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Neural processing and benefits of singing in the ageing brain

Nella Moisseinen

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Pre-examiners

Professor Pascale Tremblay, PhD
Département de Readaptation
Faculté de Médecine
Université Laval, Canada

Associate Professor Rebecca Schaefer, PhD
Health, Medical & Neuropsychology Unit
Institute for Psychology
Faculty of Social and Behavioural Sciences
Leiden University, The Netherlands

Custos

Professor Teppo Särkämö, PhD
Cognitive Brain Research Unit
Centre of Excellence in Music, Mind, Body and Brain
Department of Psychology
Faculty of Medicine
University of Helsinki

Supervisors

Professor Teppo Särkämö, PhD
Cognitive Brain Research Unit
Centre of Excellence in Music, Mind, Body and Brain
Department of Psychology
Faculty of Medicine
University of Helsinki, Finland

Postdoctoral Researcher Noelia Martínez Molina, PhD
Center for Brain and Cognition
Department of Information and Communication Technologies
Universitat Pompeu Fabra, Spain

University Researcher Aleksi Sihvonen, MD, PhD
Cognitive Brain Research Unit
Centre of Excellence in Music, Mind, Body and Brain
Department Psychology
Faculty of Medicine
University of Helsinki, Finland
and
Department of Neurology
University of Helsinki & Helsinki University Hospital, Finland

Associate Professor Boris Kleber, PhD
Center for Music in the Brain
Department of Clinical Medicine
Aarhus University and The Royal Academy of Music Aarhus/Aalborg, Denmark

Opponent

Professor Stefan Koelsch, PhD
Department of Biological and Medical Psychology
Faculty of Psychology
University of Bergen, Norway

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To my grandparents

Abstract

The brain is a highly adaptive organ that aims to respond to the parallel and intertwined declines in normal ageing. According to the prevailing models of ageing, the interactions of associated neural atrophy and preservation emerge across adulthood and are influenced by accelerating and mediating factors, such as sensory deficits and lifestyle. Emerging evidence suggests that singing, like many cognitively engaging musical activities, may promote a healthy ageing trajectory. The positive influence of music on socioemotional well-being has directed particular attention towards choir singing, yet a systematic account on its associations with neurocognitive ageing is currently missing while the direct effects of ageing on the neural substrates of singing remain unknown.

This thesis, comprising three studies, aimed to map the ageing effects of singing and the associations of choir singing experience with brain structure, cognitive function, and socioemotional well-being across adulthood (N = 100, age 21–88 years). Study I used a 2 x 3 overt production task design to learn about the ageing effects of singing versus speech across three types of associated cognitive demands: repetition and completion of familiar and improvisation of new items. Despite extensive overlap across the age range, singing and speech showed differential effects of age: (i) increasing activation in the medial prefrontal cortex and angular gyri in the completion task in singing with no significant difference to speech, (ii) systematic adaptation effects in left-lateralised somatosensory cortices across all speech tasks but not in singing, and (iii) a larger left-to-right shift in lateral prefrontal vocal production regions in the improvisation task in speech compared to singing.

Studies II and III addressed the associations between choir singing experience (duration, frequency) and brain structure (regional grey matter volume, white matter structural connectivity), cognitive function (verbal fluency, episodic memory, working memory, processing speed, executive function), and subjective socioemotional well-being [depression, quality of life (QOL)]. The results suggested that lifetime choir singing duration was associated with joint enhancements of associative, commissural, projection, and cerebellar pathways as well as episodic memory and verbal fluency, which also mediated the effects on memory. Choir singing frequency, by contrast, was associated with enhanced psychological and overall QOL as well as reduced depressive symptoms, which also mediated the effects on QOL.

Taken together, these results illustrate functional differences between singing and speech in the ageing brain, despite the heavy overlap of the associated vocal production networks. Further, the results provide the first systematic account of how choir singing is associated with enhancements across the neural, cognitive, and well-being domains, showing mutually interacting mechanisms by which choir singing as well as other cognitively engaging leisure activities may promote a healthy ageing trajectory.

Tiivistelmä

Aivot muovautuvat läpi elämän sopeutuen myös ikääntymisen mukanaan tuomiin muutoksiin. Nykykäsityksen mukaan aivojen ikääntymiseen kuuluvien muutosten keskinäiset vuorovaikutussuhteet elävät läpi aikuisuuden ja riippuvat osittain kiihdyttävistä ja välittävistä tekijöistä, kuten aistien heikkenemisestä ja elintavoista. Lisääntyvä tutkimusnäyttö kognitiivisesti stimuloivien vapaa-ajan aktiviteettien kuten musiikin kyvystä tukea tervettä ikääntymistä onkin herättänyt kasvavaa mielenkiintoa. Erityisesti kuorolaulamisen on osoitettu tukevan sosioemotionaalista hyvinvointia, mutta laajempi systemaattinen tutkimusnäyttö sen yhteyksistä terveeseen neurokognitiiviseen ikääntymiseen ja toisaalta ikääntymisen vaikutuksista laulamisen aivoperustaan puuttuu.

Tämä väitöskirja koostuu kolmesta tutkimuksesta, jotka yhdessä pyrkivät kartoittamaan ikääntymisen vaikutuksia laulamisen aivoperustaan (tutkimus I) ja kuorolaulamisen yhteyksiä aivojen rakenteeseen, kognitiiviseen toimintakykyyn ja sosioemotionaaliseen hyvinvointiin terveillä aikuisilla (tutkimukset II–III; *N* = 100, ikä 21–88 vuotta). Tutkimus I hyödynsi toiminnallista magneettikuvantamista verratakseen laulamisen ja puhumisen ikävaikutuksia kolmessa kognitiivisilta vaatimuksiltaan erilaisessa tehtävässä: tutun ärsykkeen toistamisessa ja muistinvaraisessa täydentämisessä sekä uuden improvisoinnissa. Vokaalisen tuoton herättämän aktivaation laajasta päällekkäisyydestä huolimatta laulaminen ja puhuminen erosivat ikävaikutuksiltaan: (i) muistinvarainen täydentäminen laulamalla herätti iäkkäämmillä voimakkaampaa aktivaatiota mediaalisella etuotsalohkolla ja kulmapoimussa, kun taas (ii) kaikissa puhetehtävissä nähtiin järjestelmällisiä muutoksia somatosensorisella aivokuorella ja (iii) puheimprovisaatiossa suurempi siirtymä oikeanpuoleisten vokaalisen tuoton alueiden käyttöön lateraalisella etuotsalohkolla kuin lauluimprovisaatiossa.

Tutkimukset II ja III selvittivät edelleen kuorolauluharrastuksen yhteyksiä terveeseen ikääntymiseen. Kuorolauluharrastuksen kesto oli positiivisesti yhteydessä valkean aineen eheyteen assosiatiivisissa, aivopuoliskot yhdistävissä, projektio- ja pikkuaivojen radoissa sekä sanasujuvuuteen ja episodiseen muistiin, jossa havaittiin myös mediaatiovaikutus sanasujuvuuden kautta. Kuorolaulamisen taajuus (tuntia viikossa) puolestaan oli negatiivisesti yhteydessä masennusoireisiin ja positiivisesti yhteydessä elämänlaatuun, jossa havaittin mediaatiovaikutus vähentyneiden masennusoireiden kautta.

Näiden tulosten perusteella ikääntyminen ei vaikuta laulamiseen samalla lailla kuin puhumiseen, vaikka niiden aivoperusta on laajalti päällekkäinen. Sen sijaan kuorolauluharrastus oli positiivisesti yhteydessä aivojen valkean aineen rakenteelliseen kytkeytyneisyyteen, episodisen muistiin ja sanasujuvuuteen sekä sosioemotionaaliseen hyvinvointiin. Lisäksi kognitiivisen toimintakyvyn ja sosioemotionaalisen hyvinvoinnin tulokset osoittivat keskinäisiä riippuvuussuhteita viitaten siihen, että kuorolaulamisen kaltaisten, kognitiivisesti stimuloivien aktiviteettien yhteydet terveeseen ikääntymiseen voivat selittyä useamman tekijän yhteisvaikutuksella.

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Järvenpää, January 2026
Nella Moisseinen

List of abbreviations

ACC	anterior cingulate cortex
AD	Alzheimer’s disease
AF	arcuate fasciculus
AG	angular gyrus
AMI	Advanced Magnetic Imaging centre
AP	anterior-posterior
AR	autoregressive model
ART	Artifact Detection Tool
BOLD	blood oxygenation level dependent
CAT	Computational Anatomy Toolbox
CBRU	Cognitive Brain Research Unit
CinC	cingulate cortex
CC	corpus callosum
CES-D	Center for Epidemiological Studies: depression
CI	confidence interval
CPT	corticopontine tract
CR	Cognitive Reserve theory
CRA	compound remote associate
CRUNCH	Compensation-Related Utilization of Neural Circuits Hypothesis
CSF	cerebrospinal fluid
CST	corticospinal tract
CStrT	corticostriatal tract
DLPFC	dorsolateral prefrontal cortex
DMN	default mode network
dMRI	diffusion-weighted magnetic resonance imaging
DRTT	dentatorubrothalamic tract
EC	extreme capsule
EPI	echo-planar imaging
ERCEA	European Research Council Executive Agency
FA	fractional anisotropy
FAT	Flexible Attention Test
FDR	false discovery rate

FG	fusiform gyrus
fMRI	functional magnetic resonance imaging
FOV	field of view
FSL	FMRIB Software Library
FWE	family-wise error
FWHM	full width at half maximum
GLM	general linear model
GM	grey matter
GMV	grey matter volume
Gold-MSI	Goldsmith's Musical Sophistication Index
HAROLD	Hemispheric Asymmetry Reduction in Older Adults model
HCB	hippocampal cingulum bundle
HG	Heschl’s gyrus
HRF	hemodynamic response function
IFG	inferior frontal gyrus
IFOF	inferior fronto-occipital fasciculus
ILF	inferior longitudinal fasciculus
IOG	inferior occipital gyrus
IPL	inferior parietal lobule
ITG	inferior temporal gyrus
LI	Laterality Index
MCI	mild cognitive impairment
MedFG	medial frontal gyrus
MedOG	medial orbital gyrus
MFG	middle frontal gyrus
MIT	Massachusetts Institute of Technology
ML	medial lemniscus
MNI	Montreal Neurological Institute
MOG	middle occipital gyrus
MPFC	medial prefrontal cortex
MP-PCA	Marchenko-Pastur principal component analysis
MPRAGE	magnetisation-prepared rapid gradient echo
MR	magnetic resonance
MRI	magnetic resonance imaging
MTG	middle temporal gyrus
OFG	orbitofrontal gyrus
PA	posterior-anterior
PCC	posterior cingulate cortex
PFC	prefrontal cortex
PHG	parahippocampal gyrus
PoCG	postcentral gyrus

PrCG	precentral gyrus
pSTS	posterior superior temporal sulcus
QA	quantitative anisotropy
QOL	quality of life
RCT	randomised controlled trial
ROI	region of interest
RSFC	resting-state functional connectivity
SD	standard deviation
SE	standard error
SFG	superior frontal gyrus
SLF	superior longitudinal fasciculus
sMRI	structural magnetic resonance imaging
SMA	supplementary motor area
SpiN	speech in noise task
SPL	superior parietal lobule
SPM	Statistical Parametric Mapping
STAC-R	Scaffolding Theory of Aging and Cognition (revised)
STG	superior temporal gyrus
STS	superior temporal sulcus
tb-fMRI	task-based functional magnetic resonance imaging
T1w	T1-weighted
TA	time of acquisition
TE	time of echo
TIV	total intracranial volume
TMT	Trail-Making Test
TOI	tract of interest
TP	temporal pole
TPM	tissue probability map
TR	time of repetition
ThR	thalamic radiation
UCL	University College London
UF	uncinate fasciculus
VBM	voxel-based morphometry
WAIS-IV	Wechsler Adult Intelligence Scale, 4th edition
WHO	World Health Organization
WHOQOL-BREF	World Health Organization quality of life: brief version
WM	white matter
WMS-III	Wechsler Memory Scale, 3rd edition

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List of original publications

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I Moisseinen N., Särkämö T., Kauramäki J., Kleber B., Sihvonen AJ., and Martínez-Molina N. (2023) Differential effects of ageing on the neural processing of speech and singing production. Frontiers in Aging Neuroscience 15: 1236971. DOI: 10.3389/fnagi.2023.1236971

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[†] Aleksi J. Sihvonen and Teppo Särkämö contributed equally to this study.
[‡] Alli Haavisto and Silja Heimala contributed equally to this study.

The publications are referred to in the text by their roman numerals.

1 Introduction

1.1 Parallel and intertwined declines of the ageing brain

The brain is a highly adaptive organ that makes use of available resources to meet the requirements of daily life. Its unique ageing trajectory unfolds throughout adulthood, following the net influence of accelerating and mediating factors, such as ageing-related sensory deficits, genetic determinants, and lifestyle (Corley et al., 2018; Kaufmann et al., 2019; Livingston et al., 2020). Parallel declines in maintenance processes and alterations in neuronal excitability (Mattson & Arumugam, 2018) are eventually followed by the degradation of functional neural networks (Marstaller et al., 2015; for a review, see also Mattson & Arumugam, 2018) and the underlying grey matter (GM) and white matter (WM) structures (Bethlehem et al., 2022; Vinke et al., 2018). Peaking before adulthood, GM generally shows faster atrophy compared to WM (Bethlehem et al., 2022). Frontal, temporal, and parietal regions including inferior and middle frontal and postcentral gyri (Minkova et al., 2017) typically show earlier signs of ageing compared to other GM regions. Likewise, early maturing WM structures such as the fornix, the main pathway of the hippocampus, also degrade earlier. Partially owing to these changes, normal brain ageing involves progressive declines in episodic and working memory (Nicolas et al., 2020), fluid intelligence (Ritchie et al., 2015), and executive function (Berger et al., 2022; Manard et al., 2016; see also Koini et al., 2018).

