing language experience, the caudate nucleus is the first structure to expand and subsequently renormalise due to its key role in cognitive control. This should be later followed by effects in other subcortical regions, such as the putamen and globus pallidus, which subserve more secondary tasks of bilingualism, including articulatory control for language production [25]. Conversely, a more recent study only reported a linear relationship between the duration of bilingual engagement and the volume of caudate nucleus, but not the putamen, globus pallidus and thalamus, among young adults with variable dual language use experiences [26]. The lack of these additional effects, and of renormalisation of the caudate nucleus, could be attributed to the overall degree of

bilingual experience in the sample, meaning that such effects could be observed at even higher levels of bilingual experiences or the way that bilingual experience was measured, which differed from Ref. [7]. This showcases some important shortcomings in the literature, in that different methodologies may yield different patterns, accompanied by the observation that lack of effects in a certain region could either mean that the region has not been affected or that it has already re-normalised [27], two possibilities that cannot be distinguished in cross-sectional studies. It should be reminded though that, where a region is in the expansion–renormalisation cycle will inevitably relate to *both* its function *and* the amount of bilingual experiences (see Ref. [5]), and it may be that some regions (e.g. the caudate nucleus) are very important even at lower levels of bilingual experience, and therefore more susceptible to restructuring, compared with the cerebellum or the thalamus for example. These observations may explain a lot of inconsistencies in the field and call for careful thinking of the designs and the samples that are used (see Section *Wrapping up*).

Multilinguals and interpreters

While the number of studies on subcortical structural adaptations in multilinguals remains small, emerging evidence suggests parallels with findings from immersed or experienced bilinguals. For example, in a cross-sectional study comparing German–Italian–English trilinguals to Italian monolinguals, the former were found to have larger putamen volumes, and more activation in the putamen during picture naming in the weaker languages, with both findings possibly reflecting additional needs for articulatory control [25]. In another study, the volume of caudate nucleus in multilinguals was reported to correlate positively with their language experience (measured as earlier Age of Acquisition (AoA) and higher proficiency), and this was attributed to increasing needs for handling of lexico-semantic alternatives in multiple languages [21]. Moreover, a recent study [27] compared monolinguals, bilinguals, trilinguals, and quadrilinguals and reported patterns of expansion–renormalisation for the nucleus accumbens, putamen and globus pallidus, in that volumes in quadrilinguals were smaller than in trilinguals and comparable to monolinguals. Given the roles played by these structures in language control, lexical-semantic operations and articulation, the authors interpreted these as the optimisation of relevant neural resources as language experience increases, echoing the DRM predictions.

A unique multilingual population with arguably higher levels of language experience are translators and interpreters, who possess exceptional language-switching abilities and use them frequently. Simultaneous interpreters, in particular, face the challenging task of translating in real time. A recent study compared the volumes

of the caudate nucleus and putamen among interpreters, translators and bilingual controls and reported that caudate volumes increased with bilingual experiences across all groups but returned to baseline levels specifically in interpreters and translators at higher experience levels [28]. Crucially, the putamen, a structure subserving simultaneity and articulatory control, showed an expansion–renormalisation pattern in interpreters only, while translators and nonprofessional controls exhibited a linear volumetric increase as a function of increasing experience, further highlighting the region-specific nature of bilingualism-related brain adaptations. A study with individuals undergoing simultaneous interpreting training reported significant increases in structural connectivity in two subnetworks that involve the basal ganglia and the cerebellum [29]. More specifically, the first subnetwork, which connects between frontal regions and the basal ganglia, has been linked to cognitive and language control, while the second subnetwork, which involves the cerebellum, has been posited to be an essential language control network. These changes in specific control-related neural networks have been suggested to manage the extreme language control that occurs during interpreter training.

Bilingualism and brain metabolism

Expanding on the findings of experience-based structural neuroplasticity, the study of changes in indices of metabolic activity related to structural adaptations provides further depth to our understanding. Indeed, the above-described pruning processes correspond to regional changes in the concentrations of certain metabolites. In the case of bilingualism, only one study to date has focused on a large cluster overlapping with parts of the caudate nucleus and the putamen, and measured concentrations of metabolites that are related to processes of ageing, neuronal death and experience-based neuroplasticity [30]. That study reported steeper changes with ageing for bilinguals versus monolinguals (increases in myo-Inositol and decreases in N-acetylaspartate), while the concentrations for both metabolites were significantly predicted by a measure of bilingual experience. This pattern was interpreted as evidence for the increasing pruning processes that take place in subcortical structures as a result of the bilingual experience, effects that are distinguishable from, and additive to, the expected effects of ageing.

