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Subcortical gray matter aging and attentional control in amateur musicians and nonmusicians

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Abstract

Aging is associated with declines in attentional control. While most studies have explored the relationship between brain structure and attention at the cortical level, subcortical structures remain largely overlooked. Leisure activities, such as musical practice, are thought to promote brain reorganization and help preserve cognitive function in aging. However, evidence for such effects at the subcortical level remains limited. In this cross-sectional study, we examined the relationship between age, subcortical gray matter, and attentional control in amateur musicians and nonmusicians. A total of 108 adults (20–88 years) were recruited, including 34 singers, 37 instrumentalists, and 37 active nonmusicians. Participants completed an auditory selective attention task and a visual inhibition task. Anatomical magnetic resonance imaging (MRI) images were acquired to examine the relationship between subcortical volumes and attentional measures. Our results indicate that aging is associated with worse attentional control and smaller subcortical volumes. While no group differences in subcortical volume were observed, significant interactions emerged between musical activity and subcortical volume in relation to attentional control, particularly in inhibition. Notably, in singers, greater musical experience and smaller subcortical volumes were linked to better inhibition. These results refine our understanding of subcortical contributions to attentional control in aging musicians and nonmusicians.

KEYWORDS
aging, amygdala, attention control, basal ganglia, cerebellum, musicians, thalamus

INTRODUCTION

Attentional control involves selecting specific stimuli, shifting focus based on the salience of a stimulus, and inhibiting distractions. While several models like the Attention System[1] and the Ventral and Dorsal Attention Pathways[2] describe the cortical dynamics of attention, subcortical mechanisms remain less well understood. A recent review highlighted this knowledge gap, noting that most studies investigating neurocognitive mechanisms have primarily focused on the cortex, while overlooking subcortical structures.[3]

Emerging evidence suggests that the caudate nucleus, the putamen, the pallidum, different thalamic nuclei and the cortico–centro–medial nuclear group of the amygdala play a role in attention.[3] The cerebellum, especially in lobules VI, VIIB, VIIIA, and crus I-II, has also been implicated.[4] The cerebellum is reported to be functionally connected to the ventral and dorsal attentional network.[4] It has also been proposed that the basal ganglia, especially the pallidum, would be implicated in attention switching.[5,6] The thalamus is thought to link memory and attentional processes, as evidenced by studies in rodents[7] and

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humans.[8–10] Specific nuclei, including the anterior, intralaminar, ventral lateral, lateral dorsal, pulvinar, and lateral geniculate (LGN) nuclei, are associated with memory-driven and orientation of attention. Moreover, larger medial thalamic nuclei volume was found in children and teenagers with attention deficit hyperactivity disorder,[11] suggesting these nuclei play a central role in attention processes. Finally, the amygdala is also believed to play a role in attention. Animal studies have suggested that the central[12] and the anterior nuclei[13] of the amygdala are implicated in bottom-up attention. Others have suggested a role in top-down attention and selective attention.[14] In sum, the subcortical attentional system is complex and wide-ranging, with multiple structures interacting to support various aspects of attention.

Attentional control, like most cognitive abilities, declines in older age, often impacting older adults' autonomy.[15] Several studies have suggested that practicing a cognitively demanding leisure activity, like musical activities, could reduce age-related cognitive decline (for a review, see ref.[16]). Salthouse[17] developed a framework that is helpful to interpret the impact of practicing a cognitively demanding activity on cognitive aging. The first hypothesis proposed by Salthouse, the *differential–preservation hypothesis*, suggests that the practice of a cognitively demanding activity reduces the rate of age-related decline, observable through an interaction between age and group (those who practice a cognitively demanding activity and those who do not). The *preserved differentiation hypothesis*, in contrast, proposes that the practice of a cognitively demanding activity is associated with better cognitive performance but not with a reduced rate of age-related decline, observable through a main effect of group. According to Salthouse, only patterns that are consistent with the differential–preservation hypothesis are indicative of a reduction of cognitive aging. This general paradigm was later adapted to musicians.[18]

While these cognitive models help characterize how musical practice might influence cognitive trajectories in aging, they do not account for the underlying neurobiological mechanisms. Complementary frameworks have been developed to examine the effects of leisure activities on brain structure and function, providing a neural-level perspective on plasticity in aging. According to the Scaffolding Theory of Aging and Cognition (STAC-r),[19,20] life experiences, such as leisure activity, can moderate brain decline by having positive effects on brain structure and function, as well as triggering compensatory scaffolding.[19,20] The concept of compensatory scaffolding, or compensatory plasticity, refers to the expansion of networks to include homologue regions of the other hemisphere and strengthened within-network connectivity. The brain reserve (BR) hypothesis proposes that engaging in a cognitively demanding activity can mitigate, at least in part, age-related atrophy.[21] According to this view, brain regions that benefit from practicing an activity should be larger in those who engage in an activity compared to those who do not. In contrast, the Expansion–Renormalization model (ERM) proposes that learning initially induces structural expansion, followed by a return to baseline once performance stabilizes.[22] Consequently, a person with extensive experience in an activity would not have a larger regional brain volume compared to a person of the same age with no experience. In a previous study, we found evidence of structural plasticity at the cortical level in amateur singers, consistent with the ERM. In contrast, results in nonmusicians were aligned with the BR hypothesis while findings in instrumentalists were consistent with neither model.[23] In that study, a global experience score (EXP) was used as a proxy of performance, under the assumption that individuals with higher experience would be closer to their peak performance. Interestingly, despite having the lowest EXP, singers showed the least age-related cortical decline in specific structures, including the bilateral superior frontal sulcus and the right superior temporal sulcus. Another study also reported findings consistent with the ERM.[24] In this study, professional musicians with higher proficiency in an absolute pitch task had a thinner cortex in several frontal and parietal regions compared to less proficient musicians. However, most studies have shown higher gray matter volumes in professional musicians than nonmusicians in specific regions in the frontal, temporal, somatosensory, and auditory cortices as well in the cerebellum,[24–28] supporting the BR hypothesis. A study comparing professional and amateur musicians to nonmusicians reported evidence of coexisting positive (BR) and negative (ERM) effects of expertise on gray matter density.[29] In sum, while some evidence suggests a pattern of plasticity resembling BR in professional musicians, too few studies have explored plasticity in amateur singers to draw firm conclusions about the nature of the neural changes associated with an amateur-level musical practice—whether expansion, renormalization, or both.

Musical practice, with its high attentional demand, provides a valuable model for studying experience-induced plasticity in the subcortical attention system. Beyond attentional control, the role of subcortical structures in processing tempo and pitch suggests that musical training may further enhance plasticity in these regions. Brown et al.[30] proposed that the basal ganglia are engaged in perceiving and controlling predictable temporal sequences, while the cerebellum would process less predictable sequences. Both structures interact with other motor regions, such as the supplementary motor area, which is important in rhythm and pitch processing, via the cortico–subcortical loop. According to Brown et al., all musicians engage this system, with greater interactions between these regions as expertise increases from amateur to professional. Further, it has been shown that musical practice is associated with stronger connectivity between the left thalamus and the precuneus and the posterior cingulate cortex.[31] Finally, for the amygdala, a study found that the superficial, medial, central, and laterobasal nuclei of the amygdala were larger in professional musicians compared to nonmusicians.[32] In sum, musical practice may promote structural and functional plasticity in these subcortical and cortical regions, potentially supporting enhanced attentional capacities.

The first objective of this study was to examine the aging of subcortical gray matter in the thalamus, caudate, putamen, pallidum, amygdala, and cerebellar cortex, in singers, instrumentalists and nonmusician active controls. The first hypothesis was that aging would be negatively associated with the structure of the subcortical executive network, with reduced age effects in musicians, consistent with the differential preservation perspective.[17] The second objective was to examine the relationship between the subcortical attention network and attentional control in these groups. The second hypothesis was that the

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negative impact of aging on brain structure would be associated with worse attention/inhibition performance. The third hypothesis was that the relationships between brain structure, attentional performance, and musical experience would be activity-specific rather than domain-specific. This hypothesis is based on a previous study with the same sample that focused on the cortex.[23] Specifically, singers would show a pattern consistent with the ERM, nonmusicians would show a pattern consistent with the BR hypothesis and instrumentalists would show a pattern inconsistent with both models. To achieve these goals, healthy adults engaged in a musical activity (singing or playing a musical instrument), were compared to healthy adults engaged in a nonmusical activity, like knitting, golfing, and billiards.

METHOD

This study is part of the PICCOLO Project (Projet de recherche sur les effets de la Pratique d'un Instrument ou du Chant sur la COgnition, le Langage et l'Organisation cérébrale),[23,33–35] approved by the Comité d'éthique de la recherche sectoriel en neurosciences et santé mentale, Institut Universitaire en Santé Mentale de Québec (#2019-1733). All participants provided written informed consent.

Participants

A total of 122 healthy adults between 20 and 88 years old were recruited. All were Quebec French speakers, with normal or corrected-to-normal vision, no diagnosed language, speech, hearing, neurodegenerative, psychological or psychiatric disorder. According to the Edinburgh Handedness Inventory,[36] all participants were right-handed or ambidexter writing with their right hand. All participants passed the Montreal Cognitive Assessment (MoCA)[37] using the Quebec norms for middle-aged and elderly Quebec French speakers.[38] Although it was not an exclusion criteria, all participants were administered the 15 items geriatric depression screening scale (GDS)[39] to assess their mood.

Participants were separated in three groups based on their main activity: singers, instrumentalists, and people practicing a nonmusical cognitive-motor activity. To be included, participants had to practice at least 3 h per week for the past 5 years. Participants could not engage in any other activity, musical or not, more than half the time they spent on their main activity. The activity needed to be practiced at an amateur level, meaning that their main source of income was not tied to the practice of this activity. Because 13 participants did not complete the magnetic resonance imaging (MRI) visit, they were not included in the present study. One instrumentalist was removed as an outlier ($<Q1 - 1.5 \times IQR$, where IQR stands for intraquartile range) for the experience score (the participant had a very low amount of experience compared to the rest of the sample). The final sample for this study ($N = 108$) is therefore composed of 34 singers (mean age = 61.62 ± 16.19; 23–88; 65% females), 37 instrumentalists (mean age = 52.05 ± 18.90; 20–88; 30% females), and 37 controls (mean age = 55.57 ± 18.97; 20–87; 49% females). Participants' characteristics are provided in Table 1. The groups were comparable in terms of age, education, number of spoken languages, cognition (MoCA), depression symptoms (GDS), self-reported health, life habits score (LHS), and pure tone hearing. The LHS was used as a general life habits index and is based on nine of the twelve potentially modifiable risk factors identified by the 2020 Lancet Commission for dementia, intervention, and care.[40] Details of the calculations are presented in Supporting Information 1. The groups were also comparable in terms of the number of years of practice of their main activity and the average number of hours of weekly practice in the last 5 years. However, the instrumentalists had significantly more experience, measured by a global experience score (EXP), compared to controls and singers. The EXP is a composite score that takes into account the age of onset (AO) and the ratio between the number of years of practice and the age of the participant (RP): $\frac{1}{AO - (AO \times RP)}$. A higher EXP means that a person has more experience, meaning that they have started to practice early in life and have been practicing during a large proportion of their life. To achieve a normal distribution, the raw scores were transformed using the natural logarithm.

Procedures

The study included two visits. The first visit took place at the Speech and Hearing Neuroscience Laboratory in Quebec City, Canada and was divided into two parts, for a total of approximately 3 h. The first part took place in a quiet interview room where questionnaires and cognitive tests were administered. The second part took place in a double-walled sound-attenuated room where an audiometric assessment and a second set of cognitive assessment (computer tasks) were administered, as well as speech, language and voice tasks not discussed here.[34] The full cognitive assessment analysis has been published elsewhere.[33] This study revealed a significant group difference mainly in two tasks: the Test of Attention in Listening (TAiL), a selective auditory attention computer task, and the Color-Word Interference Test (CWIT), a visual inhibition task. Therefore, only these two tasks will be analyzed in this study. The second visit was a multimodal MRI session at the IRM Québec Clinic in Quebec City, Canada.

Audiometric assessment

Audiometric assessment consisted of finding the pure tone thresholds in dB HL with a calibrated clinical audiometer (AC40, Interacoustic). For each ear, the pure tone average (PTA) was computed with the thresholds of six different frequencies (0.5, 1, 2, 3, 4, 6 kHz).

Test of Attention in Listening

The French version of the TAiL[41] was used to assess auditory selective attention. The TAiL is a computer task that is composed of three tests: auditory processing speed (Cued RT), attend frequency (AF),

TABLE 1 Participants' characteristics.

	Controls				Singers				Instrumentalists				ANOVA	
	N = 37 (49% ♀)				N = 34 (65% ♀)				N = 37 (32% ♀)					
Characteristics	*M*	SD	Min	Max	*M*	SD	Min	Max	*M*	SD	Min	Max	*F*	*p*
Age	55.57	18.97	20	87	61.62	16.19	23	88	52.05	18.90	20.00	88.00	2.511	0.0861
Education (years)[a]	14.7	2.22	11	18	14.85	2.44	10	18	15.22	2.30	11.00	21.00	0.478	0.621
Nb languages[b]	2.16	0.55	1	4	2.35	0.6	1	3	2.32	0.53	1.00	3.00	1.224	0.298
MoCA[c] (/30)	27.41	1.57	25	30	27.82	1.77	24	30	27.95	1.75	22.00	30.00	1.029	0.361
GDS[d] (/15)	1	1.62	0	7	0.97	1.57	0	7	0.78	0.98	0.00	3.00	0.253	0.777
Self-reported health[e]	5.15	0.82	3	7	5.27	1.14	3	7	5.21	1.05	3.00	7.00	0.133	0.875
Life habits score (/100)	9.48	6.55	0	28.39	9.83	7.47	0	29.82	8.07	4.93	0.00	16.20	0.775	0.463
Right ear PTA[g]	19.19	15.08	−4.17	59.17	19.44	13.63	−0.83	54.17	16.60	9.71	−2.50	33.33	0.532	0.589
Left ear PTA[g]	19.8	15.33	−3.33	70.83	19.85	14.16	0	53.33	17.84	12.39	−0.83	51.67	0.245	0.783
Better ear PTA[h]	16.82	13.09	−4.17	50	17.57	13.28	−0.83	53.33	14.71	10.00	−2.50	33.33	0.536	0.587
Years of practice[i]	25.07	15.99	8	80	27.62	16.23	5.08	72	32.19	17.77	6.00	65.00	1.722	0.184
Ratio of pratice[j]	0.47	0.24	0.11	0.92	0.45	0.22	0.08	0.83	0.61	0.21	0.14	0.86	5.374	**0.006**
Intensity of activity[k]	10.04	8.26	2.5	40	9.71	8.18	1.38	45.6	8.28	8.28	1.80	50.80	0.475	0.623
Age of onset[l]	25.97	19.34	5	62	27.51	19.17	3	69	12.82	7.31	5.00	40.00	9.031	**0.0002**
Experience[m]	−2.17	1.35	−4.01	0.91	−2.35	1.09	−4.09	−0.34	−1.37	0.88	−3.46	0.15	7.889	**0.0006**
Musical practice intensity[n]	0.18	0.32	0	1.36	4.64	3.56	0.64	16.75	6.32	6.79	0.25	35.44	18.72	**<0.0001**

Note: M, mean; SD, standard deviation of the mean; *N*, number of participants per group; ♀, female participants. *p*-values in bold indicate a statistically significant group difference.