The net effects of neurocognitive decline are further shaped by mutual dependencies of functions in everyday cognition: for example, performance in semantic verbal fluency tasks is associated with executive function (Amunts et al., 2020), while the various types of semantic processing feed differentially to the formation of spoken content (e.g., Humphreys et al., 2024). Such dependencies are also found along the ageing continuum, where performance in tasks measuring one function can predict performance in another. Following clinical observations in mild cognitive impairment (MCI) and Alzheimer's type dementia, an increasing amount of interest is being directed towards using (semantic) verbal fluency performance to predict later performance in episodic memory (Folia et al., 2023; Gustavson et al., 2020; Sutin et al., 2019). While the source of the association between episodic memory and semantic fluency remains poorly understood (Folia et al., 2023), it illustrates the importance of considering ageing not only by segregated structures or functions but the heavily intertwined network it impacts.

1.2 Neurocognitive reserve and adaptation with advancing age

Contemporary theories of neurocognitive ageing posit that, while handling the challenges associated with structural and functional decline, the ageing brain remains highly adaptive. Prevailing models, such as Cognitive Reserve (CR) theory (Stern, 2009; see also Stern et al., 2020) and the revised version of the Scaffolding Theory of Aging and Cognition (STAC-R; Reuter-Lorenz & Park, 2014, 2024), suggest that a unique ageing trajectory involves components of both reserve, i.e., existing resources, and a degree of compensation, i.e., structural and functional plasticity that aims to support the existing resources (for a comparison and review on CR and STAC-R, see Oosterhuis et al., 2023). Within this framework, compensatory mechanisms can be supported with sustained enrichment promoting healthy brain structure and function (cf. Reuter-Lorenz & Park, 2014); indeed, enrichment through cognitively engaging leisure activities, such as reading, dancing, playing board games or a musical instrument have been associated with a reduced risk of developing dementia (Hall et al., 2009; Verghese et al., 2003; for a review, see also Rodriguez et al., 2025).

Neuroimaging studies have provided partially converging evidence, suggesting that enrichment through cognitively engaging activities can, to some extent, reduce volumetric loss in prefrontal GM (Chaddock-Heyman et al., 2021; Kühn et al., 2017; Tabei et al., 2017) and enhance the microstructure of major WM tracts, such as corpus callosum (Lövdén et al., 2010), inferior longitudinal fasciculus (ILF), and hippocampal cingulum bundle (HCB; de Lange et al., 2018) in the ageing brain. As such effects are typically local, carrying the heavy influence from early-life determinants (Walhovd et al., 2023), reaching a healthy ageing trajectory inevitably involves adjustment to structural changes. According to the current models of ageing, the brain can respond with functional compensation (compensatory scaffolding in STAC-R), which involves the configuration of supplementary neural circuitry to adapt to emerging declines. Within the STAC-R framework, both needs and capacity for adaptation are partially dictated by available resources, however: ageing brains can differ in their adaptive abilities (see also Walhovd et al., 2023).

A classic form of functional compensation in neurocognitive literature is overactivation, well-known examples comprising additional engagement of prefrontal regions, or more bilateral activation in the case of initially lateralized functions (for discussion, see Reuter-Lorenz & Park, 2014). It remains unclear, however, to what extent such compensatory mechanisms *can* compensate for deteriorating resources. Increasing bilaterality, also described by Cabeza (2002) in the Hemispheric Asymmetry Reduction of Older Adults (HAROLD) model, has been reported across various cognitively challenging production tasks, such as rapid word production (Hoyau et al., 2017; Wierenga et al., 2008), with mixed results on its ability to support performance. While this discrepancy could partially owe to differential adaptive properties, as discussed above, other ageing studies (e.g., Meunier et al., 2014; Morcom & Henson, 2018) have pointed out that a more widely distributed functional network, such as that recruiting the contralateral hemisphere, may be less efficient, leaving the compensatory utility of such reorganisation questionable.

This is also recognized in STAC-R, which posits that compensatory mechanisms aim to support the primary network without making direct assumptions on their success (Reuter-Lorenz and Park, 2014), and that sufficient cognitive engagement, on the other hand, can reduce the reliance on compensatory scaffolding (Reuter-Lorenz and Park, 2024). On the other hand, growing task demands (load) can elicit overactivation irrespective of age, and then decrease again; this is hypothesised to stem from available resources not being able to respond to the growing demands (Compensation-Related Utilization of Neural Circuits Hypothesis, CRUNCH; Reuter-Lorenz & Cappell, 2008). Taken together, estimating the actual compensatory capacity of a given functional assembly, even when restricted to the frontal networks, is challenging on its own. This renders a combination of neuroimaging and behavioural measures commendable, the former ideally providing an explanatory framework for the latter (see also Meunier et al., 2014), especially when the aim is to assess the utility of neurocognitive enrichment, personal lifestyle, or interventions.

1.3 Vocal production as a marker for ageing-associated decline

Vocal production, sometimes considered equal to speech, falls at the intersection of overlapping cognitive demands, language, and precise motor control. Highly specialised in the association of acoustic features and meaning, the vocal production networks translate memory and contextual information into fine motor sequences, enabling sophisticated communication through speech or singing, for instance. The classical dual stream model of language (Hickok & Poeppel, 2004, 2007), also largely applied to singing (Loui, 2015; Musso et al., 2015), holds that a majority of language-related processing, centrally involved in vocal production, occurs through bidirectional dorsal and ventral processing streams that receive input from the auditory cortices as well as one another.

The dorsal stream, flowing dorsally between the posterior Sylvian regions and posterior frontal regions, including posterior parts of the inferior frontal gyrus (IFG; pars opercularis, triangularis) as well as the posteriorly adjacent premotor cortex, is thought to contribute to the mapping of auditory/phonological and motor information, including articulation and feedback control. Its main pathways include arcuate fasciculus (AF) and the superior longitudinal fasciculus (SLF), allowing it to convey information across the more dorsal portions of, primarily, the left (dominant) hemisphere. The ventral stream, by contrast, is thought to map auditory information to meaning in a more bilateral fashion (Hickok & Poeppel, 2007). It engages the primary auditory cortices along with more anterior parts of the middle and inferior temporal regions through the inferior fronto-occipital fasciculus (IFOF), for instance. Crucially, the ventral stream supports vocal production by receiving auditory input although not being directly involved in motor processing.

The dual stream model offers a convenient framework for understanding speech, especially the key processes involved in the motor aspects of vocal production. With respect to the cognitive demands of vocal production, it remains more limited, however, not describing how intrinsic information is handled and combined with auditory input. Indeed, meaningful vocal production centrally involves interactions of the attention, working memory, episodic memory, and even affective systems that go beyond the hypothesised functions and anatomy of the ventral stream. This is well illustrated in evidence from aphasic patients (Dresang et al., 2021; Hula et al., 2020) suggesting the involvement of limbic and other subcortical pathways, including the fornices and splenium of the corpus callosum (CC) as well as frontal and parietal cortico-subcortical projection pathways in semantic processing and retrieval. A recent neuroimaging study on live speech perception (Steiner et al., 2022) also showed selective subcortical responses to different affective cues of pseudoword sentences in amygdala and striatum, further illustrating the semantic dimensions of speech (for a review and model on nonverbal vocal communication, see also Frühholz & Schweinberger, 2021).

Cognitive task demands intrinsic to production, on the other hand, can diversify the composition of the support network directly. In an innovative functional magnetic resonance imaging (fMRI) study on freestyle rap, Liu et al. (2012) found that improvised versus conventional production (recall) elicited left-lateralised activity increases along the medial prefrontal cortices (MPFC) and widespread right-lateralised activity decreases across dorsolateral prefrontal cortex (DLPFC) regions, concluding that improvisation entails information synthesis and guidance of self-generated behaviour with reduced volitional control (for a review on creativity and cognitive control, see also Beaty et al., 2016). Further, ageing-associated effects of compensatory overactivation in speech production can also depend on the type of task demands. For instance, Tremblay et al. (2017) assessed the effects of ageing on speech production using nonwords of varying motor and sequential complexity (articulatory complexity of syllables and variability of syllables within a sequence, respectively) with a combination of behavioural (movement time) and neural activity measures (fMRI). While compensatory effects were associated with high sequential but not motor complexity alone, most pronounced effects of age, spreading across left somatomotor as well as executive regions (right middle frontal gyrus, MFG; bilateral posterior cingulate cortex, PCC), were found when task complexity in both domains was high, despite unchanged performance levels. Thus, the authors concluded, increasing executive and motor demands of speech show differential ageing mechanisms that can, in turn, influence the overall effects of ageing on speech.

Finally, ageing effects in speech are subject to bias from experimental tasks. Building on the observation that syntactic processing is highly automatic and typically well-preserved in ageing, Davis et al. (2014) ran a neuroimaging study where adults of various ages (20–86 years) listened to spoken sentences, some of which were syntactically ambiguous. When participants were asked to judge whether a sentence was an acceptable sentence, older participants showed increased bilateral PFC activity, mediated by partially overlapping decreases in GM density. When participants listened to the same sentences without a simultaneous task (assessing the sentences explicitly only afterwards), no ageing effect was found. As predicted, neither performance in the assessment tasks nor activation in the frontotemporal language network were associated with the experimental condition in the sample, suggesting that ageing-associated overactivation of the prefrontal cortex (PFC) was due to the presence of an explicit experimental task, not an influence of ageing on syntactic processing per se.

The diverse dependencies of speech processing on the associated affective and cognitive processes, as illustrated in the above examples, offer a flexible framework for studying the net and mediating effects of ageing within a natural context. However, the mechanisms guiding these phenomena, especially with respect to the ageing continuum, remain poorly understood. This is hardly a surprise, considering the inherent complexity of these associations, especially when reflected on the ageing continuum (for reviews, see Peelle, 2019; Shafto & Tyler, 2014), with the sometimes-problematic combinations of experimental task demands and the age-sensitivity of mutually intertwined functions (as illustrated by Davis et al., 2014). Crucially, determining these mechanisms will require systematic accounts involving the manipulation of associated cognitive task demands within a similar task context. To learn about the potential influence of underlying interactions between cognitive and vocal production systems, it would be also informative to compare the ageing effects in speech to another domain of vocal production, such as singing, across the same task demands.

1.4 Asymmetries of speech and singing networks

Also complying with the dual stream model (Loui, 2015; Zarate, 2013), singing elicits temporal, frontal, and parietal activation largely overlapping with speech in the young adult brain (see also Peretz et al., 2015). Indeed, evolutionary accounts on singing hypothesise that music may have indeed evolved as a communicative domain in parallel to speech, supporting various forms of social bonding from group communication to nurturing and communication in parent-infant dyads (Mehr et al., 2021) and forming and maintaining long-lasting intimate relationships (Bamford et al., 2024). Neuroimaging evidence also suggests neural specialisation to the acoustic features of the human voice in the superior temporal sulci (STS), hence differentiating the auditory processing of singing from that of music more generally (Whitehead & Armony, 2018).

The extensive overlap aside, increasing evidence during the past two decades has been able to characterise a number of specialisation features to distinguish the neural bases of singing and speech. Beginning at the classical observation of singing producing generally more extensive bilateral activation compared to speech (Callan et al., 2006; Özdemir et al., 2006), developments in neuroimaging have enabled the recognition of a number of specific hemispheric preferences, such as the right IFG activating together with its left-hemisphere homologue in singing but being suppressed in speech, and the left and right anterior insula selectively supporting articulation in speech and the integration of auditory and somatosensory information in singing, respectively (for a review, see Harris et al., 2023). Returning to the observations of ageing-associated overactivation in right-lateralised PFC regions in speech production tasks (e.g., Hoyau et al., 2017) discussed above, such differences in laterality raise the question of whether the ageing effects of speech can apply to vocal production at large. Specifically, existing examples on compensatory overactivation, shown to associate with variable cognitive demands in speech tasks, make no prediction on whether similar effects would arise under similar cognitive demands in singing.

Crucially, clinical evidence from aphasic patients suggests that singing ability can be preserved despite difficulties in speech production (Martínez-Molina et al., 2022) and that singing can be used to support the recovery of speech networks in aphasia (Marchina et al., 2023; Sihvonen et al., 2024). Emerging evidence suggests that such transfer effects are enabled by the asymmetry of lateralisation in speech versus singing, i.e., speech relying more heavily on the damaged left hemisphere (for a review, see Schlaug et al., 2010), or differential recruitment of the left dorsal stream, which is essentially thought to support speech production (Pitkäniemi et al., 2023). Further, evidence from normal ageing suggests that, besides the well-established transfer effects from music to speech processing (Patel, 2011; Peretz et al., 2015), such as enhanced perception of speech in noise (SpiN; Perron et al., 2022; Worschech et al., 2021; L. Zhang et al., 2021), singing can support speech processing through specific influence on networks supporting vocal production. For instance, singers have been shown to excel in imitating foreign language pronunciation, outperforming instrumentalists despite having equal skills in perception (Christiner & Reiterer, 2015). On the other hand, singing has been associated with enhanced semantic verbal fluency in healthy ageing (Fu et al., 2018; Tremblay et al., 2025) and Alzheimer's disease (Lyu et al., 2018), tentatively suggesting a beneficial effect on word retrieval despite ongoing declines (however, see Tremblay et al., 2025). Although mainly assessed in professional singers, these findings are partially corroborated by neuroimaging evidence suggesting singing-associated structural enhancements in structures overlapping with the vocal production network: increased GM volume in auditory and somatosensory cortices (Kleber et al., 2016) and WM volume (Halwani et al., 2011) and structural integrity (as measured by fractional anisotropy, FA) in the arcuate fasciculus (Halwani et al., 2011; Perron et al., 2021), one of the main pathways of the dorsal stream. By contrast, existing evidence suggests no transfer effects in the opposite direction.

Considering the asymmetries between speech and singing, involving both differential lateralisation and employment of left-lateralised language network structures, the initial contexts for developing ageing-associated declines within these modalities of vocal production are far from identical. This notion argues against shared ageing mechanisms in speech and singing, suggesting that currently known ageing effects in speech may not apply to vocal production at large. Considering that the ageing effects of speech are directly influenced by task demands, as discussed above, this raises a question: is singing similarly vulnerable to the ageing effects of associated cognitive task demands, or can the singing network overcome these effects within its more widespread bilateral network? Ideally, this setting would be tested by targeting vocal production task demands on age-sensitive cognitive functions, such as episodic memory and fluid ability.

