Amateur Singing Benefits Speech Perception in Aging Under Certain Conditions of Practice: Behavioural and Neurobiological Mechanisms.

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Research Article

Keywords: Aging, Speech perception, Brain plasticity, Music, Singing, Cortical thickness

Posted Date: May 25th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-507257/v1>

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Abstract

Limited evidence has shown that practising musical activities in aging, such as choral singing, could lessen age-related speech perception in noise (SPiN) difficulties. However, the robustness and underlying mechanism of action of this phenomenon remain unclear. In this study, we used surface-based morphometry combined with a moderated mediation analytic approach to examine whether singing-related plasticity in auditory and dorsal speech stream regions can mitigate age-related SPiN difficulties. 36 choral singers and 36 non-singers aged 20–87 years underwent cognitive, auditory, and SPiN assessments. Our results provide important new insights into experience-dependent plasticity by revealing that, under certain conditions of practice, amateur choral singing is associated with age-dependent structural plasticity within auditory and dorsal speech regions, which is associated with better SPiN performance in aging. Specifically, the conditions of practice that were beneficial for SPiN included frequent weekly practice at home, several hours of weekly group singing practice, singing in multiple languages, and having received formal singing training. These results suggest that the effect of amateur choral singing on SPiN is related to a dual mechanism involving auditory processing and auditory-motor integration and may be dose dependent, with more intense singing associated with greater benefit. Our results thus reveal that the relationship between musical practice and SPiN is complex, and underscore the importance of considering musical practice behaviours in understanding the effects of musical activities on the brain-behaviour relationship.

1. Introduction

Speech perception in noise (SPiN) difficulties are common among elderly adults. The causes of these difficulties remain unclear, but a growing body of evidence suggests that brain aging within different functional networks may be the main source of these difficulties. Though brain senescence is unavoidable, the aging brain retains the ability to reorganize itself via a variety of physical, intellectual, artistic, and social activities (for a review, see e.g. Kramer et al. 2004; Scarmeas and Stern 2003), a phenomenon known as *experience-dependent plasticity*, which could play a part in mitigating the effects of brain senescence on human cognition and behaviour, including SPiN.

Musical activities are one kind of plasticity-inducing activities that have been studied relatively extensively over the past decade using brain imaging methods. Studies have shown structural differences in several brain networks related to music, cognitive and sensory processing in young musical instrument players (professional and amateur) compared to non-musicians (e.g. Gaser and Schlaug 2003; Bermudez et al. 2009; Schlaug et al. 1995), and in young opera singers compared to non-singers (Kleber et al. 2016). Importantly, a study revealed that structural brain aging, evaluated using the BrainAge framework (Franke et al. 2010), was decelerated for both amateur and professional musical instrument players compared to non-musicians (Rogenmoser et al. 2017). Although the effects of musical activities on SPiN are heterogeneous (for a review, see Coffey et al. 2017), a number of studies have shown that playing a musical instrument (Bidelman and Alain 2015; Fleming et al. 2019; Fostick 2019; Parbery-Clark et al. 2011; Zendel et al. 2019; Zendel and Alain 2012; White-Schwoch et al. 2013; Alain et al. 2014) or singing in a choir (Dubinsky et al. 2019), can mitigate age-related SPiN difficulties. However, the nature of the underlying mechanisms, as well as the type and amount of practice required to positively influence SPiN capabilities, remain unknown.

Though there is no consensus on the mechanisms of action, one hypothesis is that musical activities reduce the impact of aging on the function and structure of auditory and dorsal speech stream regions, which are important networks involved in auditory processing and auditory-motor integration. The dorsal speech stream connects the superior temporal gyrus (STG) directly to the precentral gyrus (PrG) and inferior frontal gyrus (IFG), and indirectly through the inferior parietal lobule. Several neuroimaging studies have linked functional and structural aging within auditory and dorsal speech stream regions to SPiN difficulties (e.g. Du et al. 2016; Wong et al. 2010; Wong et al. 2009;

Hwang et al. 2007; Erb and Obleser 2013; Tremblay et al. 2019; Bilodeau-Mercure et al. 2015; Salvi et al. 2002; Manan et al. 2015; Manan et al. 2017; Sheppard et al. 2011; Tremblay et al. 2021). For instance, the volume of the left IFG has been found to predict SPiN performance in older but not in younger adults (Wong et al. 2010). Moreover, a decreased activity in the left STG during SPiN has been observed in older compared to younger adults (Wong et al. 2009; Hwang et al. 2007), as well as an increased activity associated with better performance for older adults in the right (Wong et al. 2009) and left PrG (Du et al. 2016). The dorsal speech stream is believed to be involved in the mapping of auditory speech sounds into auditory-motor speech representations (Hickok and Poeppel 2007; Rauschecker and Scott 2009). This process could serve to facilitate disambiguation of incoming speech sounds during SPiN through top-down motor information (for a review, see McGettigan and Tremblay 2018).

Playing a musical instrument and singing also require a functional auditory-motor integration mechanism in which motor commands and auditory feedback are continuously compared to monitor performance and make precise sensorimotor adjustments. Auditory-motor integration involved in musical performance has been shown to recruit a brain network similar to the dorsal speech stream (Zatorre et al. 2007). The practice of musical activities could therefore refine SPiN processing through enhanced auditory-motor integration. Consistent with this idea, a recent study has shown that a SPiN advantage for young professional musicians compared to young non-musician was associated with slightly increased activity in right auditory associative and frontal motor cortices (Du and Zatorre 2017), supporting the notion that musical activities may influence SPiN through their effect on auditory and dorsal speech stream regions. Relatedly, a recent study from our group found anatomical differences in the structure of the bilateral arcuate fasciculus - which forms the framework for dorsal speech stream- between young and older adult non-singers and adult amateur choral singers (Perron et al. 2021). However, these differences were not associated with a beneficial effect of singing on SPiN performance. Evidence of a positive impact of amateur singing on the dorsal speech stream, and, more generally, on SPiN, is scarce. While it is possible that amateur singing does not influence SPiN to the same extent as musical instrument playing, it is also possible that the effect of musical activities on SPiN follows a dose-dependent relationship, with more intense or more frequent practice being associated with increased benefits. This is consistent with the findings that, compared to non-musicians, both amateur singers and professional instrumentalists exhibit differences in the function or structure of the dorsal speech stream, but that these differences were associated to a SPiN advantage only in professionals, not in amateurs (Du and Zatorre 2017; Perron et al. 2021). The notion of a dose-dependent effect of musical practice on SPiN is also consistent with the literature on music-induced plasticity, which shows that differences in brain anatomy between instrumentists and non-musicians are related to several practice-related behaviours, such that increased plasticity is related to lower age of onset of musical practice, a higher number of years of practice, a higher number of weekly hours of practice, etc. (Amunts et al. 1997; Schlaug et al. 1995; Steele et al. 2013; for a review, see Merrett et al. 2013). This notion is in line with the Overlap, Precision, Emotion, Repetition, Attention (OPERA) hypothesis (Patel 2014, 2012, 2011), which suggests that musical activities affect speech skills by driving plasticity within speech networks when musical practice is frequent. In our previous study (Perron et al. 2021), although we found that the number of years of continuous singing was associated to a small extent with the structure of the arcuate fasciculus, we did not identify a relationship between the number of years of continuous singing and SPiN. However, several other singing practice behaviours, such as frequency of singing, duration of choral practice, age at onset of singing, etc., could drive plasticity within auditory and dorsal speech stream regions and, in turn, lead to better SPiN performance. Additional studies are needed to understand whether the effect of musical practice on SPiN is dose-dependent, and which singing practice behaviours are more important. This information is critical for the development of music-based rehabilitation interventions to maintain SPiN throughout aging.