[a]Number of years of education, standardized. Elementary = 6; High school = 11; CEGEP (general) = 13; CEGEP (technique) = 14; Undergraduate = 16; Master = 18 (includes medical doctors); PhD = 21; Medical doctors with specialization = 23.

[b]Number of spoken languages.

[c]MoCA, Montreal Cognitive Assessment. Higher scores indicate better cognitive functions.

[d]GDS, geriatric depression scale. The GDS-15 includes 15 yes/no questions. Each "negative" answer is worth one point; thus, a higher score indicates a more depressed state. For example, question one asks whether the person is globally satisfied with his/her life. A "no" answer is worth one point, whereas a "yes" answer is worth no point. The normal score is 3 ± 2, a score of 7 ± 3 suggests a mild depression, and a score of 12 ± 2 indicates a severe depression. No participant scored above 7.

[e]Self-reported health = self-reported physical health status on a scale of 0–7 (0 being lowest physical health level).

[f]Life habits score = measure of life habits dementia protection (LHS) based on the 2020 Lancet Commission for dementia prevention, intervention, and care.[40] Nine of the 12 factors were measured in our sample, corresponding to low education, hearing loss, traumatic brain injury, depression, social isolation, Type 2 diabetes, physical inactivity, alcohol consumption, and obesity. The details of the calculation are provided in Supporting Information 1.

[g]PTA, pure tone average thresholds measured in decibels at 0.5, 1, 2, 3, 4, 6 kHz for each ear.

[h]Better ear PTA = pure tone average thresholds (PTA) at 0.5, 1, 2, 3, 4, 6 kHz for the better ear, measured in decibels (dB).

[i]Years of practice = total years of active practice of signing, playing a musical instrument or practicing a cognitive-motor activity.

[j]Ratio of practice = ratio between years of practice and age.

[k]Intensity of activity = mean number of hours spent singing, playing a musical instrument or practicing a cognitive-motor activity (principal activity) each week over the past 5 years.

[l]Age of onset = age at which singers, instrumentalists or control participants began to practice their activity.

[m]Experience (EXP) = combination of the age of onset (AO) and the ratio of practice (RP) of the main activity. It consists of the multiplicative inverse of the subtraction between the age of onset and the product of the age of onset and the ratio of practice (1/(AO − (AO × RP)). A natural logarithm transformation was then performed to achieve normal distribution. A higher score indicates that a person started practicing early and has practiced for a large proportion of his life.

[n]Musical practice intensity = mean number of hours spent practicing a musical activity each week over the past 5 years.

and attend localization (AL). Each test consists of 40 pairs of pure tones, identical or not, presented in the same or different ears. In the Cued RT test, participant needed to press on a button as fast as they heard the second tone of the pair. In the AF test, the participant is asked to indicate if the two sounds of each pair are identical, that is, the same frequency, or not. To avoid perceptual difficulties, the spectral gap between the two tons of each trial was between 2 and 8 equivalent rectangular bandwidths, which is well above the frequency discrimination threshold. In the AL test, the participant is asked to indicate if the two sounds of each pair are presented in the same ear or not. Before each test, the sound level was adjusted at a comfortable level and a five-trial practice was performed. For the three tests,

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the reaction time (RT) of the corrects trials and the error rate (ER) was obtained. According to TAiL directives, trials with a RT over 2 s in Cued RT was considered a failure. For the three tests, trials with a RT over or below ±3 SD than the participant's mean were excluded; none were removed. The TAiL provides measurements of two components of selective attention: distractibility and conflict resolution. Each component is calculated for each task as a cost in RT and ER. The distractibility score represents the cost of attention when there is a change in a distracting modality (different localization in AF, different frequencies in AL). The conflict resolution score represents the cost of attention when there is incongruence between both modalities. For AF and AL, there is congruence when two identical tones are presented in the same ear (same–same) and when two different tones are presented in different ears (different–different). There is incongruence when two identical tones are presented in different ears (same–different) and when two different tones are presented in the same ear (different–same). A higher distractibility or conflict resolution scores indicate a higher cost of attention. Equations to obtain both scores are presented in Supporting Information 2. Based on previous analysis with the same sample,[33] group effects were observed only in AF. Therefore, only scores from the AF test are analyzed here.

Color-Word Interference Test

The French version of the CWIT[42] was used to assess inhibition. The CWIT is a version of the well-known Stroop test.[43] The CWIT consists of four conditions that increase in difficulty from the first to the last: color naming (C1), word reading (C2), inhibition (C3), and inhibition/switching (C4). Each condition includes 50 stimuli presented on a white background paper. In the color naming condition (C1), squares of color, red, blue, and green, were presented and the participant had to name the color. In the word reading condition (C2), words of colors, red, blue, and green, printed in black ink are presented and participants are asked to read the words. In the inhibition condition (C3), words of colors, red, blue, and green, printed in a mismatching ink (e.g., the word red printed with blue ink) are presented. Participants are asked to name the color of the ink. In the inhibition/switching condition (C4), the stimuli are presented as C3, but some of the words were inside a box. The participants are asked to name the color of the ink, but if the word is inside a box, the participants are asked to read the word aloud. Each condition starts with a 10-stimulus practice. For each condition, the time of completion (RT) and the number of errors, corrected or not, was extracted. Prior analysis with the same sample[33] showed group effect in C4. Thus, the only measure from this condition is analyzed here.

MRI data acquisition

Structural MR images were acquired on a 3T Achieva TX Philips MRI Scanner with a T_1-weighted 3D-MPRAGE sequence (repetition time = 8.3 ms, echo time = 4.0 ms, field-of-view = 240 mm, flip angle = 8°, 240 × 240 acquisition matrix, 180 slices/volume, no gap, voxel size = 1 mm^3). The MRI session had a duration of approximately 50 min and included two blood oxygenation level–dependent (BOLD) fMRI sequences, a resting state and a speech in noise perception task, and a diffusion sequence. Only the T1w images were analyzed.

MRI data processing

FreeSurfer software 7.2.0 (https://freesurfer.net/) was used for structural MRI data processing. The FreeSurfer process includes motion correction and conformation, intensity normalization, nonbrain tissue removal, gray and white matter segmentation, and tessellations with automated topology correction. Manual verifications were performed by the two authors and followed FreeSurfer guidelines.[44] Subcortical segmentation of the caudate, putamen, and pallidum was performed using the Aseg atlas.[45] A probabilistic atlas for the thalamus[46] and the amygdala[47] were used to segment these structures, into 25 and nine bilateral nuclei, respectively. For the thalamus, we grouped some nuclei to form nuclei groups of interest based on the atlas grouping: anterior (anteroventral nucleus), intralaminar (central medial and lateral, centromedian, and parafascicular nuclei), medial (reuniens, mediodorsal medial magnocellular, and lateral parvocellular nuclei), ventral lateral (ventral lateral anterior and posterior), and pulvinar (pulvinar anterior, medial, lateral and inferior). For the amygdala, we have grouped the medial, the central and the cortical nuclei, and the cortico–amygdaloid transition into the cortico–centro–medial nuclei group. Figure 1 illustrates all structures of interest and Supporting Information 3 indicates nuclei included in grouping. The bilateral volume, in mm^3, of the caudate, the putamen, the pallidum, the thalamus and its anterior (ant), intralaminar (intT), medial (medT), pulvinar (Pu), ventral lateral (VL), laterodorsal (LD), and LGN nuclei, and the amygdala and its cortico–centro–medial nuclei (CCMA) were extracted. The bilateral volume of the medial geniculate nuclei (MGN) of the thalamus was also extracted because of its involvement in auditory processing. Because the volume of brain regions is highly correlated with the total head volume, the estimate total intracranial volume (eTIV) in mm^3 was extracted and used as a covariate in the statistical analysis.

The DeepCERES pipeline[48] of the volBrain platform[49] was used for the cerebellum segmentation. DeepCERES is an automatic pipeline that includes inhomogeneity correction, intensity normalization, super-resolution extrapolation, cerebellum isolation, and atlas generation and segmentation. The bilateral volume of the lobules VI, VIIB, and VIIIA, and the crus 1–2, as well as for the whole cerebellum were first extracted in cm^3, then transform in mm^3.

Statistical analyses

Analyses were conducted in R studio (v 4.3.1).[50] For each subcortical structure, nuclei group, cerebellum lobules, and crus, and for eTIV, the volume difference to the average of all participants was calculated. To achieve a normal distribution, a natural logarithm transformation was applied to the CWIT-C4 RT. For the CWIT-C4, the transformed RT and

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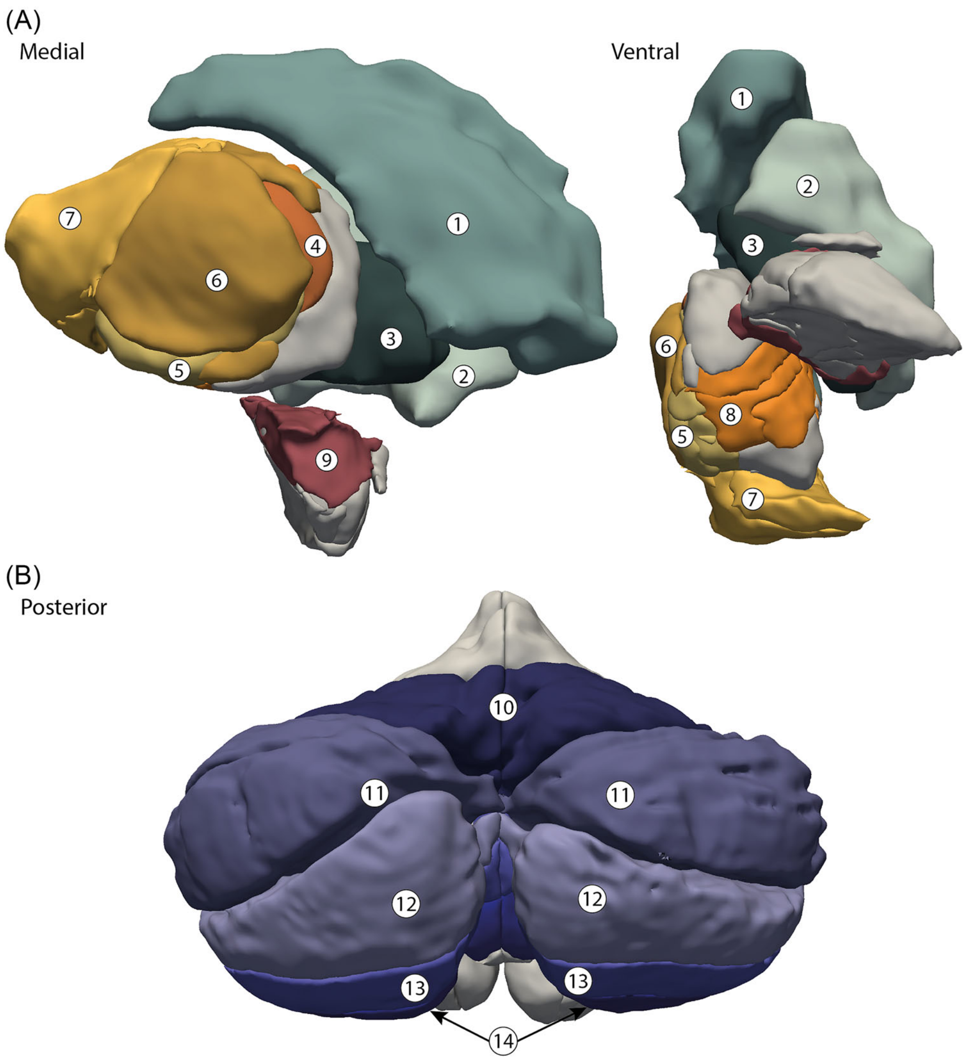

FIGURE 1 Subcortical structures of interest. (A) Medial and ventral view of the basal ganglia, thalamus, and amygdala of the average left brain calculated from the entire sample. (1) Caudate nucleus, (2) putamen, (3) pallidum, (4) anterior thalamic nucleic group (antT), (5) intralaminar thalamic nucleic group (intT), (6) medial thalamic nucleic group (medT), (7) pulvinar nucleus (Pu), (8) ventral lateral nucleus (VL), and (9) cortico–centro–medial nuclei of the amygdala (CCMA). Note that the medial geniculate nucleus (MGN), the lateral geniculate nucleus (LGN), and the laterodorsal nucleus (LD) were not observable on the average brain. (B) Posterior view of the cerebellum of a participant. (10) lobule VI, (11) crus I, (12) crus II, (13) lobule VIIB, and (14) lobule VIIIA.

the number of errors were analyzed. For the TAiL, we could not obtain a normal distribution for the cost in RT, thus only distractibility and conflict resolution in cost in ER were analyzed.