1.5 Using music to promote healthy ageing

From a public-health perspective, interventions that foster or maintain cognitive reserve make for a promising avenue to mitigate the societal and economic burden associated with the rapid ageing of populations worldwide (World Health Organization, 2019). Following increasing evidence on its efficacy in supporting healthy ageing, healthcare organizations including WHO (Fancourt & Finn, 2019) and Global Council on Brain Health (2020) now advocate the use of music for promoting a healthy ageing trajectory. Regular and sustained engagement in musical activities, such as singing and playing an instrument, can support specific cognitive functioning, including auditory-linguistic skills (Perron et al., 2022; Worschech et al., 2021) and verbal fluency (Fu et al., 2018; Hanna-Pladdy & Gajewski, 2012; Tremblay et al., 2025), episodic memory and learning (Hanna-

Pladdy & Gajewski, 2012; Mansens et al., 2018; for a review on dementia risk, see also Arafa et al., 2022), working memory (Hanna-Pladdy & Gajewski, 2012; Joyal et al., 2024; Mansens et al., 2018), processing speed, and executive function (Joyal et al., 2024; Mansens et al., 2018), with increasing evidence from healthy ageing (for reviews, see Román-Caballero et al., 2018; Vetere et al., 2024) to mild cognitive impairment (Doi et al., 2017; for a review, see also Dorris et al., 2021).

Although well established, the underlying mechanisms as well as sufficient doses of practice (cf. Perron et al., 2022; Strong, 2022) and the potential overall significance of these effects (cf. Joyal et al., 2024; Tremblay et al., 2025) for promoting a healthy ageing trajectory remain unclear. Taking memory as an example, Mansens et al. (2018) studied the associations between music making (amateur or professional level) and cognitive function in older adults (*N* = 1101), reporting a positive association between immediate verbal recall and music making (yes/no). In contrast to the hypothesis, however, this effect was not explained by the frequency of musical practice. Similarly, Hanna-Pladdy & Gajewski (2012) compared older non-musicians (*n* = 37) and formerly or presently active advanced musicians (*n* = 33; minimum experience of 10 years at amateur or professional level), finding a significant difference in immediate verbal recall in musicians' favour. In another correlational study (Strong, 2022), musical experience was not a significant predictor of immediate verbal recall in a sample involving older non-musicians (*N* = 58), while the subgroup of older instrumental musicians (*n* = 45; amateur or professional level) did show a positive association between recall and the years of formal training. Finally, longitudinal studies on choir singing have reported null effects on immediate and delayed verbal memory during a 6-month randomised controlled trial (RCT; Johnson et al., 2020) and within the follow-up periods of 1–2 years in ageing amateur-level choir singers (Pentikäinen et al., 2023).

Taken together, a positive association between practicing music and recall is not found in all circumstances but may be more likely in the case of long-term musical practice (Mansens et al., 2018; Perron et al., 2022; Strong, 2022). This trend aligns well with magnetic resonance imaging (MRI) evidence from musically active older adults showing long-evolving plastic effects in neural networks associated with recall and memory. For instance, sustained engagement in musical activities has been associated with enhanced resting-state functional connectivity (RSFC) of the MPFC (Liebscher et al., 2024; see also Quinci et al., 2022) and, to some degree, of other default mode network (DMN) regions (e.g., X. Zhang & Tremblay, 2023). Whether such effects could explain the benefits associated with singing remains unclear (cf. X. Zhang & Tremblay, 2023). However, the role of DMN in supporting the internal narrative, including episodic memory (for reviews, see Menon, 2023; Smallwood et al., 2021), and of MPFC in processing musical memories and pleasure (Hennessy et al., 2025; Quinci et al., 2022) considered, the ability to enhance memory-supporting network function seems to offer a potential mechanism for the effects of musical engagement on memory.

Structural MRI (sMRI) studies have also associated long-term music activities with memory-supporting systems, reporting increased grey matter volume (GMV) in the parahippocampal cortices in highly trained amateurs (Chaddock-Heyman et al., 2021). However, RCTs on dance and piano playing have shown enhanced microstructure of the fornices (Burzynska et al., 2017; Jünemann et al., 2022), the major pathways of the hippocampi, showing also a mild positive association with episodic memory performance after only six months' practice (Jünemann et al., 2022). Tentatively, these effects suggest that music-induced benefits on memory-supporting mechanisms may be strengthened by but not limited to long-term practice. Considering the vulnerability of episodic memory in normal and pathological ageing, the influence of musical activities on these mechanisms may hold great potential for promoting healthy neurocognitive ageing.

Furthermore, musical memories and emotions are well-preserved from normal ageing to the advanced stages of Alzheimer's disease (AD), thus providing unique means for supporting socioemotional well-being with advancing age (for suggested mechanisms of preservation in AD, see Jacobsen et al., 2015). In recent years, increasing qualitative evidence on the positive influence of music on socioemotional well-being has directed particular attention towards choir singing. Contributing to the inherent social features of singing (cf. Bamford et al., 2024; Mehr et al., 2021) and the motivational and mood-enhancing influence of music (Koelsch, 2014; see also Koelsch et al., 2021), choir singing promotes psychological well-being by enhanced emotional expression through singing, reduced negative and increased positive affect, as well as experiences of ease and uplift (Livesey et al., 2012; Moss et al., 2018). RCT results showing positive effects of choir singing on mood (e.g., reduced depression, anxiety, and loneliness) and quality of life (QOL) attribute these effects to an interplay of affect and other components of psychological well-being (Coulton et al., 2015; Galinha et al., 2023; Skingley et al., 2016; see also Johnson et al., 2013, 2020). Previous reports also note that psychological well-being may begin to decline shortly after singing is discontinued, hence indicating the importance of active engagement (Coulton et al., 2015). When interviewed on feelings regarding the end of a group-singing-based RCT, also the participants from Skingley et al. (2016) expressed regret and concerns about a negative influence in mood; resuming singing activities, on the other hand, was expected to restore positive mood. Thus, choir singing seems to best support socioemotional well-being in ageing when it is a continuous activity.

To summarise, sustained and regular engagement in musical activities can support cognitive function, such as episodic memory, and socioemotional well-being with advancing age. While a systematic account bridging neural, cognitive, and qualitative evidence on music in ageing is currently missing, existing evidence suggests that differential dose effects may apply (see also Ferreri et al., 2019). For instance, effects on episodic memory, as discussed above, have raised speculations about whether longer *duration* of the experience would lead to greater benefits. Qualitative evidence on the socioemotional benefits of choir singing, on the other hand, have shown direct associations between the *frequency* of singing and psychological well-being. In order to verify this asymmetry, however, a systematic account addressing dose effects across different measures within a same sample is needed. With most of the current evidence focusing on instrumental activities, such as piano playing, such accounts would be of particular value for the underrepresented but ecologically valid music activities such as singing, which could be easily implemented across ageing populations globally (see also Shaffer, 2022). Moreover, existing neuroimaging evidence on the influence of music on the ageing brain is largely based on anatomically confined effects focusing on regions (ROIs) or tracts of interest (TOIs). Considering that music elicits large-scale activation across the young adult brain and is associated with enhanced structural connectivity in the ageing brain, advancing our knowledge on how music may benefit neurocognitive ageing requires whole-brain accounts to complement behavioural data.

2 Aims

This dissertation explores how ageing affects the neural processing of speech and singing in vocal production tasks varying in their cognitive demands and how singing experience is associated with brain structure, cognitive performance, and subjective well-being across adulthood.

The main aims of this thesis were to:

I. Systematically map the functional neural overlap and differences of speech and singing production while varying the cognitive demands associated with the production tasks (Study I)
II. Systematically map the effects of ageing on the neural underpinnings of speech and singing production while varying the cognitive demands associated with the production task (Study I)
III. Explore the associations of the duration and frequency of singing with local volumes of grey matter as well as white matter connectivity across adulthood (Study II)
IV. Determine the associations of the duration and frequency of singing with cognitive performance and subjective well-being across adulthood (Study III).

3 Methods

3.1 Study participants

One hundred healthy adult volunteers (55 female), aged 21–88 years (mean 49.2, *SD* 17.5) were recruited to participate in the set of Studies I–III. All participants provided a written informed consent to participate in this study and to the use of their data for the scientific purposes of this study. The study was conducted in accordance with the Helsinki Declaration and approved by the European Research Council Executive Agency (ERCEA) and the University of Helsinki Ethical Review Board in the Humanities and Social and Behavioural Sciences.

Participants were required to be (i) 20–90 years old, (ii) right-handed, (iii) native Finnish-speakers, (iv) able to cooperate and understand the purpose of the study; and to have no self-reported diagnosis of (v) a hearing impairment, (vi) language or (vii) neurological disorder, (viii) cognitive decline, or (ix) dementia, (x) no self-reported history with alcohol or substance abuse, and (xi) no contraindications for MRI. Recruitment was carried out with balanced subsamples for three age-specific subgroups (young adults aged 20–39 years, middle-aged adults aged 40–59 years, and older adults aged 60–90 years) by distributing digital advertisements through email lists and the research unit's social media channels and printed advertisements placed in public venues, such as libraries, grocery stores, and community colleges in the Helsinki metropolitan area, as well as through in-person presentations of the study for local amateur choirs.

Prior to recruitment, the eligibility of each candidate was assessed with a phone interview. Persons with a professional background in music (education and/or other) were not permitted to participate in this study. For persons reporting choir singing experience in adulthood, a minimum requirement was one weekly hour for the past one year; persons with earlier choir singing experience in adulthood reporting a recent gap in active engagement were not invited to participate. Former and ongoing engagement in other musical leisure activities as well as childhood choir singing experience were allowed for all participants. The demographic characteristics and information on the musical background of the final recruited sample are outlined in Table 1.

Table 1 Demographic characteristics and musical background of the full sample and subgroups based on age and choir singing. The ageing effects of speech and singing (Study I) were assessed across the full age range. The associations of choir singing experience with brain structure, cognitive function and well-being (Studies II–III) were analysed across the full age range and within age-specific subgroups. Associations of choir singing with cognitive function and well-being (Study III) were additionally assessed within choir singers alone; statistics from non-singers are provided for comparison. All values represent mean (*SD*), minimum–maximum, unless otherwise specified.

[1] Goldsmith's Musical Sophistication Index (Gold-MSI), scores calculated for $n = 84$ due to missing data.

	Full sample	Age-specific subgroups			Singing-based subgroups	
	All	Young	Middle-aged	Older	Choir singers	Non-singers[1]
Demographic						
N	100	35	34	31	54	46
Age	49.2 (17.5), 21–88	29.9 (5.5), 21–39	50.2 (6.4), 40–59	69.9 (7.4), 60–88	51.6 (17.7), 22–88	46.4 (17.0), 21–85
Gender (F/M/Other)	55/45/0	19/16/0	18/16/0	18/13/0	28/26/0	27/19/0
Education yrs	16.8 (3.6), 8–34	17.4 (2.8), 12–24	18.1 (4.0), 12–34	14.8 (3.4), 8–20	17.0 (3.1), 8–22	16.7 (4.2), 8–34
Choir singing						
total yrs active	10.3 (14.0), 0–59	6.4 (8.0), 0–29	9.0 (10.8), 0–36	16.1 (19.7), 0–59	18.4 (14.7), 1.5–59	0.8 (1.4), 0–6
% of life active	20.4 (24.1), 0–79	20.8 (24.4), 0–77	18.2 (21.5), 0–67	22.2 (26.8), 0–79	35.9 (23.2), 3–79	2.1 (4.2), 0–17
lifetime max. hrs/week	2.7 (2.7), 0–10	2.7 (2.6), 0–8	2.5 (2.6), 0–10	2.8 (2.8), 0–10	4.6 (2.1), 1.5–10	0.4 (0.9), 0–4
current hrs/week	1.7 (2.0), 0–8	1.1 (1.5), 0–5	1.8 (2.0), 0–8	2.1 (2.3), 0–8	3.1 (1.7), 0.5–8	0.0 (0.1), 0–1
Solo singing						
total yrs active	4.2 (9.6), 0–50	3.5 (6.1), 0–26	6.4 (12.5), 0–50	2.6 (9.0), 0–50	5.7 (9.6), 0–50	2.5 (9.4), 0–50
% of life active	9.7 (20.6), 0–94	11.8 (20.1), 0–87	12.8 (24.9), 0–94	4.0 (14.5), 0–81	13.1 (21.2), 0–87	10.1 (18.3), 0–94

	Full sample	Age-specific subgroups			Singing-based subgroups	
	All	Young	Middle-aged	Older	Choir singers	Non-singers[1]
Solo singing (continued)						
lifetime max. hrs/week	1.7 (3.4), 0–15	2.0 (3.7), 0–15	1.8 (3.4), 0–15	1.3 (3.3), 0–15	2.3 (3.7), 0–15	1.0 (2.9), 0–15
current hrs/week	0.6 (1.4), 0–8	0.8 (1.6), 0–8	0.5 (1.2), 0–5	0.4 (1.4), 0–6	0.7 (1.4), 0–6	0.4 (1.4), 0–8
Playing an instrument						
total yrs active	9.7 (13.4), 0–60	9.5 (8.6), 0–30	9.5 (13.7), 0–48	10.2 (17.7), 0–60	14.3 (15.2), 0–60	4.2 (7.8), 0–43
% of life active	21.7 (27.0), 0–87	32.1 (28.2), 0–80	19.1 (26.3), 0–87	13.0 (23.1), 0–82	31.6 (29.4), 0–87	10.1 (18.3), 0–81
lifetime max. hrs/week	2.9 (4.0), 0–20	3.3 (4.1), 0–20	3.4 (4.8), 0–20	1.7 (2.3), 0–10	3.8 (4.5), 0–20	1.8 (3.1), 0–15
current hrs/week	0.6 (1.5), 0–10	0.5 (0.7), 0–2	0.8 (2.0), 0–10	0.5 (1.5), 0–7	0.7 (1.6), 0–10	0.5 (1.4), 0–7
Self-reported musical sophistication[1]						
Active engagement	33.2 (9.4), 12–57	32.9 (9.7), 12–48	33.7 (10.4), 12–57	32.8 (7.9), 12–47	37.4 (6.2), 22–49	27.7 (10.0), 12–57
Perceptual abilities	47.8 (9.7), 15.8–61.9	48.3 (9.4), 29.3–61.9	49.7 (8.7), 23.6–60.8	44.6 (10.8), 15.8–61.9	52.9 (6.3), 37.1–61.9	41.4 (9.4), 15.8–60.8
Musical training	22.3 (10.5), 7–43	24.2 (12.4), 7–43	21.4 (8.9), 7–37	21.1 (10.2), 7–38	28.6 (8.2), 12–43	14.4 (7.4), 7–32
Singing abilities	29.9 (9.7), 7–45	31.2 (9.6), 11–45	29.8 (9.1), 7–44	28.3 (10.7), 8–42	35.3 (8.2), 12–45	22.9 (9.5), 7–44
Emotions	33.0 (7.5), 17–41	33.8 (5.0), 22–40	34.3 (5.5), 17–41	30.0 (5.9), 18–40	34.4 (4.7), 21–41	31.2 (6.5), 17–41
Musical sophistication (General factor)	73.5 (22.7), 20–111	76.3 (25.1), 27–110	73.8 (20.8), 20–111	69.5 (22.4), 22–101	86.8 (12.9), 58–110	56.5 (21.0), 20–111