The overall goal of the present study was therefore to identify whether specific singing practice behaviours (e.g. singing frequency) are associated with beneficial effects on SPiN performance through neuroplastic effects on the structure of

auditory and dorsal speech stream regions. The specific aims were threefold: 1) to investigate the effect of choral singing on SPiN performance in aging, 2) to determine what aspects of a persons' singing experience affects SPiN performance, and 3) to determine if the benefits of choral singing on SPiN performance are associated with the cortical thickness, surface, and volume of auditory and dorsal speech stream regions. We expected that, by decomposing the musical practice into different singing behaviours, behavioural differences would be found for singers with a higher level of engagement in musical practice compared to those less engaged. Specifically, we expected that frequent singing practice would be associated with better SPiN performance, through a less negative age effect on the structure of auditory and dorsal speech stream.

2. Material And Methods

2.1. Participants

72 healthy native French-speaking adults aged 20–87 years old (mean: 54.10 ± 18.42 , 41 females (F)) were recruited. All participants were recruited from a companion study (#192–2018) aiming to investigate the impact of choral singing on speech production, articulation, and cognition in aging. Participants were recruited through recruitment advertisements distributed in the community and in ~ 175 choirs in the Quebec City area.

All participants were right-handed according to the *Edinburgh Handedness Inventory* (Oldfield 1971). Participants had no self-reported history of hearing, language, speech, psychological, neurological, or neurodegenerative disorder at the time of the MRI. Participants were also screened for cognition using the *Montreal Cognitive Assessment* (MoCA) (Nasreddine et al. 2005). For the MoCA, a less strict cut off (20/30) than the original cut-off score (26/30) was used to avoid false positives (Waldron-Perrine and Axelrod 2012). Participants were divided into two groups: 36 choral singers (mean: 53.19 ± 18.78 , range: [20,86], 19 F) and 36 non-singers (mean: 55.00 ± 18.27 , range: [22,87], 22 F). Choral singers were defined as individuals singing in a choir for at least 2 years and with a weekly choral practice of at least 60 consecutive minutes. Non-singers were defined as individuals not involved in any form of group singing, and not performing professional or solo singing regularly. None of the participants were professional musicians or regular musical instrument players. Singers and non-singers did not differ in age, education, handedness, number of spoken languages, cognition, and hearing (all $p \geq 0.30$). A summary of participants' information is provided in Table 1. The study was approved by the *Comité d'éthique de la recherche sectoriel en neurosciences et santé mentale, Institut Universitaire en Santé Mentale de Québec* (#192–2017; #1495–2018). All participants provided informed consent and received a small monetary compensation for their participation. Behavioural and diffusion MRI collected as part of this project have been published elsewhere (Perron et al. 2021).

Table 1

Participant's characteristics separately for each group. Independent t-tests were conducted to compare the groups on each variable.

Characteristic	Non-singers (N = 36, 19F)				Singers (N = 36, 22F)				Group differences (independent t-test)	
	M	SD	Min	Max	M	SD	Min	Max	t	p
Age	53.19	18.78	20.00	86.00	55.00	18.27	22.00	87.00	-0.41	0.68
Education ^a	15.17	2.43	11.00	21.00	15.17	2.83	6.00	23.00	0.00	1.00
Handedness ^b	93.44	9.86	60.00	100.00	95.74	8.71	66.67	100.00	-1.05	0.30
Nb spoken languages ^c	2.39	0.90	1.00	5.00	2.25	0.65	1.00	4.00	0.75	0.46
MoCA ^d (/30)	27.50	2.09	21.00	30.00	27.53	1.81	23.00	30.00	-0.06	0.95
Health ^e (/7)	5.14	0.88	3.00	7.00	5.19	0.98	3.00	7.00	-0.25	0.80
Right ear PTA ^f	17.44	13.44	1.00	57.00	15.58	10.93	0.00	45.00	0.65	0.52
Left ear PTA	17.86	13.50	1.00	65.00	15.14	10.46	-1.00	38.00	0.96	0.34
Best ear PTA ^g	15.44	12.53	1.00	57.00	13.50	9.44	-1.00	32.00	0.74	0.46
Notes. M = mean, SD = standard deviation of the mean, N = number of participants per group; F = number of female participants.										
^a Education = Number of years of education based on the highest degree obtained in Quebec.										
^b Handedness = The handedness was measured with the Edinburgh Handedness Inventory. Participants report which hand they use to perform ten actions on a scale: always the same hand (2 points), usually the same hand (1 point), without preference (0 point). Based on results a lateralization quotient is calculated: $100 * (\text{score for the right hand} - \text{score for the left hand}) / 20$. A quotient of 60% or more indicates laterality on the right.										
^c Nb spoken languages = number of spoken languages including the native language (french).										
^d MoCA = Montreal Cognitive Assessment scale. The MOCA is a short cognitive test that is scored on a 30-point scale. Higher scores indicate better cognitive functions.										
^e Health = self-reported general health status on a scale of 0 to 7, with 0 being the lowest health level and 7 the maximal one.										
^f PTA = pure tone average thresholds (PTA) at .5, 1, 2, 4 and 6 kHz for each ear individually, measured in decibels (dB).										
^g Best ear PTA = pure tone average thresholds (PTA) at .5, 1, 2, 4 and 6 kHz for the best ear, measured in decibels (dB).										