The analytical pipeline is presented in Figure 2. Linear mixed models (LMM) were used for all analysis. The buildmer package (v 2.9)[51] and the lme4 package (v. 1.1-34)[52] were used. For post hoc analysis, the emmeans package (v 1.8.8)[53] and the interactions packages (1.1.5)[54] were used to decompose interactions. Two LMM were created to address our objectives. The first (Model 1) was used to identify group differences in brain structure as a function of age (objective 1). The second (Model 2) was used to determine whether the subcortical structure was associated with attention and inhibition, and if that relationship was moderated by group and age (objective 2). Both models included sex, LHS, and eTIV (to control for head size) as covariates and participants as a random factor. Sex was included because the groups were not balanced on this variable ($X^2 = 7{,}3978$; $p = 0.02475$). LHS is a composite index that captures nine factors known to influence brain health in aging: education, audition, traumatic brain injury, obesity, depression, social isolation, diabetes, physical inactivity, and alcohol consumption. Rather than including each variable separately, we used the LHS as a summary covariate to limit model complexity and reduce the risk of overfitting, especially given our sample size,[55]—while accounting for protective and risk factors that could confound group comparisons. The eTIV covariate is a well-established covariate in volumetric analysis and was used to control head size.[56]

Therefore, the full (initial) Model 1 was as follows:

$$Volume \sim Age \times Group \times EXP + Sex + LHS + eTIV + 1|\text{Participant}.$$

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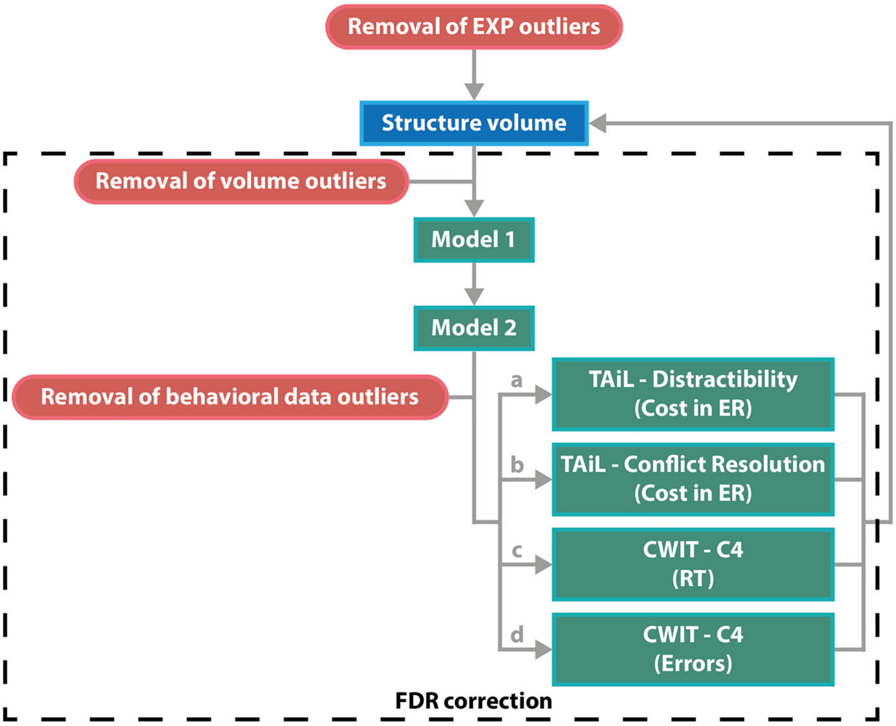

FIGURE 2 Analytic pipeline. ER, error rate; EXP, global experience score.

The full (initial) Model 2 was as follows:

$$Behavior \sim Volume \times Age \times Group + Volume \times Age \times EXP + Volume \times Group \times EXP + Sex + LHS + eTIV + 1|\text{Participant}.$$

For Model 2, the behavior included the TAiL distractibility (cost in ER), TAiL conflict resolution (cost in ER), CWIT-C4 errors, and CWIT-C4 RT. Although no group effect was found for TAiL distractibility in cost in ER and CWIT-C4 errors in our previous analysis,[33] they were included in this study. The absence of group differences at the behavioral level does not imply that there are no morphological differences. Previous analyses of the same dataset found interaction between cortical thickness and group for both measures.[23] For each structure, a Benjamini–Hochberg false discovery rate (FDR)[57] was applied to control for multiple comparisons on all tests of interest. In Model 1, the tests of interest were all effects and interactions possible; in Model 2, the tests of interest were the effects and interactions that included regional volumes.

Outliers, defined as below Q1 – 1.5 × IQR or above Q3 + 1.5 × IQR, were removed before analysis from all variables (subcortical volume, cerebellum volume, attention, and inhibition measures). For Model 1, outliers in volume measures were removed independently for each brain structure. For Model 2, outliers in each behavioral variable were identified and excluded separately. Importantly, participants removed from Model 1 were also removed from all subsequent models (Model 2) to ensure consistency. However, exclusion in one submodel of Model 2 did not propagate across the others. Removal of outliers did not exceed two participants per group in Model 1, except for the left amygdala and bilateral crus II and lobule VIIB in which up to three participants per group was removed. Removal of outliers did not exceed two participants, mainly none, per group in Model 2, except that five instrumentalists were constantly removing from conflict resolution and four singers were constantly removing from CWIT errors.

RESULTS

The results are presented by regions starting with the basal ganglia, followed by the thalamus, the amygdala, and ending with the cerebellum. Significant effects and interactions are displayed as heatmaps for each model (Figures 3 and 4). Only effects and interactions surviving the FDR correction are discussed. Main effects and post hoc analysis Tables are displayed in Supporting Information 4–8.

Basal ganglia

For Model 1, a main effect of Age was found in the bilateral caudate, putamen and pallidum while controlling for head size. Only the right putamen showed an Age × Group interaction. In instrumentalists, Age was more negatively associated with Volume compared to controls (Figure 5A).

For Model 2A and B, the bilateral pallidum showed a Volume × Group interaction for the TAiL (Figure 5B,C). In both cases, controls showed a positive relationship between regional volume and TAiL

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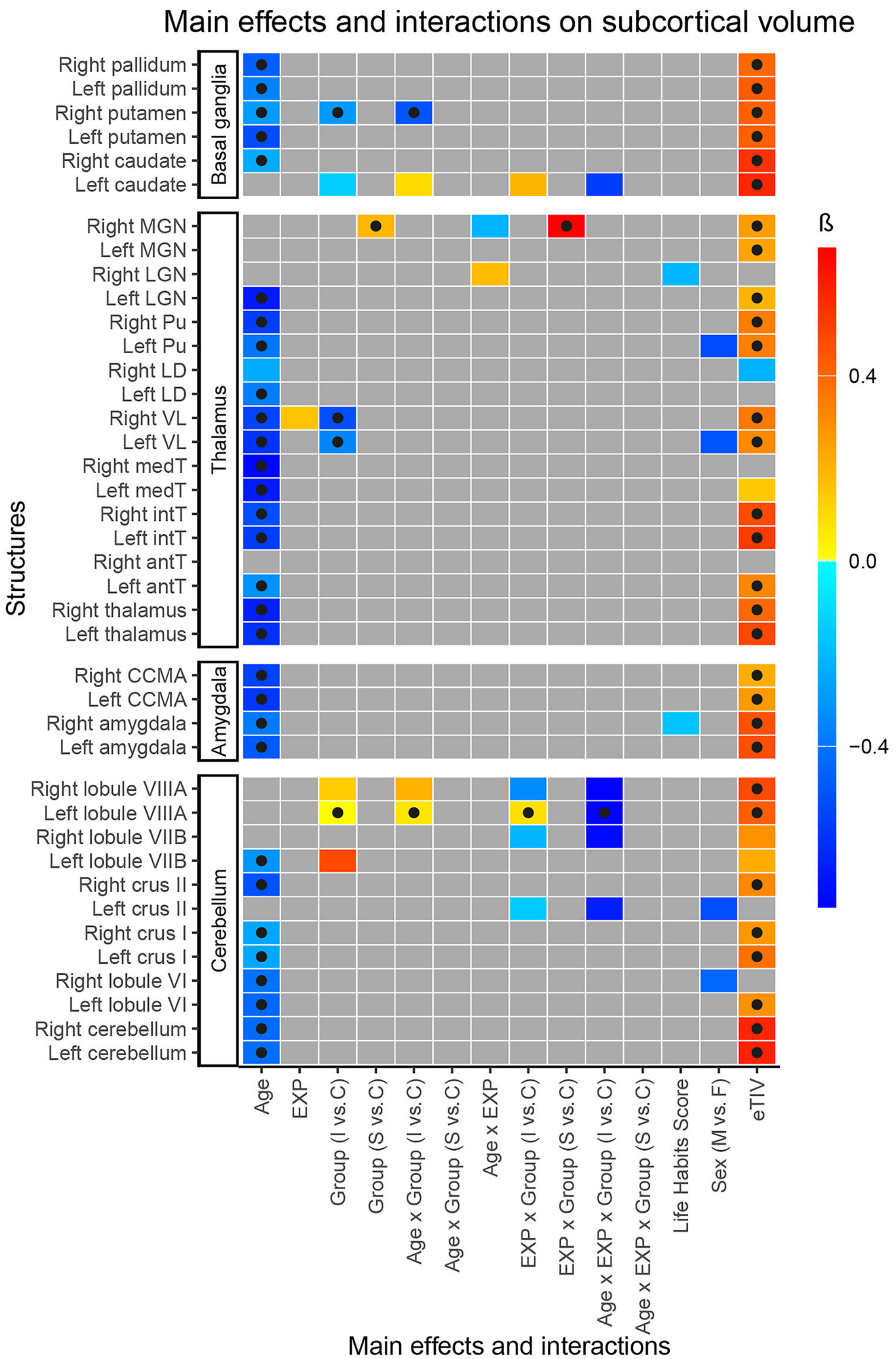

FIGURE 3 Heatmap of the significant main effects and interactions on subcortical volume. Contrasts between instrumentalists and singers are not shown, as they are absent from the main analysis Tables. β = standardized estimate. Positive β values are illustrated with red shades, while negative β values are illustrated with blue shades. Gray-colored cells indicate insignificant effect/interaction. Black dots indicate that the effect/interaction survived the false discovery rate (FDR) correction. C, controls; eTIV, estimated total intracranial volume; EXP, global experience score; I, instrumentalists; S, singers.

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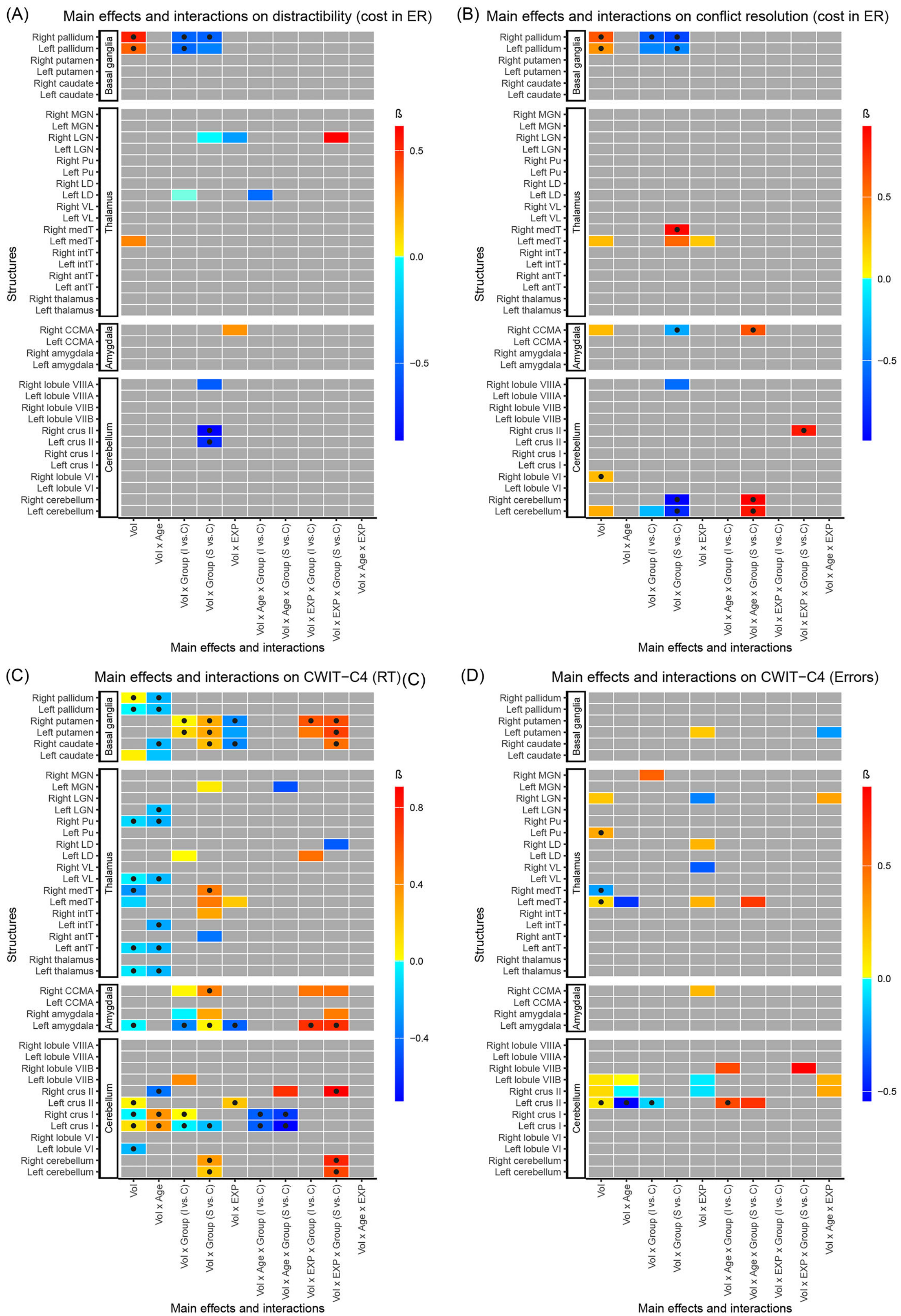

FIGURE 4 Heatmap of the significant main effects and interactions of Model 2. (A) Results for distractibility. (B) Results for conflict resolution. (C) Results for Color-Word Interference Test (CWIT)-C4 reaction time (RT). (D) Results for CWIT-C4 errors. Contrasts between instrumentalists and singers are not shown, as they are absent from the main analysis Tables. β = standardized estimate. Positive β values are illustrated with red shades, while negative β values are illustrated with blue shades. Gray-colored cells indicate insignificant effect/interaction. Black dots indicate that the effect/interaction survived the false discovery rate (FDR) correction. C, controls; EXP, global experience score; I, instrumentalists; S, singers.