Controlling for the main demographic characteristics during recruitment yielded balanced age and gender distributions across the full sample (Figure 1). Consistent with the present demographic structure in Finland (Statistics Finland, 2020, 2021), age was negatively associated with education years [$r_S\,(98) = -.279$, $p = .005$] with middle-aged participants reporting the highest mean. 54 participants reported being active choir singers (*n* = 16 young, *n* = 19 middle-aged, and *n* = 19 older adults) and 46 reported being non-singers (*n* = 19 young, *n* = 15 middle-aged, and *n* = 12 older adults). Lifetime experience in choir singing (% of age), which was used as the main study variable in Studies II–III, was not associated with age or education. Five self-reported non-singer participants reported having some earlier experience in choir singing, and one also reported irregular ongoing participation in singing. Older participants reported less experience in solo singing [$r_S\,(98) = -.218$, $p = .029$] and playing an instrument [$r_S\,(98) = -.266$, $p = .007$].

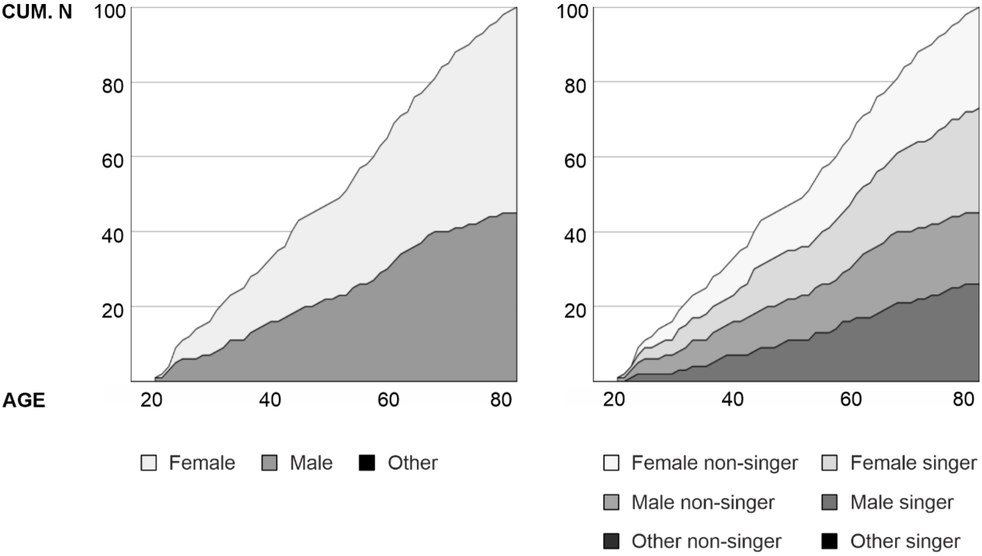

Figure 1 Distributions of age across the sample and of gender with respect to age. Age and gender in the full sample on left, and in choir singers and non-singers on right.

The sample sizes were partially reduced across the three studies due to generally higher level of head movement as well as issues in performing fMRI tasks (Study I, *N* = 85–100), with further reductions due to failures in subsequent laterality index (LI) computation (Study I, *N* = 78–91), as well as failing to complete diffusion-weighted MRI (dMRI) data acquisition and the detection of quality issues in acquired dMRI data (Study II, *N* = 95). Further, using an identical sample across all correlational analyses on choir singing was preferred (Studies II–III), yet a technical failure reduced the sample size in two computerised behavioural tasks assessing executive function (Study III, *N* = 93–95).

3.2 Questionnaires

Prior to visiting the research laboratories, all participants filled out a questionnaire battery surveying demographic information and musical background (see Table 1) and assessing subjective experience of socioemotional well-being. Musical sophistication was assessed with the Goldsmith's Musical Sophistication Index questionnaire (Gold-MSI; Müllensiefen et al., 2014) and the types of main musical leisure activities (choir singing, solo singing, playing an instrument) with dedicated questions for the duration (years) and ongoing and most active frequency (hours/week) for each type of activity. The well-being measures addressed recent depressive symptoms (Center for Epidemiological Studies: Depression, CES-D; Radloff, 1977) and QOL (WHOQOL-BREF; The WHOQOL Group, 1998), comprising designated subscales for five domains: overall, physical, and psychological QOL, social relationships, and environment. In addition, participants were asked to rate their personal feeling of familiarity with 40 + 40 common proverbs and song phrases on a Likert scale of 1–4 (1 = *completely unfamiliar*; 4 = *extremely familiar*) for Study I. At this point, participants were not informed that the items of the familiarity questionnaire would also be used in the fMRI tasks (Study I).

3.3 Neuropsychological assessments

Neuropsychological assessments were administered in a quiet room at the laboratory of Cognitive Brain Research Unit (CBRU), University of Helsinki, Helsinki, Finland, by psychology graduate students who had been trained by a licensed clinical psychologist. The psychologist was also consulted upon any uncertainties regarding scoring.

The neuropsychological test battery assessed verbal fluency (phonemic: letter S, semantic: animals), processing speed (Wechsler Adult Intelligence Scale, 4th edition [WAIS-IV]: Symbol search, Digit symbol coding; Wechsler, 2008), working memory (WAIS-IV: Digit span, Arithmetic; Wechsler, 2008), immediate and delayed episodic memory (Wechsler Memory Scale, 3rd edition [WMS-III]: Logical memory, Word lists; Wechsler, 1997), and executive function (Trail making tests [TMT] A and B from the flexible attention test (FAT) developed at the Finnish Institute of Occupational Health; Järnefelt et al., 2018; and Simon task; Martin et al., 2012; Simon & Rudell, 1967).

All tests were carried out in the traditional pencil-and-paper format except for tests of executive function, in which a touch screen laptop computer was used to achieve higher accuracy in time observations. To obtain indices for set shifting and inhibition, the response time difference scores were calculated as TMT B minus A and Simon task incongruent minus congruent, respectively. The duration of the assessment was approximately 1.5 hours. Given the large age range of the sample and the specific aim to study ageing effects, raw instead of standardised scores were used in analysis, and summed into thematic composite scores for each domain.

3.4 Magnetic resonance imaging (MRI)

Magnetic resonance imaging was carried out at the Advanced Magnetic Imaging (AMI) Centre of Aalto University, Espoo, Finland. Upon arrival, participants were instructed to read MRI safety instructions carefully and to fill in an MRI pre-screening questionnaire assessing contraindications for imaging and given oral instructions before scanning. MRI data was acquired with a MAGNETOM Skyra 3.0 T scanner (Siemens GmbH, Erlangen, Germany) using a 32-channel RF receiving head coil. Participant's head was supported in place with soft foam paddings inside the coil to reduce head movement and to further protect hearing. Participants were asked to report immediately should they experience any discomfort or difficulty in perceiving the auditory or visual instructions. The total duration of the visit to the MRI laboratory was approximately 2 hours, during which participants were given an opportunity to have a short break as needed.

3.4.1 Functional MRI (Study I)

3.4.1.1 Task design for speech and singing production

The neural underpinnings of speech and singing production and their associations with ageing were mapped with task-based fMRI (tb-fMRI). Here, a 2 x 3 cue-response task design comprised repetition, completion, and improvisation of both spoken and sung items; respective cues and responses in each task type are summarised in Table 2. Stimuli were presented in random order within each task. Task order was pseudo-randomised in such a way that the first task rotated, vocal modality was changed after each task, and no task type (Repetition / Completion / Improvisation) was presented two times in a row. Task order was counter-balanced between participants with and without choir singing experience in adulthood as well as between young (aged 20–39 years), middle-aged (40–59 years) and older participants (60–90 years).

Table 2 Task types used in Study I to investigate the neural underpinnings of speech and singing production across different cognitive demands. All task types were completed in both speech and singing, thus comprising a total of six overt production tasks.

Task name	Cue	Response	Demand
Repetition	Familiar phrase in full	Repeat the phrase	Short-term verbal working memory and simple motor production
Completion	Beginning of a familiar phrase	Complete the ending of the cued phrase from memory	Short-term verbal working memory and simple motor production + retrieval from long-term memory
Improvisation	Beginning of a new phrase	Complete the ending of the cued phrase by improvising	Short-term verbal working memory and simple motor production + cognitive flexibility and fluency

3.4.1.2 Auditory cues for speech and singing production

Each of the six tasks comprised 20 Finnish cue-response pairs: proverbs in speech tasks and song phrases in singing tasks. As normal ageing is associated with a degree of decline in learning and memory, naturalistic instead of newly memorized study items were used to prevent bias from direct learning outcomes in the retrieval (Completion) tasks. Further, to ensure comparable familiarity of naturalistic items across the full age range of participants, the cues for Repetition and Completion tasks were pre-selected through an online pilot questionnaire (N = 665), choosing those items which were, on average, most familiar among respondents across three age groups: young (20–39 years, n = 246), middle-aged (40–59 years, n = 294), and older adults (60 and above, n = 125).

Song phrases for Repetition and Completion tasks were selected either from the beginning of the first verse or chorus, avoiding internally repetitive phrases and non-lexical utterances such as “ooh.” The song material comprised phrases from traditional children’s songs and nursery rhymes, folk songs and evergreens, seasonal songs and Finnish pop/rock classics. Cue items for Improvisation of proverbs and song phrases were constructed and carefully matched to the items selected for the Completion tasks in phrase length, sentence structure, semantic theme, and, with song phrases, also musical style. Sample cues and target responses for each of the six tasks are outlined in Table 3.

Table 3 Sample items from the six vocal production tasks in fMRI. Items with no English equivalent translated from original language (Finnish).

Task name	Cue	Response
Repetition		
Proverb	"A friend in need is a friend indeed."	"A friend in need is a friend indeed."
Song phrase	"Väinö, Väinö, where is my Väinö?"	"Väinö, Väinö, where is my Väinö?"
Completion		
Proverb	"An apple a day…"	"…keeps the doctor away."
Song phrase	"Oh, if only once I could…"	"…make it to wonderland."
Improvisation		
Proverb	"The greater the gifts…"	"…[improvised ending]"
Song phrase	"Wind whispering in trees…"	"…[improvised ending]"

All items were recorded in female and male voice using a neutral tone, matching the two voice versions in duration and expression. Female register was used with female participants and male register with male participants. Recordings were carried out by a professional female and male musician who also composed the melodies for Song phrase Improvisation items. The average word and syllable count and durations of the recorded versions for each item type are outlined in Table 4 (for a description of the tasks, see Table 2). On average, the pre-selected Proverb items were shorter compared to Song phrase items by 1 syllable.

Table 4 Lengths and durations of naturalistic Proverb and Song phrase items in Repetition and Completion tasks, and of matched new phrases in Improvisation tasks. All values represent mean (SD) across 20 items per task. Adapted from Moisseinen et al. (2023), CC BY 4.0.

Task and item	Word count	Syllable count	Recording (ms)
Repetition			
Proverb: Cue and Target	3.70 (0.66)	8.80 (1.61)	2289 (280)
Song phrase: Cue and Target	4.60 (0.88)	10.00 (1.65)	5055 (1371)
Completion			
Proverb: Cue	2.85 (0.59)	6.30 (1.13)	1776 (352)
Proverb: Target	2.85 (0.49)	6.35 (1.14)	-
Song phrase: Cue	3.20 (0.77)	7.40 (1.47)	3168 (812)
Song phrase: Target	3.25 (0.79)	7.15 (1.14)	-
Improvisation			
Proverb: Cue	2.85 (0.59)	6.50 (1.43)	1849 (247)
Song phrase: Cue	3.10 (0.72)	7.40 (1.35)	3082 (499)

3.4.1.3 Data acquisition

The in-scanner speech and singing production tasks were created and presented with Presentation 20.3 (Neurobehavioural systems, Inc., Berkeley, CA, USA) using MR pulses from the scanner as triggers to synchronise trial onset. A sparse-sampling technique (Hall et al., 1999; see also Belin et al., 1999; D. A. Yang et al., 2000) with brief silent intervals between full volumes was adopted to reduce the direct influence of scanner noise in auditory tasks as well as excessive head movement in volumes targeting activity associated with vocal production.

The trial structure (Figure 2), adapted from Martínez-Molina et al. (2025), comprised active condition trials for (i) listening while exhaling, (ii) overtly responding, and (iii) exhaling as a baseline condition; volumes were acquired during inhalation following each phase of the trial. Times of repetition (TRs) were optimised across the active conditions as per the longest stimulus in each task (see Table 4), with systematic variation (jittering) of timings of the conditions to acquire the peak of the hemodynamic response occurring at approximately 4–7-second delay (Belin et al., 1999; Yang et al., 2000). Resulting TRs thus included a start and end jitter pair (1600 ms in total), auditory cue (duration based of longest stimulus in task), and time of acquisition (TA; 1500 ms). Acquisition was carried out using T2*-weighted functional imaging with gradient echo-planar imaging (EPI) on the whole brain: time of echo (TE) = 30.0 ms, TR = 6800–10800 ms, flip angle = 90°, voxel size = 3 × 3 × 3 mm^3, field of view (FOV) = 240 mm, and slices per volume = 44. In addition, a whole-brain T1-weighted (T1w) anatomical volume was acquired using a 3D magnetisation-prepared rapid gradient echo (MPRAGE) sequence with TE = 3.3 ms, TR = 2530.0 ms, flip angle = 7°, voxel size = 1 × 1 × 1 mm^3, FOV = 256 mm, and number of slices = 176.