2.2. Musical Activity Questionnaire

All participants answered a questionnaire on past and present singing and musical practice behaviours including singing context, formal singing training (yes, no), number of singing languages, age at onset of choral singing, number of years of singing experience, frequency per week of group singing, number of hours of weekly group singing,

frequency per week of practice at home and number of hours of weekly practice at home. A singing ratio was calculated (years of singing experience/age). Given the relatively small sample size (N = 36), to examine the effect of singing practice behaviours, most variables were dichotomized (e.g., the frequency of practice at home was dichotomized as once a week and more than once a week). A summary of the singing practice behaviours is provided in Table 2. Importantly, all participants had little to no musical instrument experience and the two groups were matched in terms of no, present and past musical instrument experience. Participants' musical instrument experience is detailed elsewhere (Perron et al. 2021).

Table 2
Participants' singing practice behaviours.

Distribution of singers according to their general singing experience				
Singing context	Choral singing	Leisure singing	Choral soloist	Practice at home
Number of participants (%)	36 (100)	31 (86)	9 (25)	28 (78)
Formal singing training	Yes	No		
Number of participants (%)	11 (31)	25 (69)		
Practice behaviours related to choral singing				
	M	SD	Min	Max
Number of singing languages	2.64	1.57	1.00	6.00
Age at onset (years)	24.03	16.96	6.00	59.00
Singing experience (years)	21.51	13.60	5.00	66.00
Singing ratio (singing experience/age) (%)	36.61	18.62	9.52	89.19
Frequency of group singing	Once a week		More than once a week	
Number of participants (%)	21 (58)		15 (42)	
Number of hours of group singing	Less than 3 hours a week		More than 3 hours a week	
Number of participants (%)	17 (47)		19 (53)	
Frequency of practice at home	Less than once a week		At least once a week	
Number of participants (%)	13 (36)		23 (64)	
Number of hours of practice at home	Less than half an hour a week		At least half an hour a week	
Number of participants (%)	18 (50)		18 (50)	

Table 3

Results of the significant moderated mediations for A) accuracy and B) sensitivity (d') for the number of singing languages.

ROI	Hemi	Metric	Conditional Indirect effects			Pairwise comparisons					
			ab ₁	ab ₂	ab ₃	ab ₂ - ab ₁	95% CI	ab ₃ - ab ₁	95% CI	ab ₃ - ab ₂	95% CI
A. Accuracy											
pIFG	R	T	-0.077	-0.020	0.043	0.057*	[0.006, 0.125]	0.120*	[0.003, 0.252]	0.063	[-0.021, 0.146]
PrG	R	T	-0.120*	-0.052*	0.027	0.068*	[0.012, 0.153]	0.147*	[0.029, 0.338]	0.079*	[0.010, 0.192]
PrG	L	T	-0.095*	-0.033	0.020	0.062*	[0.010, 0.164]	0.115	[-0.007, 0.328]	0.053	[-0.042, 0.179]
ISTG	R	T	-0.127*	-0.063	0.022	0.064*	[0.014, 0.145]	0.149*	[0.029, 0.351]	0.086*	[0.010, 0.215]
ISTG	L	T	-0.183*	-0.086*	0.073	0.097*	[0.034, 0.177]	0.256*	[0.095, 0.443]	0.159*	[0.054, 0.443]
PP	R	T	-0.069	-0.025	0.012	0.044*	[0.007, 0.107]	0.081	[-0.017, 0.216]	0.037	[-0.052, 0.123]
TTG	R	T	-0.088*	-0.038	0.029	0.050*	[0.007, 0.105]	0.117*	[0.014, 0.248]	0.067*	[0.001, 0.154]
TTS	R	T	-0.111*	-0.059	0.004	0.052*	[0.006, 0.131]	0.115*	[0.010, 0.322]	0.063	[-0.003, 0.199]
B. Sensitivity (d')											
PrG	R	T	-0.010	-0.005	0.001	0.005*	[0.001, 0.011]	0.010*	[0.002, 0.024]	0.006*	[0.001, 0.014]
PrG	L	T	-0.007*	-0.002	0.002	0.004*	[0.001, 0.012]	0.008	[-0.000, 0.024]	0.004	[-0.003, 0.013]
ISTG	R	T	-0.006	-0.002	0.002	0.003*	[< 0.001, 0.009]	0.008*	[< 0.001, 0.022]	0.004	[-0.000, 0.014]
ISTG	L	T	-0.013*	-0.006	0.006	0.007*	[0.002, 0.013]	0.019*	[0.005, 0.032]	0.012*	[0.003, 0.020]

Notes. ROI = Region of interest, Hemi = Hemisphere, R = Right, L = Left, T = Thickness. Conditional indirect effects for each level of the number of singing languages (ab_1 = 1 language, ab_2 = 2 languages and ab_3 = 4 languages) and the pairwise comparisons between levels are reported for (A) accuracy and (B) sensitivity (d'). A moderated mediation is confirmed if one pairwise comparison is statistically different. The asterisks indicate statistical significance based on confidence intervals (95% CI).

2.3. Experimental Design

The experiment consisted of three visits on three separate days. The first and third visit took place at the Speech and Hearing Neuroscience Laboratory at the CERVO Research Centre. All procedures took place in a double-walled soundproof room. Participants completed questionnaires, underwent audiometric evaluations, completed a SPiN task and voice and speech production tasks. These two visits had a duration of 3 hours and included several breaks. The second visit was a 1 hour MRI session at the IRM Québec-Mailloux Clinic in Quebec City.

2.4. Audiometric Evaluation

Pure-tone thresholds in dB HL were measured with a calibrated clinical audiometer (AC40, Interacoustic, Denmark). The following frequencies: .25, .5, 1, 2, 3, 4, 6, 8 kHz were assessed in each ear separately. None of the participants wore hearing aids or cochlear implants and none had been diagnosed with any type of hearing loss. Peripheral hearing was operationalized as an extended pure tone average threshold (PTA) at .5, 1, 2, 4 and 6 kHz of the best ear (best ear PTA). According to this measure, nine participants showed signs of mild hearing loss (PTA between 26 and 40 dB) and 1 participant showed signs of moderate hearing loss (PTA between 41 and 60 dB). Among these participants, 6 were non-singers aged between 62 and 86 years and 4 were singers aged between 73 and 80 years. No difference for the extended PTA of each ear and the extended best ear PTA was found between singers and non-singers (Table 1). The extended best ear PTA was included in all statistical analyses as covariate to control for the impact of hearing on SPiN performance.