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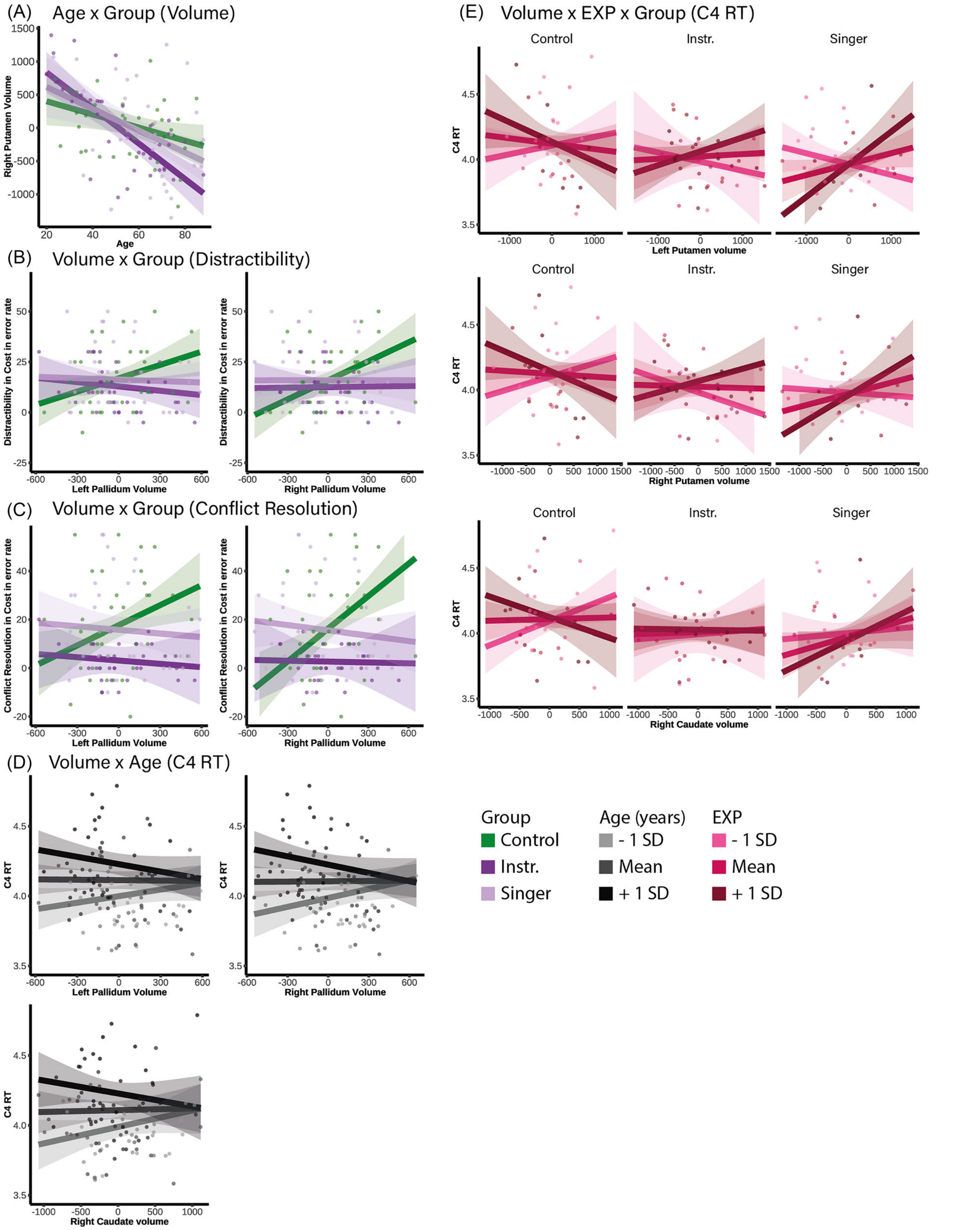

FIGURE 5 Results for the basal ganglia volume. (A) Age × Group interaction on volume for the right putamen. (B) Volume × Group interaction on distractibility for the bilateral pallidum. (C) Volume × Group interaction on conflict resolution for the bilateral pallidum. (D) Volume × Age interaction on Color-Word Interference Test (CWIT)-C4 reaction time (RT) for the bilateral pallidum and right caudate. (E) Volume × EXP × Group interaction on CWIT-C4 RT for the bilateral putamen and right caudate. *Note*: Volume expressed in mm^3. EXP, global experience score; Instr., instrumentalist.

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scores, whereas no such relationship was observed for instrumentalists and singers, apart from two nonsignificant contrasts in the left pallidum ($p = 0.058$): control—singer for distractibility and control—instrumentalist for conflict resolution. For Model 2C, a Volume × Age interaction was observed in the right caudate and bilateral pallidum. Across all structures, the relationship between volume and RT shifted from positive to negative with increasing age (Figure 5D). A Volume × EXP × Group interaction was also observed in the bilateral putamen and the right caudate. In the bilateral putamen, in singers and instrumentalists, the relationship between Volume and RT shifted from a negative to a positive relationship as EXP increased, whereas the opposite was found for controls (Figure 5E). In the right caudate, a similar pattern was observed for singers and controls, but there was no relationship between Volume, RT and EXP in instrumentalists (Figure 5E).

Thalamus

For Model 1, a negative main effect of age was observed on thalamic volumes bilaterally. An age effect was also observed in all nuclei groups, except in the right antT, right LGN, and the bilateral MGN. A main effect of group was found in the bilateral VL. In instrumentalists, lower volume was observed compared to singers and controls (Figure 6A). A significant EXP × Group interaction was found in the right MGN. In singers, EXP was positively associated with Volume, whereas no relationship was observed in controls. Instrumentalists did not differ significantly from either group (Figure 6B).

For Model 2, an Age × Volume interaction on CWIT-C4 RT was observed in the left thalamus, and in the left antT, intT and VL, and in the right Pu and LGN. Results showed that the relationship between Volume and CWIT RT shifted from positive to negative with increasing Age (Figure 6E). Another interaction, Volume × Group, on CWIT-C4 RT was also observed. In singers, medT volume was positively associated with RT, whereas a negative relationship was observed for controls. Instrumentalists did not differ from either group (Figure 6D). Other effects and interactions were observed with the other behavioral measures. A Volume × Group interaction on conflict resolution was found in the bilateral medT. In singers, Volume was positively associated with conflict resolution, with a significantly different relationship compared to controls and instrumentalists. A nonsignificant trend was observed in the left medT for the singer—control contrast ($p = 0.059$; Figure 6C). A main effect of volume on CWIT-C4 errors was observed in the bilateral medT and left Pu. Errors were positively associated with left medT and Pu volume but negatively associated with right medT volume (Figure 6F).

Amygdala

For Model 1, a negative effect of Age was observed in the bilateral amygdala as a whole, as well as in the bilateral CCMA; no association with group was found. For Model 2, a Volume × EXP × Group interaction on CWIT RT (Model 2C) was observed in the left amygdala as a whole. In singers and instrumentalists, the relationship between Volume and RT shifted from negative to positive as EXP increased, whereas the opposite was found in controls (Figure 7B). A Volume × Age × Group interaction on conflict resolution was observed in the right CCMA. In singers, the relationship between Volume and Conflict resolution shifted from negative to positive as age increased, whereas the opposite pattern was observed in controls (Figure 7A). In the right CCMA, a Volume × Group interaction on both CWIT measure was observed. For CWIT RT, singer showed a positive relationship between volume and RT, contrasting with the negative relationship in controls (Figure 7C). For CWIT errors, singers exhibited a positive relationship between volume and errors, whereas instrumentalists showed a negative relationship (Figure 7D).

Cerebellum

For Model 1, a negative main effect of age was observed in both cerebellar hemispheres, and in bilateral lobule VI and crus I, right crus II and left lobule VIIB. An Age × EXP × Group interaction was observed in the left lobule VIIIA. In instrumentalists, the relationship between age and volume shifted from positive to negative as EXP increased, whereas the opposite pattern was observed in controls (Figure 8A).

For Model 2, two interactions were observed in the bilateral cerebellum as a whole: a Volume × Age × Group interaction on conflict resolution and a Volume × EXP × Group interaction on CWIT RT. For the Volume × Age × Group interaction, in singers, the relationship between volume and conflict resolution shifted from negative to positive as age increased, whereas in controls this relationship was positive across all ages (Figure 8C). For the Volume × EXP × Group interaction, also observed in the right crus II, in singers, the relationship between volume and RT shifted from negative to positive as EXP increased, whereas, in controls, this relationship was negative across all ages (Figure 9A). Other interactions and main effect were observed in specific cerebellar structures. A Volume × Group interaction on distractibility was observed in the bilateral crus II. In singers, volume was negatively associated with distractibility, whereas no relationship was observed in instrumentalists and controls (Figure 8B). A Volume × EXP × Group interaction on conflict resolution was observed in bilateral crus II. In instrumentalists, the relationship between right crus II volume and conflict resolution shifted from positive to negative as EXP increased, whereas the opposite was found in singers and controls (Figure 8D). In the left crus II, the same pattern was observed as in the right crus II, but only instrumentalists and singers differed (Figure 8D). A positive association between the right lobule VI volume and conflict resolution was found (Figure 8E). A Volume × Age × Group interaction on CWIT RT was found in the bilateral crus I. In instrumentalists and singers—more prominently in singers—the relationship between volume and RT shifted from positive to negative as age increased, whereas the opposite pattern was observed in controls (Figure 9B). A Volume × EXP interaction on CWIT RT was observed in the left crus II; in all participants, the relationship between volume and RT shifted from negative to positive as EXP increased (Figure 9C). A negative effect of

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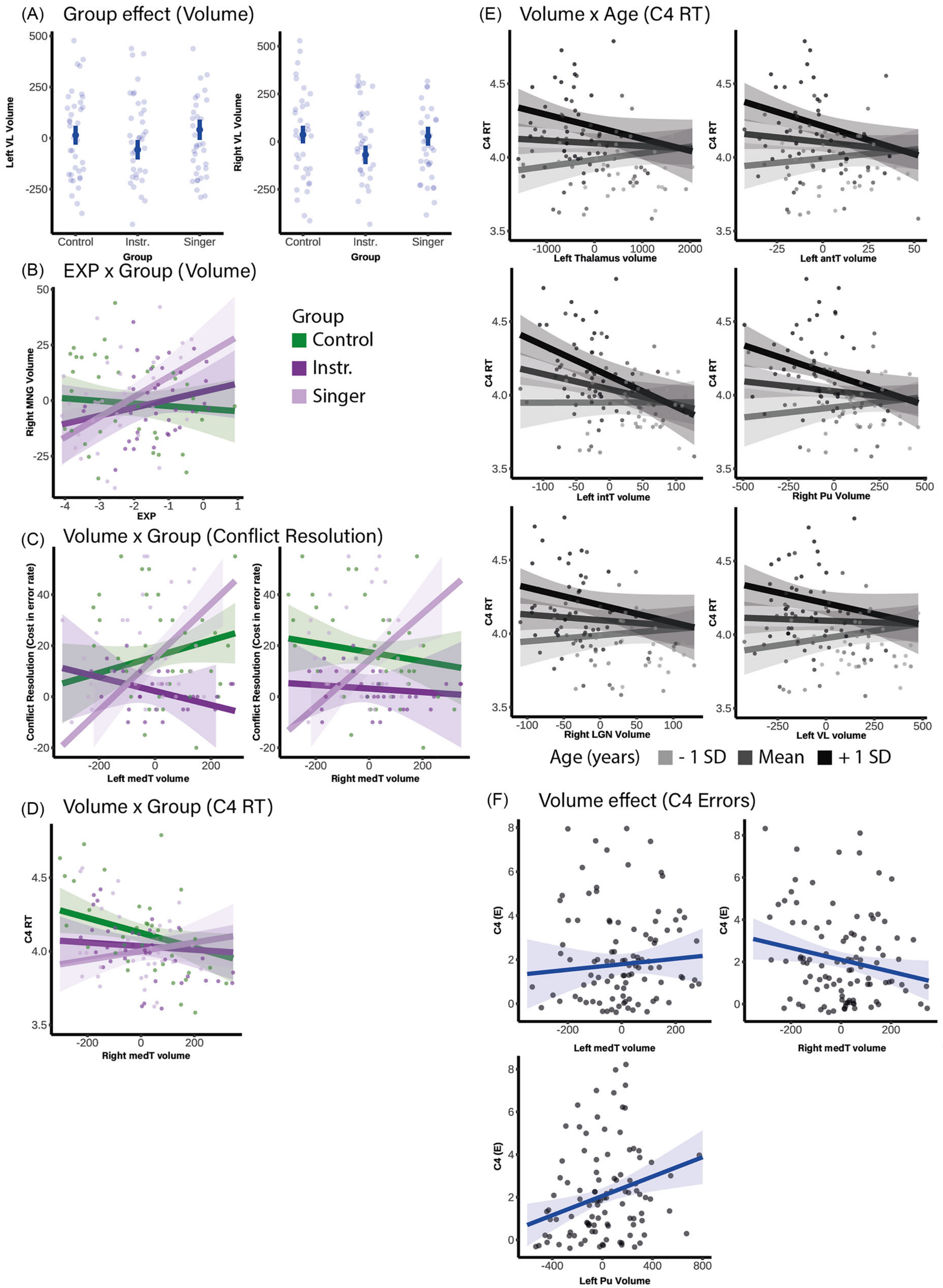

FIGURE 6 Results for the thalamus volume. (A) Main effect of Group on Volume for the bilateral ventral lateral (VL). (B) EXP × Group interaction on volume for the right medial geniculate nucleus (MGN). (C) Volume × Group interaction on conflict resolution for the bilateral medT. (D) Volume × Group interaction on Color-Word Interference Test (CWIT)-C4 reaction time (RT) for the right medT. (E) Volume × Age interaction on CWIT-C4 RT for the whole left thalamus, ant, intT and VL, and right pulvinar (Pu) and lateral geniculate nucleus (LGN). (F) Main effect of Volume on CWIT-C4 errors for the bilateral MEDT and left Pu. *Note*: Volume expressed in mm^3. Instr., instrumentalist.