Bilingualism and brain function at rest

Whilst the relationship between bilingualism-induced changes to brain structure and function is still not fully understood, there are some notable changes in the connectivity patterns observed in bilinguals, with differing effects as language experience increases. Functional connectivity at rest provides an overview of functionally coupled regions, allowing researchers to

determine functional connectivity patterns in intra- and inter-hemispheric brain networks that represent the baseline state of the bilingual brain [31], without the confounds of task-specific demands and effects; besides, the latter do not apply to structural effects either, so looking at connectivity at rest allows for the study of the functional equivalents of structural effects. This intrinsic state of connectivity in bilinguals reflects the overall functional effects of bilingualism as a lifelong experience, which shapes neural communication and efficiency. For example, more widespread functional networks have been reported in bilinguals compared to monolinguals [32], with increased functional connectivity found in posterior regions. These functional changes were also correlated with the size of the caudate nucleus in the bilingual group, stressing its role in the control of multiple language use. Moreover, Gullifer et al. [33] reported that social diversity of bilingual language use positively correlates to connectivity between the anterior cingulate cortex and the bilateral putamen, regions involved in language and executive control functions, and conflict monitoring, but also to connectivity between the caudate nucleus and bilateral superior temporal gyrus, which is involved in auditory processing and the encoding of speech sounds. A more recent study revealed stronger connections from pre-frontal regions to temporal, occipital, cerebellar and some bilateral limbic regions at rest, combined with weaker subcortical connectivity in bilingual compared to monolingual children [34]. These patterns suggest more long-distance functional connections in bilinguals and more short-distance interhemispheric functional connections in monolinguals, supporting the results of Frutos-Lucas et al. in finding more widespread connectivity as bilingual experience increases. Together, these studies illustrate that the functional connectivity of the bilingual brain is constantly changing in response to the pressures placed on it by managing multiple languages, including changes to whole-brain and subcortical connectivity, which appear to reflect an increase in efficiency as the result of concurrent changes to the structural dynamics of the brain.

Ageing and neurodegeneration

The above-discussed findings point towards processes that change the structure and function of subcortical structures in order to provide more efficient and potentially more resilient networks. However, given that subcortical structures also tend to be primary targets for healthy ageing and also progressive neurodegenerative diseases, an interesting question emerges: do the effects of bilingualism and ageing interact, and in a way that mitigates the effects of ageing [35]? This is in the light of suggestions that bilingualism acts as a form of cognitive reserve in older age and in neurodegenerative diseases such as Huntington's disease [36] and multiple

sclerosis [37] (for review, see Ref. [38]). Some corroborating evidence has been presented for the neighbouring region of the hippocampus for healthy ageing bilinguals and bilinguals diagnosed with MCI [39,40], but the literature remains extremely limited as far as the basal ganglia and the cerebellum are concerned. For example, while some studies report no structural differences between older bilinguals and monolinguals [41], Anderson et al. [42] reported smaller volumes of the caudate nucleus and putamen in healthy older bilinguals compared to monolinguals while having equal or even better performance in cognitive tasks. This pattern suggests preserved cognitive abilities for bilinguals with a declining brain (or a *cognitive reserve*) [43]. Conversely, *greater* volumes have been reported in the thalamus and globus pallidus for bilingual versus monolingual patients with Alzheimer's disease matched in terms of cognitive impairment [44]. This suggests better preservation of brain tissue in neurodegenerative diseases, or a *brain reserve* [45]. Moreover, more severe hypometabolism but better memory abilities have been reported for bilinguals compared to monolinguals in brain regions, including the putamen and the cerebellum [46], pointing towards a cognitive reserve. The scarcity of the evidence does not allow for strong conclusions; however, given recent suggestions that the basal ganglia are key regions in a shift from frontal to subcortical and posterior regions in bilinguals [47], which also appears to reverse the typical posterior to anterior shift that has been reported in ageing individuals [48], it remains important for these structures to be further investigated with respect to how bilingualism affects them. This will also help update the models on experience-based neuroplasticity, which have largely been based on evidence from younger healthy bilinguals.