2.5. SPiN Task

Participants completed a classic AX discrimination task in noise task in a double-walled soundproof room. The standardization and creation of the stimuli and task are detailed in our previous work (Perron et al. 2021). The task consisted in the discrimination of 300 minimal pairs (150 identical, 150 different) of monosyllabic Quebec-French Consonant-Vowel-Consonant (CVC) syllables created using the lab's Quebec-French oral language database SyllabO+ (Bédard et al., 2017). The syllables were presented using Presentation Software (Neurobehavioral System, USA) through high quality headphones (DT 770 Pro, Beyer Dynamic Inc., Germany). Participants were given a maximum of 3 seconds to determine if the second syllable was identical or different to the first using a response box (RB-840, Cedrus Corporation, USA). The syllables were presented in the absence of noise or simultaneously with a multi-talker babble noise created by Perrin and Grimault (2005) under two signal-to-noise ratios (SNR; $\text{Pressure}_{\text{signal}}/\text{Pressure}_{\text{noise}}$): +3 dB and -3 dB. All stimuli and experiment files are available on the Scholar Portal Dataverse :

<https://doi.org/10.5683/SP2/8IX6QZ>.

2.6. MRI Data Acquisition

The data were acquired on an Achieva TX Philips 3.0 Tesla Scanner at the *IRM Québec-Mailloux Clinic* in Quebec City. Structural MR images were acquired with a T₁-weighted 3D-MPRAGE sequence (TR = 8.3 ms, TE = 4.0 ms, FOV = 240 mm, flip angle = 8°, 240 × 240 acquisition matrix, 180 slices/ volume, no gap, voxel size = 1 mm³). Throughout the procedure, the head of each participant was immobilized using a set of cushions. The complete image acquisition protocol had a 45-minute duration and also included BOLD fMRI (with a task and resting-state) and diffusion MRI sequences. Some of the diffusion MRI data (focusing on the bilateral arcuate fasciculus) has been analyzed and published elsewhere (Perron et al. 2021).

2.7. MRI Data Processing

Structural MRI data processing was performed using FreeSurfer software version 6.0.0 (<http://freesurfer.net>) (Dale et al. 1999; Fischl and Dale 2000; Fischl et al. 1999), including motion correction and conformation, intensity normalization, non-brain tissue removal using skull stripping algorithms, gray and white matter segmentation and tessellations with automated topology correction. The output of each step was inspected by two of the authors (MP and PT) and manual interventions were performed when required. The native-space surface representations were then parcellated into 74 anatomical regions per hemisphere using the Destrieux 2009 atlas (Destrieux et al. 2010). To address our goal of examining plasticity within auditory and dorsal speech areas, the following ROIs were selected *a priori*: 1) the pars opercularis of the inferior frontal gyrus (pIFG), 2) the inferior frontal sulcus (IFS), 3) the ventral precentral sulcus (vPrS), 4) the dorsal precentral sulcus (dPrS), 5) the precentral gyrus (PrG), 6) the central sulcus, 7) the

supramarginal gyrus (SMG), 8) the angular gyrus (ANG), 9) the planum temporale (PT), 10) the superior temporal sulcus (STS), 11) the transverse temporal gyrus (TTG), 12) the transverse temporal sulcus (TTS), 13) the lateral aspect of the superior temporal gyrus (ISTG) and 14) the planum polare (PP). The mean anatomical location of the ROIs is represented in Fig. 1. Given that little is known about amateur singing-related structural brain plasticity in aging, we decided to investigate three structural metrics that provide distinct information: ROI cortical thickness (distance between the boundary of gray/white matter division and gray matter/pial surface), surface area (total area of the surface occupied by one brain region) and volume. Thickness and surface measures are influenced by different genetic sources (Panizzon et al. 2009), and they have distinct trajectories of anatomical changes that are influenced by several factors (Raznahan et al. 2011).

2.8. Statistical Analyses

All data were analyzed using SPSS 27 for Mac OS (IBM, New York, USA, www.ibm.com). The percentage of correct responses (accuracy) and reaction times (RT) for correct responses were analyzed. For RT, the individual data of each participant were inspected and any trial that deviated by more than two standard deviations from the mean of a condition was removed. The average RT was then calculated with the remaining trials. In addition to accuracy, we also analyzed performance within the signal detection theory framework (Macmillan & Creelman, 1991). That is, sensitivity (d') and response bias (c) were calculated for each condition. D' measures the capacity to correctly recognize whether pairs are the same or different while c reflects the internal decision-making strategy as well as biases. A high value of d' indicates a good capacity for discrimination. A negative value of c indicates a bias toward responding “identical” whereas a positive value of c represents a bias towards responding “different”. A value of zero indicates the absence of bias.

Since we previously reported no difference in SPiN performance between the singers and the non-singers in the two noise conditions for sensitivity (d') (Perron et al. 2021), here we averaged the two conditions of noise for each metric (mean accuracy, d' , c , RT). For each dependent variable (mean accuracy, d' , c , RT), normality was assessed via visual inspection of histograms and Q-Q plots and the homogeneity of variance was assessed using Levene’s test ($p \geq .05$). Any data points that were more than 1.5 box lengths from the edge of the boxplots (outliers) was removed. No more than 2 participants were excluded per metric (See Supplementary Information 1). The quiet condition was removed because of a strong ceiling effect. For RT, a square root transformation was applied to normalize the distribution.

To address the first aim of this study—to investigate the effect of choral singing on SPiN in aging—we conducted simple moderation analyses using the macro PROCESS (v.3.5) (model #1) for SPSS (Hayes 2017) (Fig. 2a). Moderation analyses were conducted separately for each dependent (Y) variable (mean accuracy, d' , c , RT), with age (mean-centered) as the continuous independent (X) variable and group (non-singers, singers) as the categorical moderator. Peripheral hearing (best ear PTA) was included as covariate.