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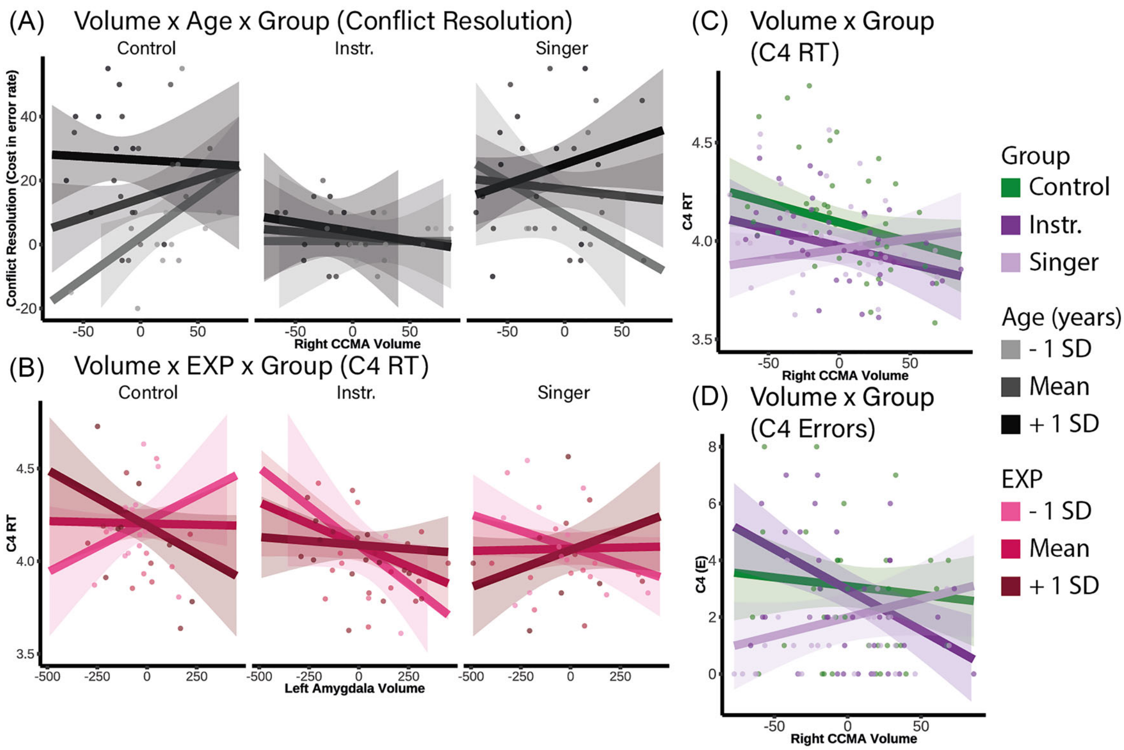

FIGURE 7 Results for the amygdala volume. (A) Volume × Age × Group interaction on conflict resolution for the right cortico–centro–medial nuclei of the amygdala (CCMA). (B) Volume × EXP × Group interaction on Color-Word Interference Test (CWIT)-C4 reaction time (RT) for the left amygdala. (C) Volume × Group interaction on CWIT-C4 RT for the right CCMA. (D) Volume × Group interaction on CWIT-C4 errors for the right CCMA. *Note*: Volume expressed in mm^3. EXP, global experience score; Instr., instrumentalist.

volume on RT was observed in the left lobule VI (Figure 9D). Finally, a Volume × Age × Group interaction on CWIT errors was observed in the left crus II. In instrumentalists, the relationship between volume and errors shifted from negative to positive as age increased, whereas the opposite pattern was observed in controls (Figure 9E).

DISCUSSION

This study aimed to examine age-related effects on the subcortical attentional system in singers, instrumentalists, and active nonmusicians, as well as their relationship to attentional control capacities. Our three key results are as follows: (1) While musical activities do not mitigate age-related decline in subcortical volume, they are associated with distinct relationships between subcortical volume and attentional control compared to nonmusicians. (2) Attentional control is associated with bilateral subcortical volumes and (3) associations with subcortical volumes are strongest with inhibition compared to attention. These findings are discussed below.

Subcortical aging and musical activities

In almost all structures, controlling for head size, the expected negative effect of age on volume was found in all three groups, in line with previous studies (for a review, see refs.[58–60]). Furthermore, our results did not reveal a global positive effect of practicing a musical activity on the subcortical attentional system. Out of the 40 structures investigated, only five showed a group difference. In three of these—the bilateral VL and the right putamen—practicing a musical instrument was associated with lower volume compared to singing or practicing a nonmusical activity. Moreover, greater experience with a musical instrument was associated with a smaller left lobule VIIIA volume compared to less experience. This finding supports the ERM,[22] which stipulates that better performance is associated with lower volume. Our results also revealed that more experienced singer had a larger right MGN compared to controls. These findings contrast with our previous analysis of the impact of musical activities on the cortical attention network in the same sample.[23] In that study, although relatively few in absolute terms, more interactions were observed between age and group, as well as between experience and group. Specifically, at cortical level, singing was associated with lesser age-related thinning in approximately 10% of the investigated regions, and distinct activity-specific mechanisms compared to controls and instrumentalists in about 6% of the regions. Taken together, these findings indicate that practicing any cognitive-motor activity, musical or not, lead to similar aging effect at the subcortical level. However, without a passive control group, we cannot determine whether aging is reduced compared to not engaging in any activity.

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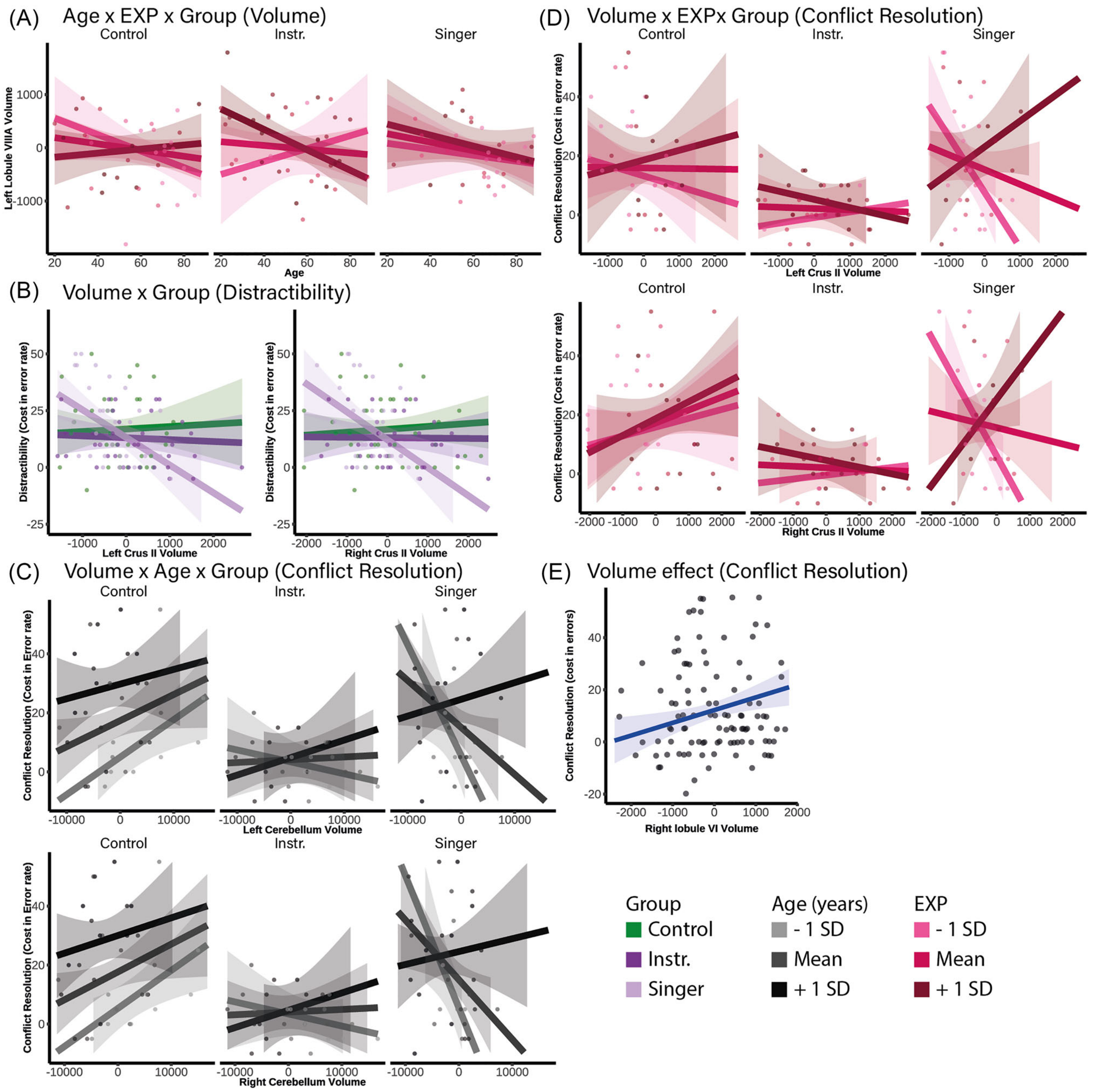

FIGURE 8 Results for Models 1, 2A and B of cerebellum volume. (A) Age × EXP × Group interaction on left lobule VIIIA Volume. (B) Volume × Group interaction on distractibility for bilateral crus II. (C) Volume × Age × Group interaction on conflict resolution for bilateral cerebellum. (D) Volume × EXP × Group interaction on conflict resolution for bilateral crus II. (E) Main effect of Volume on conflict resolution for right lobule VI. *Note*: Volume expressed in mm^3. EXP, global experience score; Instr., instrumentalist.

While the literature on the combined effect of aging and experience-induced plasticity on subcortical structures is limited, our results nevertheless align with prior studies that did not report positive effect of practicing a physical activity on the volume of the cerebellum, basal ganglia, thalamus, and amygdala.[61–63] However, some studies have reported protective effects of engaging in various kinds of musical or nonmusical activities in healthy older adults. For example, amateur instrumentalists have shown less pronounced age-related decline in cerebellar crus I volume compared to nonmusicians.[64] Additionally, a study found higher volume in the bilateral cerebellar lobules VIII and XI, and in the right caudate nucleus, in older adults who participated in piano or musical culture lessons for 6 months.[65] However, no greater volume increase was observed in the piano group compared to the musical culture group. Similarly, reduced age-related decline in subcortical volume has also been reported following cognitive[66] and physical training.[67] Importantly, however, these findings were observed in a limited set of structures, which varied across studies. Overall, few studies have investigated the effect of activity engagement in healthy older adults, as most studies have focused on clinical populations. The observed positive effects are modest. One possible explanation is that

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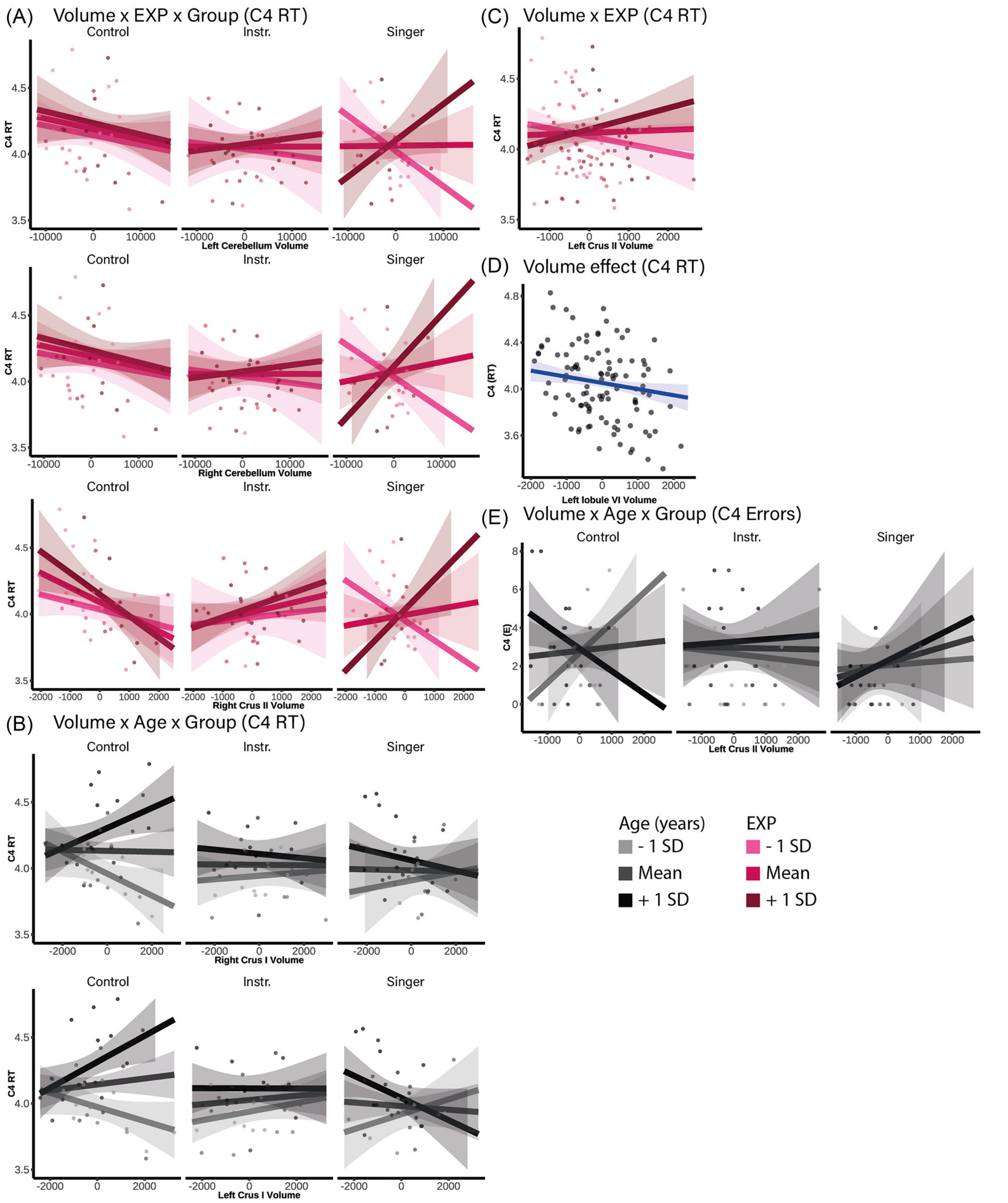

FIGURE 9 Results for Model 2C and D of cerebellum volume. (A) Volume × EXP × Group interaction on Color-Word Interference Test (CWIT) reaction time (RT) for bilateral cerebellum and right crus II. (B) Volume × Age × Group interaction on CWIT RT for bilateral crus I. (C) Volume × EXP on CWIT RT for left crus II. (D) Main effect of Volume on CWIT RT for left lobule VI. (E) Volume × Age × Group interaction on CWIT Errors for left crus II. *Note*: Volume expressed in mm^3. EXP, global experience score; Instr., instrumentalist.