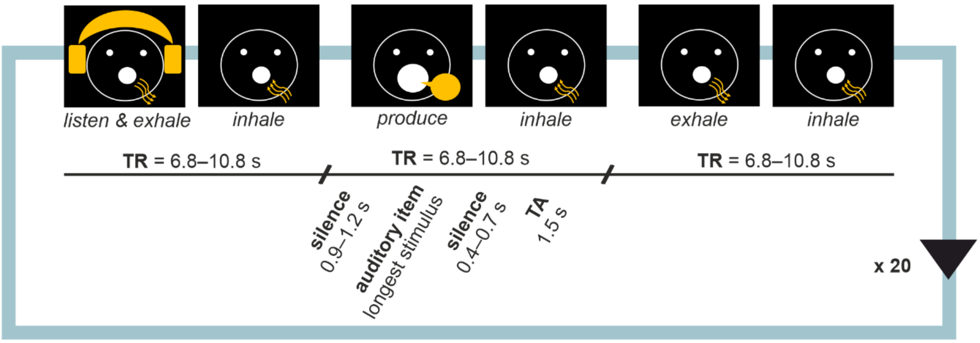

Figure 2 Trial design in fMRI speech and singing production tasks. Each task involved 20 repetitions of a listen-respond-exhale (baseline) trial triad, one for each stimulus. Each active trial was followed by a brief inhalation period, during which volume acquisition occurred. Visual cues were used to instruct actions and to help set the rhythm for breathing. Participant's voice was recorded during response (production) trials to verify timing and correctness of responses. Reproduced from Moisseinen et al. (2023), CC BY 4.0.

Prior to scanning, participants received instructions on a computer screen in a preparation room. To ensure that the participant understood the instructions and was able to follow the time-sensitive cues of the tasks, a short training session with three practice trials was administered. Regardless of singing experience, the participant was also encouraged to try their own best in all tasks. Auditory stimuli were presented using MR-compatible high-quality binaural insert earphones (KAR ADU2a), adjusting the sound level to a comfortable and clearly audible level prior to scanning. Participants' vocal responses were recorded for quality control using a high-dynamic-range noise-cancelling optic microphone (Optoacoustics FOMRI-III) manually attached to the head coil and positioned as per sound quality tests pre-scanning. The angle of a back projection mirror screen, used to present visual cues supporting the timing of actions during tasks (see Figure 2), was also adjusted as needed to ensure a comfortable level of gaze during scanning.

3.4.1.4 Data pre-processing

Functional MR volumes were pre-processed with Statistical Parametric Mapping 12 (SPM12) software package (The Wellcome Centre for Human Neuroimaging, UCL, London, UK; https://fil.ion.ucl.ac.uk/spm) running under Matlab 2019a (The MathWorks Inc., Natick, MA, USA). For each participant, T1w image was manually reoriented to the anterior commissure. For each task, EPIs were realigned to the first scan by estimating the parameters of an optimal rigid body transformation, and co-registered with the reoriented T1w image. Subsequently, segmentation was performed using unified segmentation (Ashburner & Friston, 2005) with medium regularisation and SPM12 IXI data set tissue probability maps. All EPIs were normalized to the Montreal Neurological Institute (MNI) template by applying the spatial normalisation parameters from the T1w image and resampling to 2-mm isotropic voxels using trilinear interpolation. As overt production during fMRI would cause head movement, movement outlier scans were identified with the Artifact Detection Tool (ART; Gabrieli Laboratory, MIT, Cambridge, MA, USA; https://www.nitrc.org/projects/artifact_detect/) using a 3-mm framewise displacement threshold with a global blood oxygenation level dependent (BOLD) signal change threshold of 4 SD, and applied in motion correction. Participants showing and outlier scan rate of over 20 % in each task were rejected. Finally, EPIs were spatially smoothed using spatial convolution with an 8-mm full width at half maximum (FWHM) Gaussian kernel to minimize effects of inter-individual anatomical differences.

3.4.1.5 In-scanner task performance

As expected based on the results of the pre-selection questionnaire (see above), the recruited participants rated the Proverb and Song phrase items as highly familiar, with a mean familiarity score ranging from 3.6 (.3) to 3.9 (.2) on a 4-point Likert scale (1 = *completely unfamiliar*, 4 = *extremely familiar*). Performance during fMRI speech and singing production tasks was assessed with laboratory log sheets and recorded responses. Due to a technical error, recorded responses from 26 participants were unusable, and the assessments of these participants were based on log sheets alone.

Both timing and correctness of the responses were assessed. First, a trial was marked as erroneous whenever more than 25 % of the response would fall outside the dedicated response time window (Timing errors). Second, in correctness assessments, response content was required to match the target. Non-matching responses were marked as erroneous trials (Content errors) while allowing fillers such as ‘um’ as well as replacing words with synonyms. Greater emphasis was placed on lyrics than melody in singing tasks as approximately half of the sample reported little or no singing experience. Finally, participants with five or more (≥ 20 %) erroneous trials (Timing or/and Content errors) within a task were rejected and excluded from further analysis.

Accepted participants followed the turns of listening, producing, and exhaling of the sparse sampling fMRI design with minimal difficulty, making less than one error per task across the six fMRI tasks. Performance was not associated with age, apart from Improvisation of new proverbs, where age and number of errors showed a weak positive correlation, r_s (90) = .269, p = .010. Details on the familiarity scores and performance in the accepted subsamples are outlined in Table 5.

Table 5 Participant-reported stimulus familiarity and in-scanner performance in fMRI speech (Proverb) and singing (Song Phrase) production tasks within accepted subsamples. Analyses involving between-modality comparisons were based on subsamples of participants with data accepted in both modalities (Mutual). Sample sizes reported as Accepted (Original), and familiarity and performance issues as mean (*SD*).

Task	*N*	Stimulus familiarity	Timing errors	Content errors
Repetition				
Proverb	100 (100)	3.9 (0.2)	.0 (.2)	.0 (.1)
Song phrase	89 (100)	3.7 (0.4)	.0 (.0)	.0 (.1)
Mutual	89 (100)	3.8 (0.2)	.0 (.1)	.0 (.1)
Completion				
Proverb	99 (100)	3.9 (0.2)	.0 (.2)	.1 (.4)
Song phrase	85 (100)	3.6 (0.3)	.0 (.2)	.3 (.7)
Mutual	85 (100)	3.7 (0.2)	.0 (.2)	.2 (.4)
Improvisation				
Proverb	92 (100)	-	.5 (1.0)	-
Song phrase	92 (100)	-	.1 (.2)	-
Mutual	87 (100)	-	.3 (.5)	-

3.4.2 Structural MRI (Study II)

3.4.2.1 Data acquisition

A whole-brain T1w anatomical volume, also used in Study I, was acquired using a 3D MPRAGE sequence with TE = 3.3 ms, TR = 2530.0 ms, flip angle = 7°, voxel size = 1 × 1 × 1 mm^3, FOV = 256 mm, and number of slices = 176.

Multi-shell dMRI was performed using two sequences with bidirectional phase encoding in the anterior–posterior and posterior–anterior (AP/PA) directions. TE (AP) = 104.0 ms, TE (PA) = 101.0 ms; TR = 5000 ms; 13 volumes at the b-value of 0 s/mm^2 (AP) interspersed between higher b-values, 30 unique directions at b-value of 1000 s/mm^2 (AP), 100 unique directions at b-value of 2500 s/mm^2 (AP), and 7 volumes at b-value of 0 s/mm^2 (PA); voxel size = 2 × 2 × 2 mm^3; FOV = 240 mm; and number of slices = 72.

3.4.2.2 Data pre-processing

T1w images were pre-processed in SPM12 (The Wellcome Centre for Human Neuroimaging, UCL, London, UK) using the Computational Anatomy Toolbox, version 12 (CAT12; Jena University Hospital, Jena, Germany;

https://www.nitrc.org/projects/cat/), running under Matlab R2019a (The MathWorks Inc., Natick, MA, USA). T1w images were first segmented into GM, WM, and cerebrospinal fluid (CSF) using Unified Segmentation (Ashburner & Friston, 2005) and, subsequently, normalised into MNI space using Geodesic Shooting (Ashburner & Friston, 2011). Following normalisation, the images visually inspected and smoothed with an 8-mm FWHM isotropic filter. Finally, the GM, WM and CSF volumes were used to calculate the total intracranial volume (TIV) for each participant.

The dMRI data was denoised for thermal noise (MP-PCA method; Veraart et al., 2016) with the denoise tool in MRtrix 3 (Tournier et al., 2019) and corrected for Gibbs ringing based on local sub-voxel shifts (Kellner et al., 2016). Data collection with reversed phase-encode blips had resulted in image pairs with opposite-direction distortions. The susceptibility-induced off-resonance field was estimated from these image pairs in FSL (Smith et al., 2004) using a similar method as described by Andersson et al. (2003), after which the images were combined into a single corrected one. Finally, the data were corrected for motion and eddy currents using outlier detection and replacement (Andersson et al., 2016; Andersson & Sotiropoulos, 2016) and bias (Smith et al., 2004).

Next, the diffusion data were reconstructed into MNI space in DSI Studio (version Chen, December 2022; http://dsi-studio.labsolver.org) with q-space diffeomorphic reconstruction to obtain the spin distribution function (Yeh et al., 2010; Yeh & Tseng, 2011). The accuracy of the b-table was checked by an automatic quality control routine (Schilling et al., 2019). For each participant, normalisation was carried out using the anisotropy map, and a diffusion sampling length ratio of 1.25 was used. The output was resampled to 2-mm isotropic resolution. Normalisation result was visually inspected for each participant, using forceps major and forceps minor as anatomical benchmarks of quality (Hula et al., 2020; Sihvonen et al., 2021), as well as using the R^2 values denoting goodness-of-fit between the participant's anisotropy map and template. The restricted diffusion was quantified with restricted diffusion imaging (Yeh et al., 2017).

Quantitative anisotropy (QA) was extracted as the local connectome fingerprint (Yeh, Vettel, et al., 2016) for the following connectometry analysis. QA was selected as the marker for WM integrity since it has been shown to outperform traditional FA by providing higher specificity to the individual's connectivity patterns (Yeh, Vettel, et al., 2016) and lower susceptibility to the partial volume effects of crossing fibres and free water, as well as to offer better resolution in tractography (Yeh et al., 2013; see also Sihvonen et al., 2023).

3.5 Statistical analyses

The statistical analyses addressed the main effects of speech and singing production (Study I) as well as the associations of choir singing experience with brain structure (Study II), cognitive performance, and well-being (Study III). As per dose effects associated with musical practice, participants' experience with all musical hobbies were addressed through continuous variables to account for this essential variation. Further, as the maximal duration of practice (years) is directly limited by age, measures of duration (years) were adjusted by age (% of age) to allow for comparable analyses across age-specific subgroups of participants. All models controlled for the effects of essential demographic factors apart from gender, which had been controlled for a priori by balancing recruitment with respect to age (Figure 1). The significance levels of each analysis were corrected for multiple comparisons as described in the subsequent sections.

3.5.1 Study I

3.5.1.1 First-level models

Main effects were estimated with the general linear model (GLM) framework. At the within-subject (first level), each condition was modelled with a boxcar function convolved with the canonical hemodynamic response function (HRF), as this is considered to yield the best model fitting with sparse sampling (Perrachione & Ghosh, 2013), and trial duration was set 0 s, thus opting for a 'slow' event-response analysis (Belin et al., 1999; Kleber et al., 2010). As per the standard value used in continuous fMRI, microtime resolution was adjusted to 125 ms per bin, with middle slice as the reference. Slow signal drifts were removed with a high-pass filter using a 128-s cut-off. Temporal autocorrelations in the BOLD signal time series were accounted for with an autoregressive [AR (1)] model to approximate the observed covariance of the functional data in the context of restricted maximum likelihood estimation. Tissue probability map (TPM) for grey matter tissue, thresholded at 15 % probability, was included as an explicit mask. No global scaling was applied. Nuisance regressors were included in the design matrix, with six realignment parameters to control for the effects of head motion, one regressor for incorrect trials (Jenkinson et al., 2002), and outlier scans. The within-participant model was estimated for each task, subsequently creating initial contrasts for each trial condition (listening, production, exhalation) and then extracting the activity associated with production by calculating the difference contrasts of production minus exhalation (baseline).

3.5.1.2 Second-level models

Group-level analyses mapped (i) the main effects of speech and singing production across the full age range, (ii) effects of ageing in speech and singing production, and (iii) ageing effects on the relative laterality (i.e., hemispheric asymmetry) of activation in speech and singing production at the whole-brain level. Firstly, the main effects for each task were calculated with one-sample t-tests from the production contrasts (production > baseline exhalation) created at first level. Further, differences between the main effects of speech and singing production (speech > singing; singing > speech) were mapped with paired t-tests for each task type (Repetition; Completion; Improvisation).

As the purpose of the study did not involve direct comparisons between the task types (Repetition, Completion, Improvisation), this was done task-by-task to maximise the sample size for each condition. All main effects models controlled for the effects of age (years), education (years), lifetime experience with musical leisure activities (% of age), and TIV (Barnes et al., 2010; Qing & Gong, 2016). Secondly, ageing effects in speech and singing production were tested with multiple linear regression models, addressing both increasing (positive) and decreasing (negative) trends in activation, while controlling for the effects of education (years), lifetime experience with musical leisure activities (% of age), and TIV. The results were thresholded at $p < .001$ (uncorrected), and the statistical significance of results were corrected for family-wise error (FWE) at cluster-level ($p < .05$).