To address the second aim of this study—to determine if different aspects of a persons’ singing experience influences SPiN—we first identified the behavioural measures that were affected by age in the singers by conducting multiple linear regression analyses separately for each dependent variable (mean accuracy, d' , c and RT) with age (mean-centered) and hearing as independent variables. Next, for each dependent (Y) variable that showed an age effect, a series of moderation analyses (model #1) (Fig. 2a) were conducted with age (mean-centered) as the independent (X) variable and each different singing parameter as moderator (M) in separate models. Peripheral hearing (best ear PTA) was included as covariate.

To address the third aim of this study—to uncover the neuroanatomical foundation of the benefits of choral singing on SPiN—a moderated mediation framework (model #58) was developed (Fig. 2b). Each behavioural metric was analyzed separately. For each behavioural metric, the models included age (mean-centered) as the independent variable (X),

singing (group or singing practice behaviours) as the moderator (M) and one ROI metrics (surface, volume, or thickness) as mediator (W). Peripheral hearing (best ear PTA) was included as a covariate. This moderated mediation model evaluated the direct effect of age on SPiN as well as conditional indirect age effects (ab) (i.e., indirect age effects for each level of a moderator) on SPiN through individual brain structures. The indirect effect of age on SPiN through brain anatomy represents the mechanisms by which age affects SPiN; the analysis determines whether this mechanism varies as function of the moderator (e.g., singing frequency). For accuracy and d', a positive indirect effect indicates that cases higher on age (i.e. older) are estimated to be better on SPiN through brain anatomy whereas a negative indirect effect indicates that cases higher on age are estimated to be worse on SPiN through brain anatomy (Hayes 2017). For RT, it is the opposite. For c, a significant indirect effect indicates a change in response strategy with age through brain anatomy. A significant moderated mediation is confirmed if at least one pairwise comparison between conditional indirect effects was statistically significant (Hayes 2015). For continuous variables, the levels of moderator were the 16th, 50th and 84th percentile of the distribution (Hayes 2017). For all analyses, we report the partially standardized regression coefficient (β) (age mean-centered). For all moderated mediations, a bootstrapping approach was used to test for the significance of the effect ($p < 0.05$), using a bias-corrected bootstrapping with 20 000 samples.

3. Results

3.1. SPiN in Aging Singers and Non-singers

Simple moderation analyses were conducted to compare SPiN performance in singers and non-singers. The descriptive statistics of SPiN performance are provided in Supplementary information 1. Holding hearing constant, the analyses revealed a significant age effects on accuracy ($\beta = -.154$, $t = -3.564$, $p < .001$), d' ($\beta = -.014$, $t = -3.821$, $p < .001$) and RT ($\beta = .272$, $t = 2.470$, $p = .016$) (Fig. 3), indicating a decrease in SPiN performance with age. In addition, hearing was negatively related to accuracy ($\beta = -.252$, $t = -3.637$, $p < .001$) and d' ($\beta = -.018$, $t = -3.278$, $p = .002$), indicating lower SPiN performance with higher PTA. There was no group effect and no interactions with group, revealing no overall behavioural differences between singers and non-singers.

3.2. SPiN in Aging Singers

Age effects on SPiN for singers were further investigated by conducting multiple linear regressions. The multiple regression models for accuracy ($F_{(2,34)} = 53.199$, adj. $R^2 = .754$, $p < .001$) and d' ($F_{(2,35)} = 53.941$, adj. $R^2 = .752$, $p < .001$) were statistically significant with a significant contribution of age and hearing. The multiple regression models for c ($F_{(2,33)} = .098$, adj. $R^2 = -.058$, $p = .907$) and RT ($F_{(2,33)} = 3.280$, adj. $R^2 = .121$, $p = .051$) were not statistically significant. Based on these results, simple moderation analyses were conducted to investigate whether singing practice behaviours are associated with less negative age effects on accuracy and d' . The results are reported below separately for the age-independent and age-dependent effects.

3.2.1. Age-Independent Effects

Holding age and hearing constant, the moderation analyses revealed main effects of the number of singing languages for accuracy ($\beta = 1.032$, $t = 3.337$, $p = .002$) and d' ($\beta = .088$, $t = 3.045$, $p = .005$), with better SPiN performance for singers who sang in different languages (Fig. 4a). The results also showed a main effect of frequency of practice at home for both accuracy ($\beta = 2.748$, $t = 2.348$, $p = .026$) and d' ($\beta = .228$, $t = 2.331$, $p = .027$) (Fig. 4b), with better SPiN performance for singers who practised at least once a week at home compared to those who practised less than once a week.

3.2.2. Age-Dependent Effects

Holding hearing constant, the number of singing languages positively moderated the relation between age and accuracy ($\beta = .065$, $t = 3.469$, $p = .002$) and d' ($\beta = .004$, $t = 2.173$, $p = .038$), revealing a decrease in the negative age effect on SPiN performance with an increase in the number of singing languages (Fig. 4a). A follow-up analysis revealed no correlation between the number of singing and spoken languages (Pearson correlation: $r = .063$, $p = .715$). The number of hours of group singing also positively moderated the relationship between age and accuracy ($\beta = .142$, $t = 2.042$, $p = .050$), revealing no significant negative age effect on accuracy for singers who sang in a choir at least three hours a week ($\beta = -.144$, $t = -2.012$, $p = .053$) compared to those who sang in a choir less than three hours a week ($\beta = -.286$, $t = -3.225$, $p = .003$) (Fig. 4c). Finally, formal singing training positively moderated the relation between age and d' ($\beta = .013$, $t = 2.139$, $p = .040$), revealing no significant negative age effect on d' for singers with formal singing training ($\beta = -.004$, $t = -.554$, $p = .584$) compared to those with no formal singing training ($\beta = -.017$, $t = -3.364$, $p = .002$) (Fig. 4d).

3.3. SPiN in Aging Singers and Non-singers Based on Practice Frequency

As one of our hypotheses was that frequent singing would mitigate age-related decline in SPiN performance, and because we observed that higher frequency of practice at home was associated with better SPiN performance, we compared non-singers, singers who frequently practised and singers who practised infrequently using an Analysis of Covariance (ANCOVA). Controlling for hearing and age, significant moderate-sized group effects were found for accuracy ($F_{(2,70)} = 3.360$, $p = .041$, $\eta_p^2 = .094$) (Fig. 5a) and d' ($F_{(2,71)} = 3.577$, $p = .034$, $\eta_p^2 = .098$) (Fig. 5b). Pairwise comparisons for accuracy showed that singers who practised frequently performed significantly better than non-singers (mean difference = 2.3%, $p = .020$) and almost significantly better than singers who practised infrequently (mean difference = 2.5%, $p = .054$). Non-singers and singers who practised infrequently did not differ on accuracy (mean difference = .2%, $p = .865$). Pairwise comparisons for d' showed that singers who practised frequently performed significantly better than non-singers (mean difference = .188, $p = .019$) and singers who practised infrequently (mean difference = .217, $p = .036$). Non-singers and singers who practised infrequently did not differ on d' (mean difference = .029, $p = .767$).