Wrapping up

Using bilingualism as a test case, this paper has highlighted the structural and functional malleability of subcortical structures as a response to challenging cognitive experiences. It has also demonstrated how the principles of neuroplasticity extend beyond motor skill learning to various domains of learning and expertise like bilingualism. Specifically, the findings reviewed here include both linear and nonlinear structural adaptations of subcortical regions that subserve functions crucial for bilingualism such as articulatory processes, procedural learning, and most crucially, language control. Furthermore, these findings underscore the importance of experience-based factors, or the 'degree' of bilingualism, which appear to predict observable patterns of adaptations, lending support to the DRM and UBET models. We also reviewed bilingualism-induced changes in resting-state functional connectivity in networks involving the same subcortical structures, which points towards more widespread functional adaptations that may be linked to structural adaptations. The evidence

remains limited, calling for more extensive investigations through functional Magnetic Resonance Imaging (fMRI) and Electroencephalogram (EEG) studies (at rest and on-task), which will allow us to understand how structural and functional adaptations correspond to each other and consequently improve on the existing models. In doing so, particular emphasis should be given on the patterns of such adaptations in the relatively understudied groups at the highest levels of bilingual experience, for example, interpreters. This requires the development of nuanced measures of bi-/multilingualism to account for the wide variation in individual language experience. Longitudinal designs will also help extend these models by adding a lifespan perspective to the proposed dynamic adaptations, which have been mainly observed in cross-sectional studies that do not necessarily account for fluctuations in individuals' experiences. Such a holistic approach will also allow for the study of how these adaptations interact with the effects of ageing on the healthy and diseased brain and better describe the mechanisms underlying the proposed neural and cognitive reserves. Summing up, the reviewed effects reflect expansion–renormalisation patterns that have been described in major theories of experience-based neuroplasticity after skill acquisition; consequently, bilingualism is highlighted as a long-term neuroplasticity-inducing experience that helps us understand the mechanisms underlying the adaptability of the human brain in dynamic and changing environments.

Funding

This work was supported by an Amsterdam University Medical Center Career Bridging Grant awarded to MK and an Economic and Social Research Council (ESRC) PhD studentship [grant number: 2604285] awarded to AS.

CRediT authorship contribution statement

Jia'en Yee: Conceptualization, Writing original draft, Writing – review & editing. **Michal Korenar:** Writing original draft, Funding acquisition. **Alex Sheehan:** Writing original draft, Funding acquisition, Writing – review & editing. **Christos Pliatsikas:** Conceptualization, Supervision, Project administration, Writing original draft, Writing – review & editing.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare none.

Acknowledgements

None.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Wenger E, Papadaki E, Werner A, Kühn S, Lindenberger U: **Observing plasticity of the auditory system: volumetric decreases along with increased functional connectivity in aspiring professional musicians.** *Cereb Cortex Commun* 2021, 2:tgab008.
2. Wenger E, Kühn S, Verrel J, Mårtensson J, Bodammer NC, Lindenberger U, Lövdén M: **Repeated structural imaging reveals nonlinear progression of experience-dependent volume changes in human motor cortex.** *Cereb Cortex* 2017, 27:2911–2925.
3. Gerber P, Schlaffke L, Heba S, Greenlee MW, Schultz T, Schmidt-Wilcke T: **Juggling revisited — a voxel-based morphometry study with expert jugglers.** *NeuroImage* 2014, 95:320–325.
4. Maguire EA, Gadian DG, Johnsrude IS, Good CD, Ashburner J, Frackowiak RSJ, Frith CD: **Navigation-related structural change in the hippocampi of taxi drivers.** *Proc Natl Acad Sci USA* 2000, 97:4398–4403.
5. Pliatsikas C: **Understanding structural plasticity in the bilingual brain: the Dynamic Restructuring Model.** *Biling Lang Cogn* 2020, 23:459–471.
6. Wenger E, Brozzoli C, Lindenberger U, Lövdén M: **Expansion and renormalization of human brain structure during skill acquisition.** *Trends Cogn Sci* 2017, 21:930–939.
7. Korenar M, Treffers-Daller J, Pliatsikas C: **Dynamic effects of bilingualism on brain structure map onto general principles of experience-based neuroplasticity.** *Sci Rep* 2023, 13:3428.
This study shows clear nonlinear patterns of experience-based neuroplasticity induced by bilingualism.
8. Chang C, Chen Y, Yen N: **Nonlinear neuroplasticity corresponding to sports experience: a voxel-based morphometry and resting-state functional connectivity study.** *Hum Brain Mapp* 2018, 39:4393–4403.
9. Schmidt S, Gull S, Herrmann K-H, Boehme M, Irintchev A, Urbach A, Reichenbach JR, Klingner CM, Gaser C, Witte OW: **Experience-dependent structural plasticity in the adult brain: how the learning brain grows.** *NeuroImage* 2021, 225:117502.
10. Wenger E, Kühn S: **Neuroplasticity.** Cognitive Training: An Overview of Features and Applications. 2nd ed, Springer Nature; 2021:69–83.
11. Green DW: **Mental control of the bilingual lexico-semantic system.** *Bilingualism* 1998, 1:67–81.
12. Marian V, Spivey M: **Competing activation in bilingual language processing: within- and between-language competition.** *Biling Lang Cogn* 2003, 6:97–115.
13. Kroll JF, Bobb SC, Hoshino N: **Two languages in mind: bilingualism as a tool to investigate language, cognition, and the brain.** *Curr Dir Psychol Sci* 2014, 23:159–163.
14. Ullman MT: **The declarative/procedural model.** *Neurobiology of Language.* Elsevier; 2016:953–968.
15. Middleton FA, Strick PL: **Basal ganglia and cerebellar loops: motor and cognitive circuits.** *Brain Res Brain Res Rev* 2000, 31:236–250.
16. Gallo F, Abutalebi J: **The unique role of bilingualism among cognitive reserve-enhancing factors.** *Biling Lang Cogn* 2024, 27:287–294.
This paper provides an excellent overview of the current knowledge on bilingualism and its neuroprotective effects.
17. Pliatsikas C, DeLuca V, Voits T: **The many shades of bilingualism: language experiences modulate adaptations in brain structure.** *Lang Learn* 2020, 70:133–149.