Finally, as classic findings suggests that ageing is associated with reduced hemispheric asymmetry, particularly with tasks of higher cognitive demand (the HAROLD model; Cabeza, 2002), the ageing effects on the relative laterality of activation were tested with a special interest in similarities or differences between speech and singing production. This was carried out, first, by calculating 25-% trimmed mean scores from bootstrapped LIs, following a histogram-based fMRI adaptation of the traditional approach:

$$\mathrm{LI} = \frac{\sum activation_{LEFT} - \sum activation_{RIGHT}}{\sum activation_{LEFT} + \sum activation_{RIGHT}}$$

(as implemented in the LI toolbox for SPM; for a detailed description, see Wilke & Lidzba, 2007; Wilke & Schmithorst, 2006; http://www.medizin.uni-tuebingen.de/kinder/en/research/neuroimaging/software/). To learn whether the similarities or differences of laterality between speech and singing production may change with advancing age, the effects of ageing were calculated in SPSS (IBM SPSS Statistics 28) with stepwise multiple linear regression models, addressing potential effects of the same confounding factors as above (education, experience with musical leisure activities, TIV).

As previous evidence suggests regional differences in ageing-associated hemispheric asymmetry reduction, whole-brain effects were localised, initially, between frontal (Cabeza, 2002; Hoyau et al., 2017; Wierenga et al., 2008) as well as temporal and parietal auditory-motor vocal production regions (Peretz et al., 2015) and, post hoc, between subregions. Models were corrected for multiple comparisons by dividing α = .05 by the number of models at each level of analysis (Bonferroni). Pre-defined ROIs were derived from the probabilistic connectivity-based Brainnetome atlas (https://atlas.brainnetome.org) as outlined in Table 6.

Table 6 Target ROIs used for studying age-associated localised changes in the laterality of activation in speech (Proverb) and singing (Song phrase) production.

Main model	Post hoc models	Brainnetome subregions
Frontal lobe	Middle frontal gyri (MFG)	15–28
	Inferior frontal gyri (IFG)	29–40
	Orbitofrontal gyri (OFG)	41–52
	Precentral gyri (PrCG)	53–64
Temporal lobe	Middle temporal gyri (MTG)	81–88
	Posterior superior temporal sulci (pSTS)	121–124
Parietal lobe	Inferior parietal lobules (IPL)	135–146
	Postcentral gyri (PoCG)	155–162

3.5.2 Study II

Associations of choir singing experience and brain structure were studied through the local volumes of grey matter and white matter connectometry. As whole-brain structural changes were expected to stem from sustained training rather than temporarily peaks in training, whole-brain multiple linear regression models were performed on lifetime choir singing duration (% of age), primarily across the full age range, and, to identify potential sources of effects along the large age range, within the three age-specific subgroups: younger (20–39 years), middle-aged (40–59 years), and older adults (60–90 years). Correction for multiple comparisons was performed by adjusting the significance level to α = .0125 (Bonferroni) across the four models. Each model controlled for the effects of age, education (years), experience in solo singing (% of age) and instrument playing (% of age), as well as TIV derived from T1w images. Potential influence of present training and/or lifetime maximal frequency (hours/week) was addressed in supplementary analyses with similar models using frequency scores for music covariates as well.

3.5.2.1 White matter connectometry

Associations of choir singing with structural connectivity was tracked with correlational tractography (Yeh et al., 2021), essentially correlating anisotropy of

WM segments with the training factors, and examined statistically with connectometry (Yeh, Badre, & Verstynen, 2016) in DSI Studio (version Chen, December 2022). The significance level was adjusted to $\alpha = .0125$ to correct for multiple comparisons across the four models (full age range; younger, middle-aged, and older adults), and a significance threshold was set to $t = 3$ as per adjusted α and the sample size of $n = 29$ in the smallest age-specific subgroup (older adults; $t = 2.67$). Seeding was based on the whole brain, and tracts were identified using a deterministic tracking algorithm (Yeh et al., 2013) to obtain correlational tractography. The resulting tracts were filtered by topology-informed pruning (Yeh et al., 2019) with 16 iterations and a length threshold of 30 voxels. To estimate the false discovery rate (FDR), 4000 randomised permutations were applied to the group label to obtain a null distribution for tract length. For each connectometric analysis, the whole-brain FDR threshold was set to $p < .0125$ to account for multiple comparisons (Bonferroni). Tracts containing fewer than five surviving fibres were excluded to further minimise false positives.

3.5.2.2 Grey matter volume

Associations of choir singing and the local volumes of grey matter were studied with voxel-based morphometry (VBM; Ashburner & Friston, 2000), by which spatially normalised anatomical images can be compared at voxel level. Following preprocessing steps (described above), multiple linear regression models were performed in SPM12 software package (The Wellcome Centre for Human Neuroimaging, UCL, London, UK) running under Matlab 2019a (The MathWorks Inc., Natick, MA, USA) with the volumetric GM data. Significance levels were corrected for multiple comparisons (full age range; younger, middle-aged, and older adults) by subsequent thresholding, $\alpha = .0125$.

3.5.3 Study III

First, associations of choir singing training factors with well-being measures and cognitive performance were analysed with linear stepwise regression models for the full age range in SPSS (IBM SPSS Statistics, version 29). Recognising the risk for population bias through participants' natural disposition for music (Schlaug, 2003, pp. 367–377), separate regression analyses were performed for choir singers who were expected to represent a more homogenous group in this regard. Finally, to identify potential sources of training effects in choir singers, the primary sources of each surviving result were studied across the three age-specific subgroups: young (20–39 years), middle-aged (40–59 years) and older adults (60–90 years). Significance levels were adjusted to $\alpha = .01$ to account for multiple comparisons across the five models (Bonferroni). To address the possibility of parallel contributions from the duration and frequency of practice, all training factors (% of age active; lifetime maximal and ongoing frequency, hours/week) were entered in the stepwise models, including also age, education (years), and the training factors of other musical hobbies (solo singing, instrument playing) as covariates. The results were inspected for violations in normality, independence of errors, and homoscedasticity. Outliers were identified with Mahalanobis distance, Cook's distance, and centred leverage, removing cases that would fall outside at least two out of the three distances.

Second, associations between effects were studied through mediation, limiting the analyses to theory-informed models to avoid testing for random or 'nearby' effects (Fiedler et al., 2011, 2018). Mediation analyses were carried out using the PROCESS macro (Hayes, 2022; https://www.processmacro.org/), version 4.2, in SPSS (IBM SPSS Statistics, version 29), with 10 000 bootstrapped samples. In this approach, mediation is proposed to exist when zero falls outside the lower and upper levels of the mediator-specific 95 % bootstrap confidence interval (CI). For a detailed description on this approach, see Hayes (2022), pp. 99–107. Each mediation model controlled for the same factors that showed a significant contribution to the initial regression effect serving as the motivation for testing mediation. Since mediation was tested selectively, any initial regression effect falling below uncorrected $\alpha = .05$ was considered for mediation analyses.

4 Results

4.1 Neural processing of speech and singing production (Study I)

4.1.1 Neural overlap and differences in speech and singing production

When controlling for the effects of age, neural processing of speech (Proverb) and singing (Song phrase) production extended over frontal, temporal, parietal, and cerebellar regions, with a high degree of overlap (Table 7, Figure 3).

Table 7 Neural overlap of speech (Proverb) and singing (Song phrase) production. Activation peaks within main effect clusters thresholded over whole brain at $p < 0.001$ (uncorrected). Peak coordinates (mm) in MNI space. Reproduced from Moisseinen et al. (2023), CC BY 4.0.

Abbreviations: FG, fusiform gyrus; ITG, inferior temporal gyrus; MedFG, medial frontal gyrus; PHG, parahippocampal gyrus; PoCG, postcentral gyrus; PrCG, precentral gyrus; SFG, superior frontal gyrus; SMA, supplementary motor area; SPL, superior parietal lobule; STG, superior temporal gyrus.

Task	Left / Right	*p* (FWE)	Cluster size (voxels)	*T*	Peak coordinates x	y	z
Proverbs: Repetition							
PoCG	L	<0.001	104762	24.129	-46	-10	35
PrCG	R			23.776	46	-8	37
STG	L			20.626	-56	-16	5
Proverbs: Completion							
PoCG	L	<0.001	116671	27.441	-50	-8	33
PrCG	L			25.223	-56	-2	21
PrCG	R			24.947	46	-10	37
Proverbs: Improvisation							
PoCG	L	<0.001	130584	25.883	-46	-10	35
SMA	L			20.619	-2	8	61
PoCG	R			20.240	50	-6	31

Task	Left / Right	*p* (FWE)	Cluster size (voxels)	*T*	Peak coordinates		
					x	y	z
Song phrases: Repetition							
PoCG	L	<0.001	68993	21.754	-50	-8	33
PrCG	L			19.106	-52	-6	47
PoCG	R			18.763	54	-4	27
PrCG	L	<0.001	725	6.660	-20	-28	57
SPL	L			4.741	-32	-46	67
SPL	L			4.405	-22	-60	67
ITG	R	0.010	399	5.168	42	-2	-39
FG	R			4.735	26	4	-43
PHG	R			4.532	24	4	-27
MedFG	R	0.027	311	4.466	8	54	29
SFG	R			4.261	22	48	23
SFG	R			3.892	30	46	23
Song phrases: Completion							
PoCG	L	<0.001	92172	21.835	-48	-10	35
PrCG	R			21.264	42	-10	37
STG	R			21.130	56	0	-3
Song phrases: Improvisation							
PoCG	L	<0.001	116526	20.772	-48	-10	39
SMA	L			18.585	-2	4	69
STG	R			18.558	60	-22	5

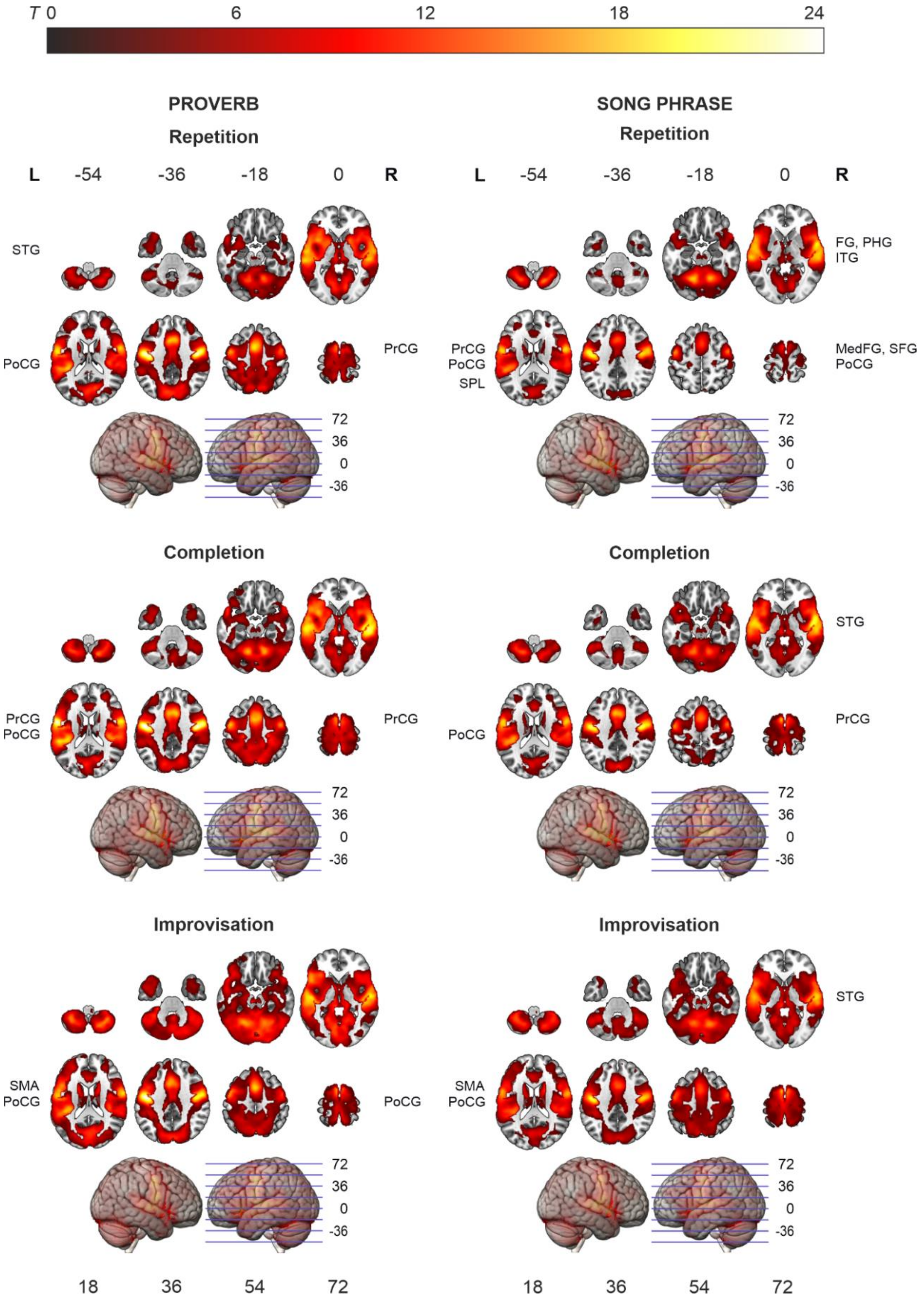

Figure 3 Activation maps of the main effects of speech (Proverb) and singing (Song phrase) production. Significant activity during production, thresholded over whole brain at $p < 0.001$ (uncorrected). Statistical significance FWE-corrected at cluster-level ($p < .05$). Highest T values displayed in yellow to white tones. Reproduced from Moisseinen et al. (2023), CC BY 4.0.

T-tests also revealed several focal differences between the two modalities (Tables 8 and 9; Figure 4). Compared to singing, the main effects of speech showed greater activation in (i) the angular gyrus (AG), cingulate cortex (CinC), rectus, cerebellum, and inferior (IOG) and middle occipital gyri (MOG) in the Repetition task; (ii) CinC and MOG extending parietally in the Completion task; and (iii) MOG in the Improvisation task (see Table 8). Compared to speech, the main effects of singing showed greater activation in (i) the superior temporal gyrus (STG), cerebellum and SMA in the Repetition task (ii) as well as in the Completion task; and (iii) STG / Rolandic operculum and cerebellum in the Improvisation task, largely bilaterally (see Table 9).