3.4. The Neuroanatomical Correlates of Singing Practice Behaviours on SPiN

Here we investigated the relationship between brain structure and SPiN performance (accuracy, d') as a function of the singing practice behaviours identified in the previous analysis as being associated with better SPiN performance (i.e., number of singing languages, practice frequency at home, number of hours of group singing, and formal singing training). All significant moderated mediations are illustrated in Fig. 6 and the results of all other pathways are summarized in Supplementary Information 2 to 4.

For accuracy, the analyses revealed that the indirect effect of age on SPiN through the thickness of the bilateral ISTG, bilateral PrG, right pIFG, right TTG, right TTS and right PP was positively moderated by the number of singing languages. The analyses also revealed that the indirect effect of age on SPiN through the thickness of the right dPrS was positively moderated by the number of hours of group singing. In all models, the positive moderated mediation suggests that the indirect effect of age on accuracy through the structure of auditory and dorsal speech stream regions was a positive function of the number of singing languages and the number of hours of group singing (i.e., less negative age effect on accuracy with increasing number of singing languages and number of hours of group singing). No moderated mediation effect was found for frequency of practice at home.

For d' , the analyses revealed that the indirect effect of age on SPiN through thickness of the bilateral PrG and ISTG was positively moderated by the number of singing languages. In all models, the positive moderated mediation suggests that the indirect effect of age on d' through the structure of auditory and dorsal speech stream regions was a positive function of the number of singing languages (i.e., less negative age effect on d' with increasing number of singing languages). The analyses also revealed that the indirect effect of age on SPiN through thickness of the right pIFG, IFS, PrG and vPrG was positively moderated by formal singing training. In all models, the indirect effect of age on d' through the structure of dorsal speech stream regions only was more positive for singers with formal singing training compared to those with no formal singing training. No moderated mediation effect was found for frequency of practice at home.

4. Discussion

This study is the first to use surface-based morphometry to investigate the relationship between amateur singing, SPiN, and brain structure in aging. Our main hypothesis was that singing would be associated with better maintained SPiN in aging through singing-induced plasticity within auditory and dorsal speech stream regions, but only under certain conditions of practice. Consistent with this idea, we found no overall beneficial effect of choral singing on SPiN. Yet, exploration of several singing practice behaviours revealed benefits for singers who frequently practised at home, who received formal singing training, who sang in a choir for at least three hours per week and for those who sang in multiple languages, which is consistent with a dose-dependent effect of amateur choral singing on SPiN. These specific singing profiles were associated with a less negative age effect on SPiN through the structure of auditory and dorsal speech stream. These results suggest that amateur singing can induce lasting structural neuroplasticity that maintains SPiN but only for aging singers in a dose-response manner. The behavioural and neurobiological results are discussed in the next sections.

4.1. Aging SPiN and Musical Practice

One of the main findings of the present study is that there was no overall behavioural difference between singers and non-singers. This finding is at odds with longitudinal and cross-sectional studies showing that playing a musical instrument as amateurs (Fostick 2019; Zendel and Alain 2012; Zendel et al. 2019) or professional (Parbery-Clark et al. 2011; Bidelman and Alain 2015) have positive effects on SPiN performance in groups of middle-aged to older adults. It is also at odds with one training study that showed that attending 10 weeks of choral singing, positively affect SPiN in aging (Dubinsky et al. 2019). It is, however, consistent with other studies that did not observe any difference between young and old musicians and non-musicians (e.g. Madsen et al. 2019; Boebinger et al. 2015; Fleming et al. 2019). Such heterogeneity in the benefits of musical activities on SPiN could be related to several factors, including personality factors (Corrigall et al. 2013), auditory or genetic predispositions (e.g. Mankel and Bidelman 2018) or methodological differences between studies, especially those related to participants' characteristics. Another potentially important explanatory factor is that different kinds of musical activities (e.g., amateur singing, opera singing, playing the violin), or different practice behaviours, may differently affect SPiN performance. The present study supports this notion since benefits in SPiN performance were found only for singers with a specific singing profile. More specifically, our results suggest that singing can be beneficial to SPiN in aging when a certain involvement in musical practice is achieved, i.e., singing in a choir for more than three hours per week, practising frequently at home, obtaining formal singing training, and singing in several languages, consistent with the notion of a dose-response relationship.

In the one (independent) prior study that examined the effect of singing training on SPiN, Dubinsky et al. (2019) showed SPiN benefits after 10 weeks of choral training including 2 hours of choral-group session and up to 1 hour of individual musical and vocal exercises per week. In the present study, singers who practised regularly are comparable

to the participants in Dubinsky et al. (2019) (i.e. at least 2 hours of choir per week and a weekly practice at home) and those had better SPiN performance than non-singers and singers with infrequent practice. Another study has shown that the number of hours of musical instrument practice per week positively correlates with SPiN performance in older amateur musicians (Zendel and Alain 2012). The frequency of practice therefore appears to be an important factor to improve SPiN, which is consistent with the OPERA hypothesis stipulating that repetition is essential to trigger lasting neuroplasticity (Patel 2014, 2012, 2011) and with evidence suggesting that the amount of practice moderates music-related neuroplasticity (for a review, see Merrett et al. 2013).

In addition to an effect of practice frequency, here we also found a SPiN advantage for aging singers who sang in multiple languages. The number of singing languages was not correlated with the number of spoken languages, indicating that singers sang without necessarily understanding the words they produced. This suggests that the SPiN advantage of singing in various languages is linked to auditory-motor learning associated with bilingualism. This hypothesis is discussed in the next section.