18. DeLuca V, Segaert K, Mazaheri A, Krott A: **Understanding bilingual brain function and structure changes? U bet! A unified bilingual experience trajectory model.** *J Neurolinguist* 2020, **56**:100930.
 19. Abutalebi J, Green DW: **Neuroimaging of language control in bilinguals: neural adaptation and reserve.** *Biling Lang Cogn* 2016, **19**:689-698.
 20. Pliatsikas C, DeLuca V, Moschopoulou E, Saddy JD: **Immersive bilingualism reshapes the core of the brain.** *Brain Struct Funct* 2017, **222**:1785-1795.
 21. Hervais-Adelman A, Egorova N, Golestani N: **Beyond bilingualism: multilingual experience correlates with caudate volume.** *Brain Struct Funct* 2018, **223**:3495-3502.
 22. Burgaleta M, Sanjuán A, Ventura-Campos N, Sebastian-Galles N, Ávila C: **Bilingualism at the core of the brain. Structural differences between bilinguals and monolinguals revealed by subcortical shape analysis.** *NeuroImage* 2016, **125**:437-445.
 23. Pliatsikas C, Johnstone T, Marinis T: **Grey matter volume in the cerebellum is related to the processing of grammatical rules in a second language: a structural voxel-based morphometry study.** *Cerebellum* 2014, **13**:55-63.
 24. Marin-Marín L, Costumero V, Ávila C, Pliatsikas C: **Dynamic effects of immersive bilingualism on cortical and subcortical grey matter volumes.** *Front Psychol* 2022, **13**:1-11.
 25. Abutalebi J, Rosa PAD, Castro Gonzaga AK, Keim R, Costa A, Perani D: **The role of the left putamen in multilingual language production.** *Brain Lang* 2013, **125**:307-315.
 26. DeLuca V, Voits T, Ni J, Carter F, Rahman F, Mazaheri A, Krott A, Segaert K: **Mapping individual aspects of bilingual experience to adaptations in brain structure.** *Cereb Cortex* 2024, **34**:bhae029.
- This study directly tests the predictions of the UBET model, and reports differentiated neuroplastic cortical subcortical effects caused by different aspects of bilingual experiences.
27. Yee J, Yap NT, Korenar M, Saddy JD, Pliatsikas C: **Subcortical restructuring as a function of multilingualism: insights from monolinguals, bilinguals, trilinguals and quadrilinguals.** *Biling Lang Cogn* 2023, **1-14**, <https://doi.org/10.1017/S136672892300086X>.
- This is the first study to directly test the effects of multilingualism on subcortical structures.
28. Korenar M, Treffers-Daller J, Pliatsikas C: **Brain structure adapts dynamically to highly demanding bilingual experiences: insights from interpreters and translators.** *Ampersand* 2023, **11**:100148.
 29. Van de Putte E, De Baene W, García-Pentón L, Woumans E, Dijkgraaf A, Duyck W: **Anatomical and functional changes in the brain after simultaneous interpreting training: a longitudinal study.** *Cortex* 2018, **99**:243-257.
 30. Pliatsikas C, Pereira Soares SM, Voits T, DeLuca V, Rothman J: **Bilingualism is a long-term cognitively challenging experience that modulates metabolite concentrations in the healthy brain.** *Sci Rep* 2021, **11**:7090.
- This is the first study to show that bilingual experiences can predict metabolite concentrations in the basal ganglia, above and beyond the effects of ageing.
31. Buckner RL, Krienen FM, Yeo BTT: **Opportunities and limitations of intrinsic functional connectivity MRI.** *Nat Neurosci* 2013, **16**:832-837.
 32. de Frutos-Lucas J, López-Sanz D, Cuesta P, Bruña R, de la Fuente S, Serrano N, López ME, Delgado-Losada ML, López-Higes R, Marcos A, et al.: **Enhancement of posterior brain functional networks in bilingual older adults.** *Bilingualism* 2020, **23**:387-400.