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activity-related changes in subcortical gray matter are too subtle to detect, especially given the well-documented strong negative effects of aging.

One distinctive feature of our study is that it focused on *amateur*, rather than *professional* musicians. While most previous studies have examined professional musicians—who typically engage in more intensive and prolonged training—few have included amateurs, and even fewer have directly compared both groups. When such comparisons have been made, stronger effects are often reported in professional.[25,29] However, focusing on amateur musicians is important for understanding the potential benefits of more accessible, nonprofessional forms of musical engagements. The fact that we did not observe clear subcortical differences may reflect the subtler neuroplastic changes associated with amateur practice, which may not be detectable with structural measures alone. Nevertheless, the inclusion of amateur musicians increases the ecological validity of our findings and highlights the need for further research examining the threshold and dose-response relationships between musical engagement and brain plasticity.

The effect of subcortical volume on attentional control

Although age-related structural decline was similar across groups, there were group differences in the relationship between volume and attention control. In general, better performance was associated with lower subcortical volume in singers. In some structures, this was observed only in older singers or in singers with more experience, a pattern that is aligned with the ERM.[22] In contrast, in controls, those with better performance had a larger volume, a pattern that is aligned with the BR hypothesis. One could argue that since the BR hypothesis is an aging hypothesis, it is irrelevant when age is not a factor. However, this hypothesis can also be interpreted from the point of view of experience. The concept of BR is tightly associated with the concept of cognitive reserve.[21,68,69] The BR is the physical reserve of the brain—its volume and synaptic density—while the *cognitive* reserve refers to the flexibility and adaptability of cognitive networks to resist negative age effects.[68] Thus, preserving the brain should allow for an enhanced *cognitive* reserve. Therefore, in the context of practicing a cognitively demanding activity, having more experience should be associated with higher BR, thus with better cognitive reserve. In instrumentalists, the brain-behavior patterns did not follow a clear or consistent pattern. These findings are in line with our analysis of the cortical attention system in the same sample.[23] However, a key difference from previous findings is the greater bilaterality of the current results. Specifically, of the 40 associations between volume and attentional control, 20 involved homologous structures (i.e., a right structure and its left counterpart are associated with a measure; Table 2). This bilaterality is most evident in the basal ganglia (pallidum and putamen) and the cerebellum (as a whole and crus I-II). At the cortical level, bilaterality was also present but not in homologous regions.[23] Specifically, six left hemisphere regions and four right hemisphere regions were associated with attentional control, but of those, only the two superior frontal sulci, left and right, were homologous regions. Our results are in line with the literature showing a contribution of the bilateral cerebellum in attention control.[4,70]

Among all attentional measures, RT in the fourth condition of the CWIT showed the most associations with subcortical volume. Of the 24 structures associated with attentional control, 21 were associated with the CWIT (Table 2). The predominant pattern was an interaction between volume and age, found in the bilateral pallidum, right caudate, Pu and LGN, and left thalamus, antT, intT, and VL. Older adults with smaller volumes in each of these regions were slower than those with larger volumes. These results are partially aligned with a previous study showing that the negative effect of age on inhibition control is mediated by a decrease in the volume of the right caudate.[71] However, in that study, no association between inhibitory control and the volume of other basal ganglia nuclei or other subcortical structures was found. Interestingly in our study, an opposite pattern emerged in the bilateral crus I, where older controls with larger volumes were slower than those with smaller volumes. This observation contradicts the BR hypothesis, suggesting that more volume is not always associated with better performance, even in older age. This observation may reflect mechanisms consistent with the ERM wherein increased volume does not necessarily indicate enhanced function. Support for the ERM in aging was also observed in the full bilateral cerebellum and the right CCMA volume in singers for conflict resolution. However, these observations are at odds with the literature which generally indicates that, with age, less cerebellar volume is associated with worst cognition (for a review, see ref.[72]). Therefore, further studies are necessary to clarify the mechanisms of cerebellar plasticity and their impact on cognitive aging. Another main observation was the interaction between volume, experience and group on RT. This observation was observed in the bilateral putamen and cerebellum, the left amygdala and the right caudate. In the left amygdala and the basal ganglia nuclei, results for singers, and instrumentalists to a lesser extent, were in line with the ERM while the controls were consistent with the BR. In the cerebellum, however, controls showed that, independently of the experience, less volume was associated with slower RT, while the results for singers were in line with the ERM.

These observations may be explained by the relationship between selective attention and inhibition, as well as the role of subcortical structures in the inhibition process. A recent study has proposed that the ability to inhibit distracting information is not under voluntary control, but rather based on previous experience with the distractor.[73] The mechanism by which distracting information is inhibited is still unknown, but proposals include the representation of the distractor in working memory, where a rejection template would match the distractor, or the amplified representation of the target in working memory to reduce the risk of distractor selection. Thus, the basal ganglia[74] and the thalamus[8,75] could provide a link between working memory and attention control by contributing to representing the distractor. The cerebellum would also play a role in representing the distractor. There is evidence that the cerebellum is activated during a Stroop task.[76] In our study, we also found that the cerebellum was the structure mainly

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TABLE 2 Summary of associations between subcortical structures and attentional control.

		Association with			
		Attention		Inhibition	
Structure	Section	Distract	Conflict	Reaction time (RT)	Errors
Basal ganglia	Left pallidum	*	*	*	
	Right pallidum	*	*	*	
	Left putamen			*	
	Right putamen			*	
	Right caudate			*	
Thalamus	Left thalamus			*	
	Left ant			*	
	Left intT			*	
	Left medT		*		*
	Right medT		*	*	*
	Left ventral lateral (VL)			*	
	Left pulvinar (Pu)				*
	Right Pu			*	
	Left lateral geniculate nucleus (LGN)			*	
Amygdala	Left amygdala			*	
	Right cortico–centro–medial nuclei of the amygdala (CCMA)		*	*	*
Cerebellum	Left cerebellum		*	*	
	Right cerebellum		*	*	
	Left lobule VI			*	
	Right lobule VI		*		
	Left crus I			*	
	Right crus I			*	
	Left crus II	*	*	*	*
	Right crus II	*	*	*	

Note: *, significant after false discovery rate (FDR) correction; Distract, distractibility (cost in error) at the attend location of the TAiL; Conflict, conflict resolution (cost in error) at the attend location of the TAiL; RT, time to pass the fourth condition of the Color-Word Interference Test (CWIT); Errors, number of errors during the fourth condition of the CWIT.

associated with conflict resolution. A measure of conflict resolution, as in the TAiL[41] and a Stroop task,[43] can assess the function of the attentional executive network.[1,77] Mannarelli et al.[78] found that inhibiting the cerebellum via noninvasive brain stimulation was associated with reduced efficiency in the executive network. Consequently, since the thalamus and basal ganglia are less associated with conflict resolution than the cerebellum, but all three are associated with inhibition, the role of each would be different in the control of attention. The basal ganglia and the thalamus would be implicated in the representation of the distractor while the cerebellum would be implicated in the resolution of conflict between a target and a distractor.

The cerebral attention system—Cortical and subcortical structure

For a long time, research on attentional control, and more generally on cognition, has focused on the cortex.[3] The objective was to find functionally activated cortical regions during attentional tasks. Although functional activity is an important indicator of the neural networks involved in an ability, it does not provide information about its underlying structural foundation. Structural MRI can reveal differences in the gray matter organization, which may underlie functional differences and provide insights into long-term developmental and neurodegen-

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erative changes. Based on the results of the current study and our previous work,[23] here we propose four observations:

- The effects of long-term practice on brain structure are primarily observable at the cortical level. This suggests that, during aging, compensatory plasticity is more sustainable at cortical than subcortical levels. An explanation could be that subcortical changes are more subtle or happen at an earlier stage. This subtlety could be explained by different plasticity mechanisms operating at the subcortical level. For example, the anterior and posterior hippocampal volumes of taxi drivers have been shown to differ from those of the general population, despite no difference in the overall hippocampal volume.[79] Specifically, taxi drivers exhibited a larger posterior hippocampus, and a smaller anterior hippocampus compared to the general population. This suggests that, rather than increasing total volume, subcortical plasticity may trigger a more complex and more subtle reorganization of neural resources.
- The absence of group differences in brain structure does not mean that brain structures contribute to attentional control in the same way across groups. In the present study, we observed multiple interactions between groups, subcortical volume and attentional control, despite minimal group differences on volume.
- Plasticity mechanisms are activity-specific at both cortical and subcortical levels. In the present and our past work,[23] we observed that results for singers were consistent with the ERM while results for our active control group aligned with the BR hypothesis. The results for instrumentalists did not follow a clear pattern. This suggests that the plasticity mechanisms involved are activity-specific but not regionally specific.
- While the relationship between subcortical volume and attentional control was primarily observed in structures involved in bottom-up attention, the relationship between cortical thickness and attentional control was found in structures involved in bottom-up and top-down attention. Practicing an activity would not be associated with the ability to better select a stimulus, but rather with better inhibition of salient stimuli. This could explain why subcortical volume was more strongly associated with the CWIT task than with the TAiL. This observation is supported by a study using the attention network test,[80] which evaluates the efficiency of the attentional networks,[1,77] with professional musicians and nonmusicians.[81] Medina and Barraza[81] showed that, compared to nonmusicians, musicians have a more efficient executive network, involved in the suppression of distracting stimuli, but showed no difference in the efficiency of the orienting network, which is linked to sensory information. In another study, it was found that musicians were less distracted by irrelevant timbre change than nonmusicians.[82] Our team also found that musicians had a better conflict resolution at the TAiL than nonmusicians, specifically instrumentalists in a study using the same sample[33] and in singers in an independent sample.[83] However, other studies have found no benefits of practicing a musical activity on inhibition.[84–87] Therefore, the benefits of practicing a musical activity on inhibition remains to be clarified through randomized training studies.

Finally, future studies should investigate the coinfluence of cortical and subcortical structures on attentional controls, ideally via randomized longitudinal studies focusing on the structural attentional systems. This approach would reduce the need for multiple comparison corrections and increase the likelihood of detecting subtle effects of musical practice.

Limitations

Given the wide age range of the participants in our study, the sample sizes may be considered relatively modest, and the conclusions should therefore be interpreted with caution. Although no significant group differences were found in participant characteristics, the absence of evidence does not imply evidence of absence. Future studies with larger samples and/or employing a Bayesian approach may be better suited to assess true equivalence between groups. Nonetheless, a key strength of the present study is its rigorous control of potentially confounding factors—including the use of our life habit score (LHS), which integrates multiple variables known to influence brain health in aging.

Another limitation relates to the exclusion of one instrumentalist with unusually low experience relative to the group. While one could argue that amateur samples should reflect a wide range of variability, this particular data point had a disproportionate influence on model assumptions, especially regarding normality and leverage. Given that experience was a central variable in the analysis, we opted to exclude this outlier to preserve the robustness of the model. Future studies may benefit from controlling for experience levels during recruitment to ensure a more balanced distribution.

CONCLUSION

This study advances our understanding of the relationship between attentional control and subcortical structures in four key ways. First, we found that engaging in a musical activity, regardless of its kind, is not associated with reduced age-related or differences in subcortical structures. Second, engaging in a musical or nonmusical activity leads to distinct relationships between attentional control and subcortical structures. Third, our findings highlight the bilaterality of the subcortical attentional system. Finally, subcortical structures were more strongly associated with inhibitory control compared to attention. Overall, our findings support the idea that musical practice is associated with circumscribed brain reorganization providing some support to cognitive abilities.

AUTHOR CONTRIBUTIONS

Alexandre Sicard: Conceptualization, methodology, investigation, formal analysis, visualization, data curation, writing—original draft preparation. **Pascale Tremblay**: Conceptualization, funding acquisition, methodology, supervision, resources, project administration, data Curation, writing—reviewing and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The raw datasets generated during the current study are not publicly available because participants did not consent to public data sharing. However, the group data (MRI and behavioral) will be available on Borealis, the Canadian Dataverse Repositor (https://doi.org/10.5683/SP3/MGIMLH).