4.2. Neuroanatomical Correlates of Singing on SPiN

We conducted surface-based morphometry analyses on 14 *a priori* selected bilateral ROIs to examine the neuroanatomical foundation of the effect of choral singing on SPiN. Our results reveal that specific practice behaviours were associated with a less negative age effect on SPiN through the structure of cortical auditory and dorsal speech stream regions. Specifically, we found that singing in multiple languages was associated with a less negative age effect on SPiN through the structure of the right TTS/TTG (i.e., primary auditory area), right PP and bilateral ISTG. These mostly right lateralized auditory regions participate in the spectro-temporal analysis of all sounds with a specialization for music features (i.e., pitch, melody, rhythm) (e.g., Liégeois-Chauvel et al. 1998; Penhune et al. 1999; Samson and Zatorre 1994). Bilingual experience has been linked to differences in the structure of brain regions supporting acoustic and auditory processing (Ressel et al. 2012; Martensson et al. 2012; Wong et al. 2008; Golestani et al. 2007). For instance, Ressel et al. (2012) found larger volume in the bilateral TTG/TTS in bilingual compared to monolingual speakers and Martensson et al. (2012) found an increase in thickness of the left STG after three months of intensive foreign language learning compared to a control group. Singing, especially in multiple languages, is a linguistic experience relying heavily on auditory processing, which could lead to a more efficient or more resilient auditory network through structural plasticity.

A few prior studies on the musical advantage on SPiN in aging have also shown that musical training is associated with an improvement in auditory processing for SPiN. For singers, Dubinsky et al. (2019) observed an increase in frequency following response (FFR) in the auditory brainstem in older adults after 10 weeks of choral training compared to a control group, which predicted improvements in pitch discrimination and, in turn, SPiN advantage. For instrumentalists, it has been shown that older adults with past musical training do not exhibit neural timing delays in the auditory brainstem compared to older adults with no past musical training in response to consonant-vowel transitions (i.e., between /d/ and /a/ in /da/) in noise and in quiet (White-Schwoch et al. 2013). Bidelman and Alain (2015) have shown that older instrumentalists are faster to categorize vowels on a continuum that was associated with higher neural encoding of speech at cortical auditory level compared to non-musicians. Altogether, musical training could enhance auditory processing through structural and functional plasticity within primary and secondary auditory areas, which, in turn, would enhance SPiN.

In the present study, we also found that three factors (singing in multiple languages; having received formal singing training and singing in a choir for at least three hours per week) are associated with a less negative age effect on SPiN through the structure of dorsal speech stream regions. The dorsal speech stream plays a role in auditory-motor integration by connecting temporal and frontal cortices (Hickok and Poeppel 2007; Rauschecker and Scott 2009). Our

results are consistent with the results of Du and Zatorre (2017), which showed that young adults with a professional musical training performed better during a SPiN task than non-musicians, and that this behavioural gain was related to increased activation in auditory and frontal cortices and a strengthened auditory-motor integration.

Singing is a musical activity characterized by precise sensory-motor adjustments to produce specific sounds, which requires a healthy auditory-motor integration mechanism. The maintenance of auditory-motor integration could represent the mechanism through which singing is associated with a mitigation of age-related SPiN decline. The notion of a relationship between speech perception and speech production mechanisms is longstanding (for a review, see McGettigan and Tremblay 2018). For example, it has been shown that speech sounds classification can be modulated by speech motor learning (Lametti et al. 2014) and speech adaptation (Grabski et al. 2013). Consistent with the notion of a benefit through auditory-motor integration, we found that singing in multiple languages was associated with better SPiN performance in aging through the structure of the left PrG (corresponding to the primary and premotor cortices). According to the Directions Into Velocities of Articulators (DIVA) model of speech production (Guenther 1994, 1995; Guenther et al. 2006), the left PrG contains speech motor representations. During SPiN, disambiguation of incoming speech sounds could be facilitated through top-down motor information (for a review, see McGettigan and Tremblay 2018). In the current study, singing in multiple languages, which involves auditory-motor learning, could strengthen auditory-motor integration, and therefore allow more efficient top-down information during SPiN.

In addition to a relationship with the structure of the left PrG, we also found that singing in different languages and attending formal singing training benefit SPiN performance in aging through the structure of the *right* PrG. A role for the right PrG in SPiN via intracortical interactions with the left motor cortex has been shown using dual-coil transcranial magnetic stimulation (Nuttall et al. 2018). In addition, increased activation in the right PrG during SPiN has also been associated with better performance in aging (Wong et al. 2009), suggesting a compensation mechanism. In sum, specific singing practice behaviours could contribute on maintaining the effectiveness of auditory-motor integration for SPiN in both hemispheres by inducing structural plasticity within the bilateral dorsal speech stream.

4.3. Effects of Singing on SPiN Through Cortical Thickness

Our analyses revealed that that SPiN benefits in aging were associated with cortical thickness, but not with cortical volume or surface. Cortical volume is usually interpreted as the product of cortical thickness and surface. According to the radial unit hypothesis (Rakic 1988), cortical surface and thickness represent distinct morphometric characteristics. While surface is determined by the number of vertical ontogenetic columns, thickness is determined by the number and size of cells in a column. Animal studies have shown that it is possible to modify the development of cortical thickness with no change to cortical surface by genetic mutations affecting the intermediate progenitor cells involved in neurogenesis (for a review, see Pontious et al. 2008), suggesting that these two cortical measures are regulated by distinct mechanisms. In line with these previous results, Panizzon et al. (2009) have found that cortical thickness and surface are influenced by different genetic sources.

The current results suggest that choral singing benefits SPiN performance through a specific mechanism of plasticity primarily associated with cortical thickness, which could reflect genesis of neurons within columns (Rakic 1988). Neurogenesis has been shown in a few regions of the human brain, including the hippocampus (e.g. Eriksson et al. 1998). Further, animal studies have shown that neurogenesis can occur in the gray matter of the cerebral cortex (Dayer et al. 2005; Gould et al. 1999). Notably, Dayer et al. (2005) found oligodendrocyte precursor cells in the neocortex of adult rats that seemed to generate new neurons. Experience-induced plasticity within cortical thickness could also reflect other mechanisms, such as preservation or modification of the neuronal morphology within columns.

4.4. Limitations

The main limitation of this study is the relatively small sample sizes ($N = 36$ per group). A consequence of the small sample is that we had to use dichotomous variables to describe singing practice behaviours (e.g., formal training vs. no training, as opposed to using a variable measuring more precisely the amount of training). Despite these limits, the validity of our results is strengthened by a strict matching of the groups (singers vs. non-singers), a rigorous verification of all MRI data with an inter-judge agreement between two of the authors, the use of a standardized SPiN task, and detailed statistical analyses.