 33. Gullifer JW, Chai XJ, Whitford V, Pivneva I, Baum S, Klein D, Titone D: **Bilingual experience and resting-state brain connectivity: impacts of L2 age of acquisition and social diversity of language use on control networks.** *Neuropsychologia* 2018, **117**:123-134.
 34. Kwon YH, Yoo K, Nguyen H, Jeong Y, Chun MM: **Predicting multilingual effects on executive function and individual connectomes in children: an ABCD study.** *Proc Natl Acad Sci* 2021, **118**:e2110811118.
 35. Gallo F, DeLuca V, Prystauka Y, Voits T, Rothman J, Abutalebi J: **Bilingualism and aging: implications for (delaying) neurocognitive decline.** *Front Hum Neurosci* 2022, **16**:819105.
 36. Calabria M, Pérez Pérez J, Martínez-Horta S, Horta-Barba A, Carceller M, Kulisevsky J, Costa A: **Language reconfiguration in bilinguals: a study with Huntington's disease patients.** *LAB* 2021, **11**:459-483.
 37. Aveledo F, Higuera Y, Marinis T, Bose A, Pliatsikas C, Meldaña-Rivera A, Martínez-Ginés ML, García-Domínguez JM, Lozano-Ros A, Cuello JP, et al.: **Multiple sclerosis and bilingualism: some initial findings.** *LAB* 2021, **11**:551-577.
 38. Voits T, Pliatsikas C, Robson H, Rothman J: **Beyond Alzheimer's disease: can bilingualism be a more generalized protective factor in neurodegeneration?** *Neuropsychologia* 2020, **147**:107593.
 39. Voits T, Robson H, Rothman J, Pliatsikas C: **The effects of bilingualism on hippocampal volume in ageing bilinguals.** *Brain Struct Funct* 2022, **227**:979-994.
 40. Voits T, Rothman J, Calabria M, Robson H, Aguirre N, Cattaneo G, Costumero V, Hernández M, Puig MJ, Marin-Marín L, et al.: **Hippocampal adaptations in mild cognitive impairment patients are modulated by bilingual language experiences.** *Biling Lang Cogn* 2023, <https://doi.org/10.1017/S1366728923000354>
 41. Del Maschio N, Sulpizio S, Gallo F, Fedeli D, Weekes BS, Abutalebi J: **Neuroplasticity across the lifespan and aging effects in bilinguals and monolinguals.** *Brain Cogn* 2018, **125**:118-126.
 42. Anderson JAE, Grundy JG, Grady CL, Craik FIM, Bialystok E: **Bilingualism contributes to reserve and working memory efficiency: evidence from structural and functional neuroimaging.** *Neuropsychologia* 2021, **163**:108071.
 43. Berkes M, Bialystok E: **Bilingualism as a contributor to cognitive reserve: what it can do and what it cannot do.** *Am J Alzheimers Dis Other Dement* 2022, **37**:15333175221091417.
 44. Raji CA, Meysami S, Merrill DA, Porter VR, Mendez MF: **Brain structure in bilingual compared to monolingual individuals with Alzheimer's disease: proof of concept.** *J Alzheimer's Dis* 2020, **76**:275-280.
 45. Macbeth A, Higby E, Atagi N, Chiarello C: **Evidence for cognitive and brain reserve supporting executive control of memory in lifelong bilinguals.** *Neuropsychologia* 2021, **160**:107958.
 46. Perani D, Farsad M, Ballarín T, Lubian F, Malpetti M, Fracchetti A, Magnani G, March A, Abutalebi J: **The impact of bilingualism on brain reserve and metabolic connectivity in Alzheimer's dementia.** *Proc Natl Acad Sci USA* 2017, **114**:1690-1695.
 47. Grundy JG, Anderson JAE, Bialystok E: **Neural correlates of cognitive processing in monolinguals and bilinguals.** *Ann N Y Acad Sci* 2017, **1396**:183-201.
 48. Grant A, Dennis NA, Li P: **Cognitive control, cognitive reserve, and memory in the aging bilingual brain.** *Front Psychol* 2014, **5**.