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REFERENCES

1. Petersen, S. E., & Posner, M. I. (2012). The attention system of the human brain: 20 years after. *Annual Review of Neuroscience*, *35*, 73–89. https://doi.org/10.1146/annurev-neuro-062111-150525
2. Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201–215. https://doi.org/10.1038/nrn755
3. Janacsek, K., Evans, T. M., Kiss, M., Shah, L., Blumenfeld, H., & Ullman, M. T. (2022). Subcortical cognition: The fruit below the rind. *Annual Review of Neuroscience*, *45*, 361–386. https://doi.org/10.1146/annurev-neuro-110920-013544
4. Habas, C. (2021). Functional connectivity of the cognitive cerebellum. *Frontiers in Systems Neuroscience*, *15*, 642225. https://doi.org/10.3389/fnsys.2021.642225
5. van Schouwenburg, M. R., den Ouden, H. E., & Cools, R. (2010). The human basal ganglia modulate frontal-posterior connectivity during attention shifting. *Journal of Neuroscience*, *30*(29), 9910–9918.
6. van Schouwenburg, M. R., den Ouden, H. E., & Cools, R. (2015). Selective attentional enhancement and inhibition of fronto-posterior connectivity by the basal ganglia during attention switching. *Cerebral Cortex*, *25*(6), 1527–1534. https://doi.org/10.1093/cercor/bht345
7. Wright, N. F., Vann, S. D., Aggleton, J. P., & Nelson, A. J. (2015). A critical role for the anterior thalamus in directing attention to task-relevant stimuli. *Journal of Neuroscience*, *35*(14), 5480–5488. https://doi.org/10.1523/jneurosci.4945-14.2015
8. de Bourbon-Teles, J., Bentley, P., Koshino, S., Shah, K., Dutta, A., Malhotra, P., Egner, T., Husain, M., & Soto, D. (2014). Thalamic control of human attention driven by memory and learning. *Current Biology*, *24*(9), 993–999. https://doi.org/10.1016/j.cub.2014.03.024
9. Kinomura, S., Larsson, J., Gulyás, B., & Roland, P. E. (1996). Activation by attention of the human reticular formation and thalamic intralaminar nuclei. *Science*, *271*(5248), 512–515. https://doi.org/10.1126/science.271.5248.512
10. O'Connor, D. H., Fukui, M. M., Pinsk, M. A., & Kastner, S. (2002). Attention modulates responses in the human lateral geniculate nucleus. *Nature Neuroscience*, *5*(11), 1203–1209.
11. Ivanov, I., Bansal, R., Hao, X., Zhu, H., Kellendonk, C., Miller, L., Sanchez-Pena, J., Miller, A. M., Chakravarty, M. M., Klahr, K., Durkin, K., Greenhill, L. L., & Peterson, B. S. (2010). Morphological abnormalities of the thalamus in youths with attention deficit hyperactivity disorder. *American Journal of Psychiatry*, *167*(4), 397–408. https://doi.org/10.1176/appi.ajp.2009.09030398
12. Gallagher, M., & Holland, P. C. (1994). The amygdala complex: Multiple roles in associative learning and attention. *Proceedings of the National Academy of Sciences*, *91*(25), 11771–11776.
13. Mosher, C. P., Zimmerman, P. E., & Gothard, K. M. (2010). Response characteristics of basolateral and centromedial neurons in the primate amygdala. *Journal of Neuroscience*, *30*(48), 16197–16207. https://doi.org/10.1523/jneurosci.3225-10.2010
14. Jacobs, R. H. A. H., Renken, R., Aleman, A., & Cornelissen, F. W. (2012). The amygdala, top-down effects, and selective attention to features. *Neuroscience & Biobehavioral Reviews*, *36*(9), 2069–2084. https://doi.org/10.1016/j.neubiorev.2012.05.011
15. Harada, C. N., Natelson Love, M. C., & Triebel, K. L. (2013). Normal cognitive aging. *Clinics in Geriatric Medicine*, *29*(4), 737–752. https://doi.org/10.1016/j.cger.2013.07.002
16. Särkämö, T. (2018). Cognitive, emotional, and neural benefits of musical leisure activities in aging and neurological rehabilitation: A critical review. *Annals of Physical and Rehabilitation Medicine*, *61*(6), 414–418. https://doi.org/10.1016/j.rehab.2017.03.006
17. Salthouse, T. A. (2006). Mental exercise and mental aging: Evaluating the validity of the "use it or lose it" hypothesis. *Perspectives on Psychological Science*, *1*(1), 68–87. https://doi.org/10.1111/j.1745-6916.2006.00005.x
18. Alain, C., Zendel, B. R., Hutka, S., & Bidelman, G. M. (2014). Turning down the noise: The benefit of musical training on the aging auditory brain. *Hearing Research*, *308*, 162–173. https://doi.org/10.1016/j.heares.2013.06.008
19. Reuter-Lorenz, P. A., & Park, D. C. (2024). Cognitive aging and the life course: A new look at the Scaffolding theory. *Current Opinion in Psychology*, *56*, 101781. https://doi.org/10.1016/j.copsyc.2023.101781
20. Reuter-Lorenz, P. A., & Park, D. C. (2014). How does it STAC up? Revisiting the scaffolding theory of aging and cognition. *Neuropsychology Review*, *24*(3), 355–370. https://doi.org/10.1007/s11065-014-9270-9
21. Stern, Y., Arenaza-Urquijo, E. M., Bartrés-Faz, D., Belleville, S., Cantilon, M., Chetelat, G., Ewers, M., Franzmeier, N., Kempermann, G., Kremen, W. S., Okonkwo, O., Scarmeas, N., Soldan, A., Udeh-Momoh, C., Valenzuela, M., Vemuri, P., & Vuoksimaa, E. (2020). Whitepaper: Defining and investigating cognitive reserve, brain reserve, and brain maintenance. *Alzheimer's & Dementia*, *16*(9), 1305–1311. https://doi.org/10.1016/j.jalz.2018.07.219
22. Wenger, E., Brozzoli, C., Lindenberger, U., & Lövdén, M. (2017). Expansion and renormalization of human brain structure during skill acquisition. *Trends in Cognitive Sciences*, *21*(12), 930–939. https://doi.org/10.1016/j.tics.2017.09.008
23. Sicard, A., & Tremblay, P. (2025). Experience-induced plasticity in the attention system of healthy adults practising musical or non-musical activities. *Aperture Neuro*, *5*. https://doi.org/10.52294/001c.127706

17496632, 0, Downloaded from https://nyaspubs.onlinelibrary.wiley.com/doi/10.1111/nyas.70023, Wiley Online Library on [24/08/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

24. Bermudez, P., Lerch, J. P., Evans, A. C., & Zatorre, R. J. (2009). Neuroanatomical correlates of musicianship as revealed by cortical thickness and voxel-based morphometry. *Cerebral Cortex*, *19*(7), 1583–1596. https://doi.org/10.1093/cercor/bhn196
25. Gaser, C., & Schlaug, G. (2003). Gray matter differences between musicians and nonmusicians. *Annals of the New York Academy of Sciences*, *999*, 514–517. https://doi.org/10.1196/annals.1284.062
26. Hutchinson, S., Lee, L. H.-L., Gaab, N., & Schlaug, G. (2003). Cerebellar volume of musicians. *Cerebral Cortex*, *13*(9), 943–949. https://doi.org/10.1093/cercor/13.9.943
27. Fauvel, B., Groussard, M., Chételat, G., Fouquet, M., Landeau, B., Eustache, F., Desgranges, B., & Platel, H. (2014). Morphological brain plasticity induced by musical expertise is accompanied by modulation of functional connectivity at rest. *Neuroimage*, *90*, 179–188. https://doi.org/10.1016/j.neuroimage.2013.12.065
28. Kleber, B., Veit, R., Moll, C. V., Gaser, C., Birbaumer, N., & Lotze, M. (2016). Voxel-based morphometry in opera singers: Increased gray-matter volume in right somatosensory and auditory cortices. *Neuroimage*, *133*, 477–483. https://doi.org/10.1016/j.neuroimage.2016.03.045
29. James, C. E., Oechslin, M. S., Van De Ville, D., Hauert, C.-A., Descloux, C., & Lazeyras, F. (2014). Musical training intensity yields opposite effects on grey matter density in cognitive versus sensorimotor networks. *Brain Structure and Function*, *219*, 353–366.
30. Brown, R. M., Zatorre, R. J., & Penhune, V. B. (2015). Expert music performance: Cognitive, neural, and developmental bases. *Progress in Brain Research*, *217*, 57–86. https://doi.org/10.1016/bs.pbr.2014.11.021
31. Tanaka, S., & Kirino, E. (2017). Reorganization of the thalamocortical network in musicians. *Brain Research*, *1664*, 48–54. https://doi.org/10.1016/j.brainres.2017.03.027
32. Vaquero, L., Hartmann, K., Ripollés, P., Rojo, N., Sierpowska, J., François, C., Càmara, E., van Vugt, F. T., Mohammadi, B., Samii, A., Münte, T. F., Rodríguez-Fornells, A., & Altenmüller, E. (2016). Structural neuroplasticity in expert pianists depends on the age of musical training onset. *Neuroimage*, *126*, 106–119. https://doi.org/10.1016/j.neuroimage.2015.11.008
33. Joyal, M., Sicard, A., Penhune, V., Jackson, P. L., & Tremblay, P. (2024). Auditory attention, working memory and inhibitory control in aging: Comparing singers, instrumentalists and active controls. *Annals of the New York Academy of Sciences.*
34. Tremblay, P., Gagnon, L., Roy, J. P., & Arseneault, A. (2023). Speech production in healthy older adults with or without amateur singing experience. *Journal of Speech, Language, and Hearing Research*, *66*(11), 4332–4352. https://doi.org/10.1044/2023_jslhr-23-00126
35. Zhang, X., & Tremblay, P. (2025). Aging of resting-state functional connectivity in amateur singers, instrumentalists and controls. *Aperture Neuro*, 5.
36. Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4
37. Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S., Whitehead, V., Collin, I., Cummings, J. L., & Chertkow, H. (2005). The Montreal Cognitive Assessment, MoCA: A brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society*, *53*(4), 695–699. https://doi.org/10.1111/j.1532-5415.2005.53221.x
38. Larouche, E., Tremblay, M.-P., Potvin, O., Laforest, S., Bergeron, D., Laforce, R., Monetta, L., Boucher, L., Tremblay, P., Belleville, S., Lorrain, D., Gagnon, J.-F., Gosselin, N., Castellano, C.-A., Cunnane, S. C., Macoir, J., & Hudon, C. (2016). Normative data for the Montreal cognitive assessment in middle-aged and elderly Quebec-French people. *Archives of Clinical Neuropsychology*, *31*(7), 819–826. https://doi.org/10.1093/arclin/acw076
39. Yesavage, J. A., Brink, T. L., Rose, T. L., Lum, O., Huang, V., Adey, M., & Leirer, V. O. (1982). Development and validation of a geriatric depression screening scale: A preliminary report. *Journal of Psychiatric Research*, *17*(1), 37–49. https://doi.org/10.1016/0022-3956(82)90033-4
40. Livingston, G., Huntley, J., Sommerlad, A., Ames, D., Ballard, C., Banerjee, S., Brayne, C., Burns, A., Cohen-Mansfield, J., Cooper, C., Costafreda, S. G., Dias, A., Fox, N., Gitlin, L. N., Howard, R., Kales, H. C., Kivimäki, M., Larson, E. B., Ogunniyi, A., … Mukadam, N. (2020). Dementia prevention, intervention, and care: 2020 report of the Lancet Commission. *Lancet*, *396*(10248), 413–446. https://doi.org/10.1016/s0140-6736(20)30367-6
41. Zhang, Y. X., Barry, J. G., Moore, D. R., & Amitay, S. (2012). A new test of attention in listening (TAIL) predicts auditory performance. *PLoS ONE*, *7*(12), e53502. https://doi.org/10.1371/journal.pone.0053502
42. Fine, E. M., & Delis, D. C. (2011). Delis–Kaplan executive functioning system. In J. S. Kreutzer, J. DeLuca, & B. Caplan (Eds.), *Encyclopedia of clinical neuropsychology* (pp. 796–801). Springer. https://doi.org/10.1007/978-0-387-79948-3_1539
43. Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, *18*, 643–662. https://doi.org/10.1037/h0054651
44. FreeSurfer. (2023). *FsTutorial/TroubleshootingDataV6.0 – Free surfer wiki.* https://surfer.nmr.mgh.harvard.edu/fswiki/FsTutorial/TroubleshootingDataV6.0
45. Fischl, B., Salat, D. H., Busa, E., Albert, M., Dieterich, M., Haselgrove, C., van der Kouwe, A., Killiany, R., Kennedy, D., Klaveness, S., Montillo, A., Makris, N., Rosen, B., & Dale, A. M. (2002). Whole brain segmentation: Automated labeling of neuroanatomical structures in the human brain. *Neuron*, *33*(3), 341–355. https://doi.org/10.1016/s0896-6273(02)00569-x
46. Iglesias, J. E., Insausti, R., Lerma-Usabiaga, G., Bocchetta, M., Van Leemput, K., Greve, D. N., van der Kouwe, A., Fischl, B., Caballero-Gaudes, C., & Paz-Alonso, P. M. (2018). A probabilistic atlas of the human thalamic nuclei combining ex vivo MRI and histology. *Neuroimage*, *183*, 314–326. https://doi.org/10.1016/j.neuroimage.2018.08.012
47. Saygin, Z. M., Kliemann, D., Iglesias, J. E., van der Kouwe, A. J. W., Boyd, E., Reuter, M., Stevens, A., Van Leemput, K., McKee, A., Frosch, M. P., Fischl, B., & Augustinack, J. C. (2017). High-resolution magnetic resonance imaging reveals nuclei of the human amygdala: Manual segmentation to automatic atlas. *Neuroimage*, *155*, 370–382. https://doi.org/10.1016/j.neuroimage.2017.04.046
48. Morell-Ortega, S., Ruiz-Perez, M., Gadea, M., Vivo-Hernando, R., Rubio, G., Aparici, F., de la Iglesia-Vaya, M., Catheline, G., Coupé, P., & Manjón, J. V. (2024). DeepCERES: A deep learning method for cerebellar lobule segmentation using ultra-high resolution multimodal MRI. *arXiv preprint arXiv:2401.12074.*
49. Manjón, J. V., & Coupé, P. (2016). volBrain: An online MRI brain volumetry system. *Frontiers in Neuroinformation*, *10*, 30. https://doi.org/10.3389/fninf.2016.00030
50. R Core Team. (2023). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. https://www.R-project.org/
51. Voeten, C. C. (2022). *buildmer: Stepwise elimination and term reordering for mixed-effects regression.* https://CRAN.R-project.org/package=buildmer
52. Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823.
53. Lenth, R. V. (2023). *emmeans: Estimated marginal means, aka least-squares means.* Version 1.8.8. https://CRAN.R-project.org/package=emmeans
54. Long, J. A. (2022). *interactions: Comprehensive, user-friendly toolkit for probing interactions.* Version 1.1.6. https://cran.r-project.org/package=interactions
55. Zhang, Z. (2014). Too much covariates in a multivariable model may cause the problem of overfitting. *Journal of Thoracic Disease*, *6*(9), E196–E197. https://doi.org/10.3978/j.issn.2072-1439.2014.08.33