Table 8 Differences between the main effects of speech (Proverb) and singing (Song phrase) production. Activation peaks within main effect clusters, thresholded over the whole brain at $p < 0.001$ (uncorrected). Peak coordinates (mm) in MNI space. Reproduced from Moisseinen et al. (2023), CC BY 4.0.

Abbreviations: AG, angular gyrus; CinC, cingulate cortex; IOG, inferior occipital gyrus; IPL, inferior parietal lobule; MOG, middle occipital gyrus, MTG, middle temporal gyrus.

Task	Left / Right	*p* (FWE)	Cluster size (voxels)	*T*	Peak coordinates		
					x	y	z
Proverbs: Repetition > Song phrases: Repetition							
AG	L	<.001	1954	7.639	-38	-72	37
AG	L			5.488	-40	-54	29
MTG	L			5.133	-52	-64	21
AG	R	<.001	2275	7.222	40	-72	37
AG	R			6.631	46	-68	31
MOG	R			5.830	50	-66	23
CinC	R	<.001	2344	6.827	2	-38	35
Precuneus	R			5.761	2	-54	41
CinC	L			5.707	-2	-32	41
Rectus	R	<.001	876	4.899	6	24	-19
Rectus	L			4.755	-10	38	-19
Rectus	R			4.728	6	32	-21
Cerebellum (crus 2)	R	.016	326	4.861	28	-88	-39
Cerebellum (crus 2)	R			4.610	44	-78	-41
Cerebellum (crus 2)	R			3.883	14	-92	-37
IOG	R	.004	447	4.430	46	-86	-5
IOG	R			4.303	40	-92	3
MOG	R			4.219	32	-98	9
IOG	L	.026	290	4.183	-46	-86	-7
MOG	L			3.837	-32	-98	-3
IOG	L			3.550	-22	-96	-7
Proverbs: Completion > Song phrases: Completion							
MOG	L	<.001	1371	5.043	-42	-76	33
IPL	L			4.985	-38	-76	41
IPL	L			4.885	-52	-58	43
CinC	L	.014	335	4.768	-2	-42	39
Precuneus	L			3.582	-6	-52	35
CinC	L			3.483	-8	-52	27

Task	Left / Right	*p* (FWE)	Cluster size (voxels)	*T*	Peak coordinates x	y	z
Proverbs: Improvisation > Song phrases: Improvisation							
MOG	R	.002	509	5.939	28	-98	5
Calcarine	R			5.487	14	-102	1

Table 9 Differences between the main effects of singing (Song phrase) and speech (Proverb) production. Activation peaks within main effect clusters, thresholded over the whole brain at $p < 0.001$ (uncorrected). Peak coordinates (mm) in MNI space. Reproduced from Moisseinen et al. (2023), CC BY 4.0.

Abbreviations: CinC, cingulate cortex; HG, Heschl's gyrus; PrCG, precentral gyrus; SMA, supplementary motor area; STG, superior temporal gyrus; TP, temporal pole.

Task	Left / Right	*p* (FWE)	Cluster size (voxels)	*T*	Peak coordinates		
					x	y	z
Song phrases: Repetition > Proverbs: Repetition							
STG	R	<.001	12967	15.482	54	0	-3
STG	R			14.311	62	-16	1
Rolandic operculum	R			13.432	62	-8	7
STG	L	<.001	12053	15.140	-64	-24	9
HG	L			14.712	-60	-12	7
PrCG	L			14.004	-52	-6	47
Cerebellum (6)	L	<.001	11060	13.211	-16	-60	-21
Cerebellum (6)	R			11.738	18	-62	-21
Cerebellum (8)	L			9.447	-22	-62	-55
SMA	R	<.001	3271	8.154	2	10	63
CinC	L/R			7.529	0	20	33
SMA	R			5.837	8	10	71
Song phrases: Completion > Proverbs: Completion							
STG	R	<.001	6540	11.770	52	-8	-1
TP	R			10.390	58	6	-3
STG	R			9.332	62	-18	5
STG	L	<.001	5470	10.655	-52	-8	1
STG	L			9.517	-62	-14	7
STG	L			7.717	-46	-38	15
SMA	R	<.001	1505	6.512	2	6	61
CinC	L			4.906	-2	12	35
SMA	L			4.834	-4	4	73
Cerebellum (6)	L	<.001	2254	5.626	-12	-60	-19
Cerebellum (6)	R			5.129	16	-64	-15
Cerebellum (6)	L			4.959	-24	-62	-21
Cerebellum (8)	L	.016	324	4.803	-22	-62	-59
Cerebellum (8)	L			4.694	-34	-52	-53
Cerebellum (8)	L			4.616	-26	-58	-53

Task	Left / Right	*p* (FWE)	Cluster size (voxels)	*T*	Peak coordinates		
					x	y	z
Song phrases: Improvisation > Proverbs: Improvisation							
STG	L	<.001	11408	8.252	-48	-10	-1
Rolandic operculum	L			8.103	-54	-4	1
STG	L			7.996	-60	-10	5
Rolandic operculum	R	<.001	4995	7.309	60	10	5
TP	R			7.174	60	8	-5
STG	R			7.104	62	-24	5
Cerebellum (3)	L	.001	598	4.598	-4	-40	-15
Cerebellum (4–5)	L			4.193	-4	-60	-13
Cerebellum (3)	R			4.035	14	-38	-23

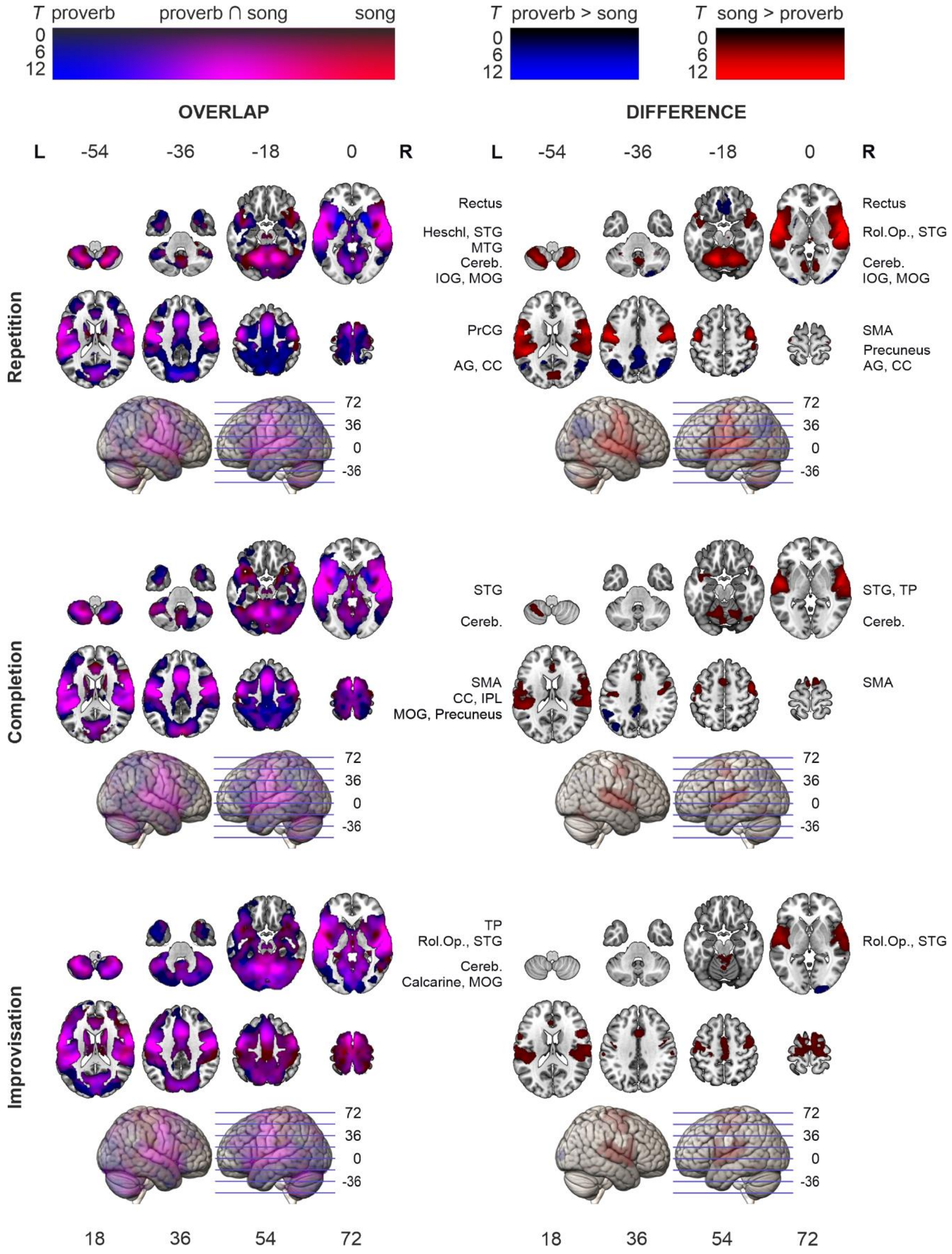

Figure 4 Activation maps showing the differences between speech (Proverb) and singing (Song phrase) production. Overlap of speech and singing in displayed in the left panel and their differences (speech > singing; singing > speech) on right. Significant activity during production, thresholded over whole brain at $p < 0.001$ (uncorrected). Statistical significance FWE-corrected at cluster-level ($p < .05$). Highest T values displayed in bright colours: blue for speech, red for singing, and magenta for an overlap. Reproduced from Moisseinen et al. (2023), CC BY 4.0.

In summary, the main effects of speech and singing production showed an extensive overlap of activation across frontal, temporal, parietal, and cerebellar regions, with an overlapping cluster in left PoCG across all task types (Repetition, Completion, Improvisation). Here, singing elicited stronger activity compared to speech production throughout the brain, the most consistent effects appearing in auditory (STG) and cerebellar regions across all task types.

4.1.2 Age-associated neural changes in speech and singing production

4.1.2.1 Speech production

Regression models showed that, across the age range of 21–88 years, activation decreased across fronto-parietal and temporal regions: PrCG and PoCG in all speech tasks as well as MFG in the Repetition task and in STG in the Improvisation task (Table 10, Figure 5). Further, regression models on the within-subject difference maps for speech production > singing production (Table 11, Figure 6) showed that activation in PrCG and PoCG decreased as a function of age in the Repetition and Completion tasks, more so for speech than for singing production. This effect was accompanied by activation decrease in MTG and cerebellum in the Repetition task.

Age-associated increases in activation were observed only in the Improvisation task (Table 10, Figure 5): in AG/MOG, fusiform gyrus (FG), and ITG. In addition, the results suggested a trend towards increasing activation in a cluster overlapping with right IFG which, however, did not survive FWE-correction (FWE $p = .065$). Regression models on the within-subject difference maps for speech production > singing production in Improvisation showed that activation in the right IFG increased as a function of age more in speech than singing production (Table 11, Figure 6).

In speech, supporting analyses on the lateralisation of activation across the whole brain (as per LI, illustrated in Figure 7) also showed an increasing rightward trend with older age [F (1, 90) = 4.968, $p = 0.028$, $R^2 = 0.052$], potentially originating in the prefrontal regions [MFG: F (1, 90) = 7.578, $p = 0.007$, $R^2 = 0.078$], with age as the sole significant predictor in the stepwise models. Respective analyses on the difference between speech and singing (speech production > singing production) showed that age predicted variation in laterality over the whole brain [F (1, 85) = 8.137, $p = 0.005$, $R^2 = 0.087$] with a significant source in the frontal lobes [F (1, 85) = 14.874, $p < 0.001$, $R^2 = 0.149$] and, more specifically, in the IFG [F (1, 77) = 20.267, $p < 0.001$, $R^2 = 0.208$] as well as MFG [F (1, 85) = 11.447, $p < 0.001$, $R^2 = 0.119$], again with no other significant predictors.

Table 10 Ageing effects in speech (Proverb) tasks. Activation peaks within main effect clusters, thresholded over whole brain at $p < 0.001$ (uncorrected). Association marked as increasing or decreasing with relation to advancing age. Peak coordinates (mm) in MNI space. Reproduced from Moisseinen et al. (2023), CC BY 4.0.

Abbreviations: AG, angular gyrus; FG, fusiform gyrus; ITG, inferior temporal gyrus; MFG, middle frontal gyrs; MOG, middle occipital gyrus; MTG, middle temporal gyrus; PoCG, postcentral gyrus; PrCG, precentral gyrus; STG, superior temporal gyrus.