4.5. Conclusion

Choral singing is a musical activity that is demanding on multiple levels: sensorimotor, cognitive, and emotional. Because of the rich experience associated with singing, choral singing has the potential to promote structural plasticity in the adult brain. Here, we investigated whether choral singing is associated with better SPiN performance in aging through experience-dependent structural plasticity within auditory and dorsal speech stream regions. Our findings highlight the importance of considering the characteristics of singers when investigating singing-induced plasticity. Our results show that choral singing is associated with structural neuroplasticity within auditory and dorsal speech stream regions which benefits SPiN in a dose-response manner through a dual mechanism involving auditory processing and auditory-motor integration. Understanding the singing practice behaviours that most influence neuroplasticity and SPiN is necessary to develop singing-based strategies to maintain SPiN, and more generally, communication-mediated activities, throughout the entire lifespan.

Declarations

Funding: This study was supported by grants to PT from the Drummond Foundation (2016RFA proposal #27) and the Natural Sciences and Engineering Research Council of Canada (NSERC grant # RGPIN-2019-06534), and two Globalink research internships from MITACS. PT holds a Career award from the Fonds de la Recherche en Santé du Québec (FRQ-S, #35016). MP was funded by graduate scholarships from the Fonds de la Recherche en Santé du Québec (FRQS) and the Canadian Institutes of Health Research (CIHR).

Conflicts of interest/Competing interests: The authors have no relevant financial or non-financial interests to disclose.

Availability of data and material: All stimuli and experiment files are publicly available on the Scholar portal Dataverse: <https://doi.org/10.5683/SP2/8IX6QZ>. Individual data are not available because informed consent obtained from participants did not include consent to public data sharing, and we were not granted the right to request it a posteriori by our local research ethics committee.

Code availability: The software used in this study is freely available online: <http://freesurfer.net>

Authors' contributions: **Maxime Perron:** Conceptualization, Methodology, Investigation, Project administration, Formal analysis, Visualization, Writing- Original draft preparation, Data Curation. **Josée Vaillancourt:** Conceptualization, Writing- Reviewing and Editing. **Pascale Tremblay:** Conceptualization, Funding acquisition, Methodology, Investigation, Supervision, Resources, Project administration, Writing- Reviewing and Editing, Data Curation.

Ethics approval: Ethic approval was obtained from the Comité d'éthique de la recherche sectoriel en neurosciences et santé mentale, Institut Universitaire en Santé Mentale de Québec (#192-2017; #1495-2018). The procedures used in this study adhere to the tenets of the Declaration of Helsinki.

Consent to participate: Informed consent was obtained from all individual participants included in the study.

Consent for publication: N/A

5. Acknowledgements

We thank Valérie Brisson for her valuable help in the development of the task and for her contribution to the recruitment and testing of participants. We also thank Julie Poulin, Emilie Belley, Lisa-Marie Deschênes, Anne-Christine Bricaud, Elena Vaccaro, and Antoine Halbaut for their contributions to the recruitment and testing of participants, as well as all others research assistants and research interns who contributed to the project. Technical support for protocol development and data acquisition was provided by the “Centre intégré en neuroimagerie et neurostimulation de Québec” (CINQ).

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Figures

Figure 1

Location of the regions of interest (ROIs) represented on the group average inflated left surface: 1) the pars opercularis of the inferior frontal gyrus (pIFG), 2) the inferior frontal sulcus (IFS), 3) the ventral precentral sulcus (vPrS), 4) the dorsal precentral sulcus (dPrS), 5) the precentral gyrus (PrG), 6) the central sulcus, 7) the supramarginal gyrus (SMG), 8) the angular gyrus (ANG), 9) the planum temporale (PT), 10) the superior temporal sulcus (STS), 11) the transverse temporal gyrus (TTG), 12) the transverse temporal sulcus (TTS), 13) the lateral aspect of the superior temporal gyrus (ISTG) and 14) the planum polare (PP)

a. Moderation model

b. Moderated mediation model

Figure 2

Conceptual and statistical analytical models for the (a) moderation and (b) moderated mediation analyses. The moderation and moderated mediation analyses were conducted separately for each dependent variable (mean accuracy, d' , c , RT) and singing practice behaviours. Different moderated mediation analyses were also conducted for each ROI metric (surface, volume, thickness)

Figure 3

Relationship between age and SPiN performance. The scatterplots show: (a) accuracy, (b) sensitivity (d'), and (c) reaction time. In each graph, the y-axis represents one of the dependent measures of performance with the effect of hearing removed (unstandardized residuals), and the x-axis shows the variable age. Dotted line represented 95% confidence intervals of the regression line

Figure 4

Relationship between age, singing practice behaviours and SPiN performance. The regression plots show measures of sensitivity (d') or accuracy on the y-axis and age on the x-axis. The graphs were produced using the command line from the output of PROCESS. (a) Main effect and moderating effect of the number of singing languages on the relationship between age and SPiN performance. (b) Main effect of frequency of practice at home on SPiN performance. (c) Moderating effect of the number of hours of group singing on the relationship between age and SPiN. (d) Moderating effect of formal singing training on the relationship between age and SPiN performance. Asterisks indicate significant age effect on SPiN performance at $p \leq 0.05$, and ns indicate non-significant age effect on SPiN performance

Figure 5

The box plots illustrate the categorical effect of singing on (a) accuracy and (b) sensitivity (d') with the effects of hearing and age removed (residuals), separately for non-singers, singers with infrequent practice at home ($< 1/\text{week}$), and singers with frequent practice at home ($\geq 1/\text{week}$). Each dot represents one participant. Asterisks indicate significance at $p \leq 0.05$, and ns indicate non-significance. Error bars represent the 95% confidence intervals of the mean

a. Number of singing languages

b. Number of hours of group singing

c. Formal Singing Training

○ Accuracy ● d' ● Accuracy + d'

Figure 6

Illustration of the ROIs showing a significant moderated mediation, presented on group average inflated brain surfaces. (a) ROIs showing an indirect effect of age on SPiN performance through cortical thickness positively moderated by the number of singing languages. (b) ROIs showing an indirect effect of age on SPiN performance through cortical thickness positively moderated by formal singing training. (c) ROIs showing an indirect effect of age on SPiN performance through cortical thickness positively moderated by the number of hours of group singing. In the figure, regions identified in white show a moderated indirect effect of age on accuracy through ROI structure, regions identified in yellow showed a moderated indirect effect of age on sensitivity through ROI structure (d'), and regions identified in blue identifies showed a moderated indirect effect of age for both accuracy and d'

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