17496632, 0, Downloaded from https://nyaspubs.onlinelibrary.wiley.com/doi/10.1111/nyas.70023, Wiley Online Library on [24/08/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

56. Wang, J., Hill-Jarrett, T., Buto, P., Pederson, A., Sims, K. D., Zimmerman, S. C., DeVost, M. A., Ferguson, E., Lacar, B., Yang, Y., Choi, M., Caunca, M. R., La Joie, R., Chen, R., Glymour, M. M., & Ackley, S. F. (2024). Comparison of approaches to control for intracranial volume in research on the association of brain volumes with cognitive outcomes. *Human Brain Mapping*, *45*(4), e26633. https://doi.org/10.1002/hbm.26633
57. Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, *57*(1), 289–300. http://www.jstor.org/stable/2346101
58. MacDonald, M. E., & Pike, G. B. (2021). MRI of healthy brain aging: A review. *NMR in Biomedicine*, *34*(9), e4564. https://doi.org/10.1002/nbm.4564
59. Ramanoël, S., Hoyau, E., Kauffmann, L., Renard, F., Pichat, C., Boudiaf, N., Krainik, A., Jaillard, A., & Baciu, M. (2018). Gray matter volume and cognitive performance during normal aging. A voxel-based morphometry study. *Frontiers in Aging Neuroscience*, *10*, 235. https://doi.org/10.3389/fnagi.2018.00235
60. Raz, N., Ghisletta, P., Rodrigue, K. M., Kennedy, K. M., & Lindenberger, U. (2010). Trajectories of brain aging in middle-aged and older adults: Regional and individual differences. *Neuroimage*, *51*(2), 501–511. https://doi.org/10.1016/j.neuroimage.2010.03.020
61. Yamamoto, M., Wada-Isoe, K., Yamashita, F., Nakashita, S., Kishi, M., Tanaka, K., Yamawaki, M., & Nakashima, K. (2017). Association between exercise habits and subcortical gray matter volumes in healthy elderly people: A population-based study in Japan. *ENeurologicalScience*, *7*, 1–6.
62. Matura, S., Fleckenstein, J., Deichmann, R., Engeroff, T., Füzéki, E., Hattingen, E., Hellweg, R., Lienerth, B., Pilatus, U., & Schwarz, S. (2017). Effects of aerobic exercise on brain metabolism and grey matter volume in older adults: Results of the randomised controlled SMART trial. *Translational Psychiatry*, *7*(7), e1172–e1172.
63. Erickson, K. I., Voss, M. W., Prakash, R. S., Basak, C., Szabo, A., Chaddock, L., Kim, J. S., Heo, S., Alves, H., White, S. M., Wojcicki, T. R., Mailey, E., Vieira, V. J., Martin, S. A., Pence, B. D., Woods, J. A., McAuley, E., & Kramer, A. F. (2011). Exercise training increases size of hippocampus and improves memory. *PNAS*, *108*(7), 3017–3022. https://doi.org/10.1073/pnas.1015950108
64. Yamashita, M., Ohsawa, C., Suzuki, M., Guo, X., Sadakata, M., Otsuka, Y., Asano, K., Abe, N., & Sekiyama, K. (2021). Neural advantages of older musicians involve the cerebellum: Implications for healthy aging through lifelong musical instrument training. *Frontiers in Human Neuroscience*, *15*, 784026. https://doi.org/10.3389/fnhum.2021.784026
65. Marie, D., Müller, C. A., Altenmüller, E., Van De Ville, D., Jünemann, K., Scholz, D. S., Krüger, T. H., Worschech, F., Kliegel, M., & Sinke, C. (2023). Music interventions in 132 healthy older adults enhance cerebellar grey matter and auditory working memory, despite general brain atrophy. *Neuroimage: Reports*, *3*(2), 100166.
66. Raz, N., Schmiedek, F., Rodrigue, K. M., Kennedy, K. M., Lindenberger, U., & Lövdén, M. (2013). Differential brain shrinkage over 6 months shows limited association with cognitive practice. *Brain and Cognition*, *82*(2), 171–180. https://doi.org/10.1016/j.bandc.2013.04.002
67. Wood, K. N., Nikolov, R., & Shoemaker, J. K. (2016). Impact of long-term endurance training vs. guideline-based physical activity on brain structure in healthy aging. *Frontiers in Aging Neuroscience*, *8*, 155.
68. Stern, Y., Barnes, C. A., Grady, C., Jones, R. N., & Raz, N. (2019). Brain reserve, cognitive reserve, compensation, and maintenance: Operationalization, validity, and mechanisms of cognitive resilience. *Neurobiology of Aging*, *83*, 124–129. https://doi.org/10.1016/j.neurobiolaging.2019.03.022
69. Pettigrew, C., & Soldan, A. (2019). Defining cognitive reserve and implications for cognitive aging. *Current Neurology and Neuroscience Reports*, *19*(1), 1. https://doi.org/10.1007/s11910-019-0917-z
70. Janata, P., Tillmann, B., & Bharucha, J. J. (2002). Listening to polyphonic music recruits domain-general attention and working memory circuits. *Cognitive, Affective, & Behavioral Neuroscience*, *2*(2), 121–140.
71. Hu, S., Ide, J. S., Chao, H. H., Castagna, B., Fischer, K. A., Zhang, S., & Li, C. R. (2018). Structural and functional cerebral bases of diminished inhibitory control during healthy aging. *Human Brain Mapping*, *39*(12), 5085–5096. https://doi.org/10.1002/hbm.24347
72. Arleo, A., Bareš, M., Bernard, J. A., Bogoian, H. R., Bruchhage, M. M. K., Bryant, P., Carlson, E. S., Chan, C. C. H., Chen, L. K., Chung, C. P., Dotson, V. M., Filip, P., Guell, X., Habas, C., Jacobs, H. I. L., Kakei, S., Lee, T. M. C., Leggio, M., Misiura, M., … Manto, M. (2024). Consensus paper: Cerebellum and ageing. *Cerebellum (London, England)*, *23*(2), 802–832. https://doi.org/10.1007/s12311-023-01577-7
73. van Moorselaar, D., & Slagter, H. A. (2020). Inhibition in selective attention. *Annals of the New York Academy of Sciences*, *1464*(1), 204–221. https://doi.org/10.1111/nyas.14304
74. Seger, C. A. (2006). The basal ganglia in human learning. *The Neuroscientist*, *12*(4), 285–290. https://doi.org/10.1177/1073858405285632
75. Strumpf, H., Mangun, G. R., Boehler, C. N., Stoppel, C., Schoenfeld, M. A., Heinze, H. J., & Hopf, J. M. (2013). The role of the pulvinar in distractor processing and visual search. *Human Brain Mapping*, *34*(5), 1115–1132. https://doi.org/10.1002/hbm.21496
76. Ravnkilde, B., Videbech, P., Rosenberg, R., Gjedde, A., & Gade, A. (2002). Putative tests of frontal lobe function: A PET-study of brain activation during Stroop's test and verbal fluency. *Journal of Clinical and Experimental Neuropsychology*, *24*(4), 534–547. https://doi.org/10.1076/jcen.24.4.534.1033
77. Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42. https://doi.org/10.1146/annurev.ne.13.030190.000325
78. Mannarelli, D., Pauletti, C., Currà, A., Marinelli, L., Corrado, A., Delle Chiaie, R., & Fattapposta, F. (2019). The cerebellum modulates attention network functioning: Evidence from a cerebellar transcranial direct current stimulation and attention network test study. *Cerebellum (London, England)*, *18*(3), 457–468. https://doi.org/10.1007/s12311-019-01014-8
79. Maguire, E. A., Gadian, D. G., Johnsrude, I. S., Good, C. D., Ashburner, J., Frackowiak, R. S. J., & Frith, C. D. (2000). Navigation-related structural change in the hippocampi of taxi drivers. *Proceedings of the National Academy of Sciences*, *97*(8), 4398–4403. https://doi.org/10.1073/pnas.070039597
80. Fan, J., McCandliss, B. D., Sommer, T., Raz, A., & Posner, M. I. (2002). Testing the efficiency and independence of attentional networks. *Journal of Cognitive Neuroscience*, *14*(3), 340–347.
81. Medina, D., & Barraza, P. (2019). Efficiency of attentional networks in musicians and non-musicians. *Heliyon*, *5*(3), e01315. https://doi.org/10.1016/j.heliyon.2019.e01315
82. Kaganovich, N., Kim, J., Herring, C., Schumaker, J., Macpherson, M., & Weber-Fox, C. (2013). Musicians show general enhancement of complex sound encoding and better inhibition of irrelevant auditory change in music: An ERP study. *European Journal of Neuroscience*, *37*(8), 1295–1307. https://doi.org/10.1111/ejn.12110
83. Tremblay, P., & Perron, M. (2023). Auditory cognitive aging in amateur singers and non-singers. *Cognition*, *230*, 105311. https://doi.org/10.1016/j.cognition.2022.105311
84. Dubinsky, E., Wood, E. A., Nespoli, G., & Russo, F. A. (2019). Short-term choir singing supports speech-in-noise perception and neural pitch strength in older adults with age-related hearing loss. *Frontiers in Neuroscience*, *13*, 1153. https://doi.org/10.3389/fnins.2019.01153
85. Johnson, J. K., Stewart, A. L., Acree, M., Nápoles, A. M., Flatt, J. D., Max, W. B., & Gregorich, S. E. (2020). A community choir intervention to promote well-being among diverse older adults: results from the community of voices trial. *Journals of Gerontology Series B, Psychological Sciences and Social Sciences*, *75*(3), 549–559. https://doi.org/10.1093/geronb/gby132

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86. Merten, N., Fischer, M. E., Dillard, L. K., Klein, B. E. K., Tweed, T. S., & Cruickshanks, K. J. (2021). Benefit of musical training for speech perception and cognition later in life. *Journal of Speech, Language, and Hearing Research*, *64*(7), 2885–2896. https://doi.org/10.1044/2021_jslhr-20-00588
87. Guo, X., Yamashita, M., Suzuki, M., Ohsawa, C., Asano, K., Abe, N., Soshi, T., & Sekiyama, K. (2021). Musical instrument training program improves verbal memory and neural efficiency in novice older adults. *Human Brain Mapping*, *42*(5), 1359–1375. https://doi.org/10.1002/hbm.25298

SUPPORTING INFORMATION

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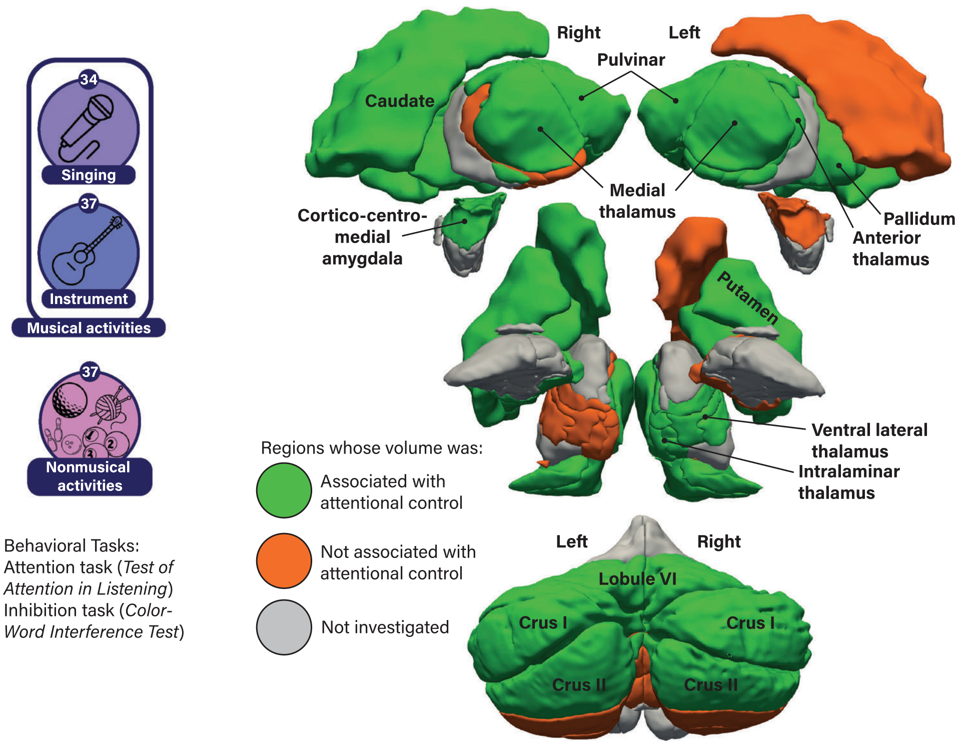

108 adults aged 20 to 88 years were recruited, including 34 singers, 37 instrumentalists, and 37 active nonmusicians. Participants completed an auditory selective attention task and a visual inhibition task. MRI images were acquired to examine the relationship between subcortical volumes and attention in these groups. Aging was associated with worse attentional control and smaller subcortical volumes. Significant interactions were found between groups and subcortical volume in relation to attention.