Task	Left / Right	*p* (FWE)	Direction of change with age	Cluster size (voxels)	*T*	Peak coordinates		
						x	y	z
Proverbs: Repetition								
PoCG	L	<0.001	decrease	2071	7.136	-56	-8	23
PoCG	L				6.285	-52	-10	35
PoCG	L				5.847	-44	-14	33
MFG	R	<0.001	decrease	1505	6.892	46	-2	51
PoCG	R				4.880	46	-12	33
PoCG	R				4.873	50	-4	25
Proverbs: Completion								
PrCG	R	0.020	decrease	311	4.968	46	-4	49
PoCG	R				3.697	58	-6	37
PoCG	L	0.009	decrease	372	4.532	-60	-4	23
PoCG	L				4.250	-48	-10	37
PoCG	L				3.957	-54	-14	49
Proverbs: Improvisation								
PoCG	L	0.010	decrease	374	5.124	-52	-10	41
PoCG	L				4.168	-54	-10	29
STG	L	0.038	decrease	266	4.626	-46	-20	5
MTG	L				4.172	-52	-16	-5
STG	L				3.928	-50	-6	-7
AG	R	<0.001	increase	2701	5.723	42	-66	35
AG	R				5.202	52	-56	31
Precuneus	R				4.727	12	-56	33
MOG	L	0.001	increase	583	4.794	-42	-74	35
AG	L				4.656	-50	-70	37
AG	L				4.025	-40	-66	47
FG	R	0.028	increase	291	4.692	38	-60	-9
FG	R				4.473	28	-66	-9
ITG	R				3.822	52	-58	-5

Task	Left / Right	*p* (FWE)	Direction of change with age	Cluster size (voxels)	*T*	Peak coordinates		
						x	y	z
Proverbs: Improvisation (continued)								
ITG	R	0.035	increase	272	4.524	52	-44	-15
ITG	R				4.215	56	-32	-19
ITG	R				3.947	58	-44	-9

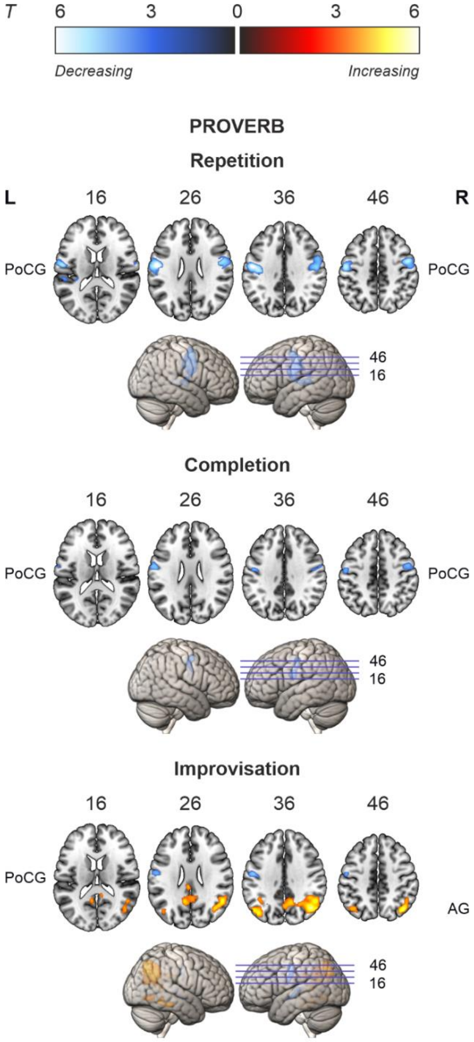

Figure 5 Ageing effects in speech (Proverb) tasks. Local activations decreasing and increasing as a function of age displayed in cold and hot colour bars, respectively. Thresholding over whole brain at $p < 0.001$ (uncorrected). Statistical significance FWE-corrected at cluster-level ($p < .05$). Highest T values displayed in light blue to white for decreasing activity and yellow to white for increasing activity. Reproduced from Moisseinen et al. (2023), CC BY 4.0.

Table 11 Ageing effects in the differences between speech (Proverb) and singing (Song phrase) production. Activation peaks within main effect clusters, thresholded over whole brain at $p < 0.001$ (uncorrected). Association marked as increasing or decreasing with relation to advancing age. Peak coordinates (mm) in MNI space. Reproduced from Moisseinen et al. (2023), CC BY 4.0.

Abbreviations: IFG, inferior frontal gyrus; MTG, middle temporal gyrus; PoCG, postcentral gyrus; PrCG, precentral gyrus.

Task	Left / Right	*p* (FWE)	Direction of change with age	Cluster size (voxels)	*T*	Peak coordinates		
						x	y	z
Proverbs: Repetition > Song phrases: Repetition								
PoCG	L	<.001	decrease	711	6.377	-48	-10	27
PrCG	L				3.553	-48	-4	51
PrCG	R	.004	decrease	440	5.079	46	-6	29
PoCG	R				4.518	60	0	19
MTG	L	.006	decrease	414	4.712	-58	-28	5
MTG	L				4.302	-52	-40	-1
MTG	L				3.590	-50	-24	-7
Cerebellum (crus 2)	R	.012	decrease	348	4.064	50	-58	-47
Cerebellum (8)	R				3.871	42	-62	-57
Cerebellum (crus 2)	R				3.792	44	-70	-43
Proverbs: Completion > Song phrases: Completion								
PoCG	L	.026	decrease	265	4.637	-44	-8	33
PoCG	L				3.881	-56	-4	43
Proverbs: Improvisation > Song phrases: Improvisation								
IFG (oper.)	R	.010	increase	367	4.698	50	12	13
IFG (oper.)	R				3.624	48	10	21

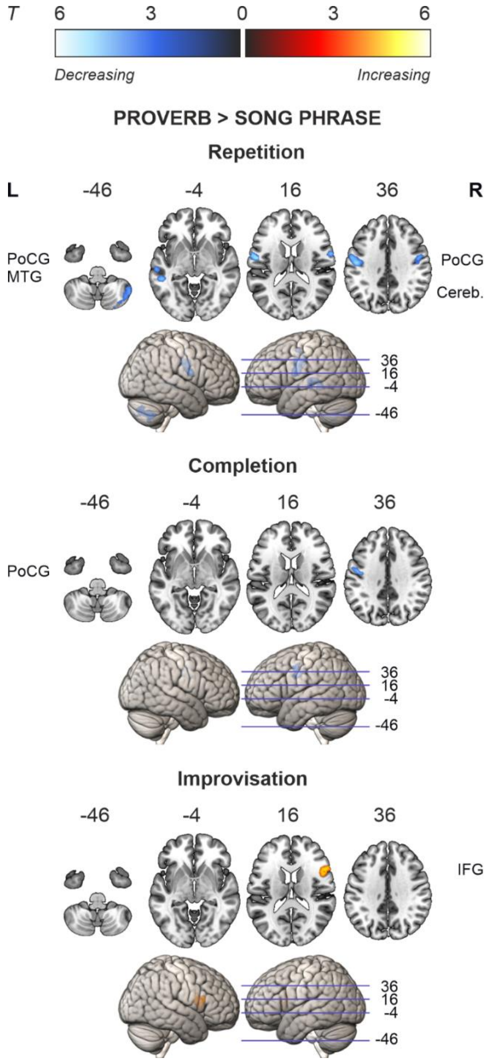

Figure 6 Ageing effects in the differences between speech (Proverb) and singing (Song phrase) tasks. Differences in local activations decreasing and increasing as a function of age displayed in cold and hot colour bars, respectively. Thresholding over whole brain at $p < 0.001$ (uncorrected). Statistical significance FWE-corrected at cluster-level ($p < .05$). Highest T values displayed in light blue to white for decreasing activity and yellow to white for increasing activity. Reproduced from Moisseinen et al. (2023), CC BY 4.0.

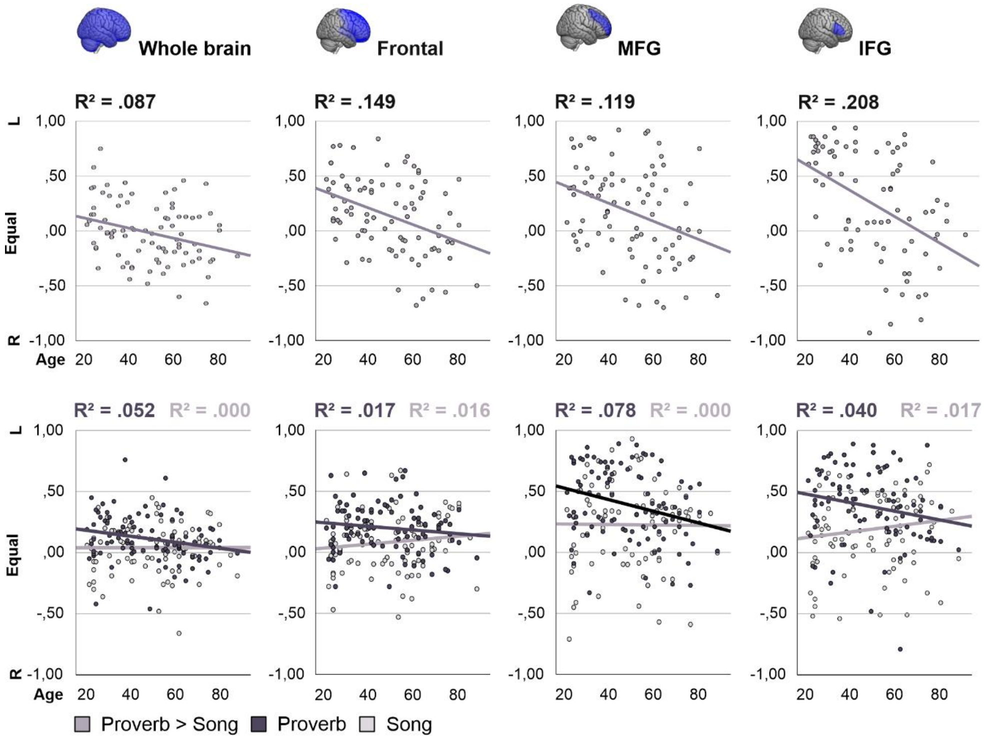

Figure 7 Ageing effects on laterality, as indicated by LI, in the Improvisation tasks. Age-associated changes in LI displayed for the whole-brain, frontal lobes, and MFG and IFG bilaterally. Positive and negative values suggest stronger contribution of the left- and right-hemisphere region, respectively. For each region, significant age-associated changes in the difference of speech and singing (Proverb > Song phrase) are displayed on top in mid grey. Respective age trends in improvised speech (Proverb) and singing (Song phrase) shown below in dark and light grey, respectively. Note that only two modality-specific effects remained significant after correction for multiple comparisons: speech-associated ageing effects in the whole brain and in MFG. Reproduced from Moisseinen et al. (2023), CC BY 4.0.

4.1.2.2 Singing production

Regression models with singing production tasks showed no systematic effects for age, including no effects of age in Repetition and Improvisation tasks. In the Completion task, completion of familiar song phrases from memory elicited clusters in superior, middle and medial frontal regions, CinC and AG as well as temporal, occipital and cerebellar regions (Table 12; Figure 8). By contrast, regression models on the difference between singing and speech production (Song phrase > Proverb) showed no ageing effects unique for singing. Further, none of the singing tasks showed changes in laterality (as indicated by LI) on their own or when contrasted against speech (Song phrase > Proverb).

Table 12 Ageing effects in singing (Song phrase) tasks. Activation peaks within main effect clusters, thresholded over whole brain at p < 0.001 (uncorrected). Association marked as increasing or decreasing with relation to advancing age. Peak coordinates (mm) in MNI space. Reproduced from Moisseinen et al. (2023), CC BY 4.0.

Abbreviations: ACC, anterior cingulate cortex; AG, angular gyrus; CinC, cingulate cortex, ITG, inferior temporal gyrus; MedFG, medial frontal gyrus; MedOG, medial orbital gyrus; MFG, middle frontal gyrus; MTG, middle temporal gyrus; SFG, superior frontal gyrus.

Task	Left / Right	*p* (FWE)	Direction of change with age	Cluster size (voxels)	*T*	Peak coordinates x	y	z
Song phrases: Completion								
AG	L	<0.001	increase	907	5.265	-48	-70	35
MTG	L				5.056	-50	-72	21
AG	L				4.951	-40	-66	33
ITG	L	0.011	increase	364	4.944	-50	-58	-13
MTG	L				4.338	-60	-44	-9
MTG	L				4.231	-54	-36	-9
Cerebellum (crus 2)	R	0.020	increase	318	4.894	38	-80	-47
Cerebellum (7b)	R				4.320	42	-66	-53
Cerebellum (8)	R				4.092	14	-78	-53
ACC	R	<0.001	increase	927	4.742	4	40	27
MedFG	L				4.618	-6	38	37
MedFG	R				4.129	4	54	35
MedOG	L	0.010	increase	412	4.554	-2	42	-9
MedOG	L				4.478	-2	60	-1
MedFG	L				3.516	-2	56	17
CinC	L/R	0.002	increase	543	4.553	0	-52	25
CinC	L				4.443	-6	-44	11
CinC	L/R				4.171	0	-40	39
MFG	L	0.023	increase	309	4.395	-32	16	53
MFG	L				4.022	-42	20	45
AG	R	0.005	increase	442	4.263	46	-68	43
AG	R				4.011	42	-60	25
AG	R				3.890	52	-62	29
SFG	R	0.003	increase	490	4.160	30	12	65
MFG	R				4.116	36	14	43
SFG	R				3.828	22	24	57

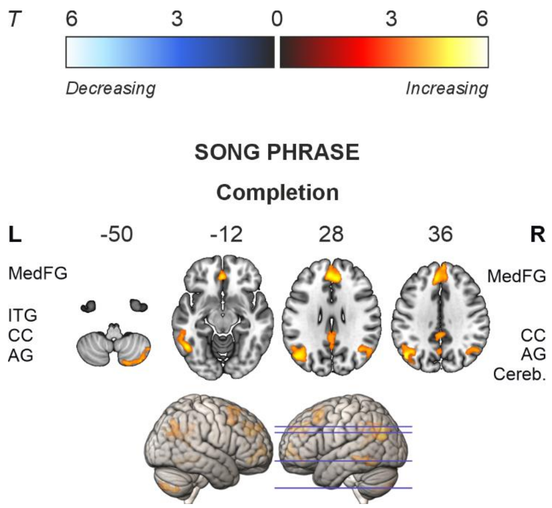

Figure 8 Activation maps of the ageing effects in singing (Song phrase) tasks, where the only significant results were found in the Completion from memory task. Thresholding over whole brain at $p < 0.001$ (uncorrected). Statistical significance FWE-corrected at cluster-level ($p < .05$). Local activations decreasing and increasing as a function of age displayed in cold and hot colour bars, with highest T values displayed in light blue to white for decreasing activity and yellow to white for increasing activity. Reproduced from Moisseinen et al. (2023), CC BY 4.0.

4.2 Associations of choir singing experience with brain structure, cognitive performance, and well-being (Studies II & III)

4.2.1 Brain structure

4.2.1.1 White matter connectometry

When controlling for the effects of age, whole-brain correlational tractography showed positive associations between choir singing duration (% of age) and WM QA in associative [left AF, right extreme capsule, as well as bilateral cingulum, inferior longitudinal fasciculi (ILF), and inferior fronto-occipital fasciculi (IFOF)], commissural [anterior commissure (AC) and corpus callosum (CC)], and projection pathways (bilateral corticopontine, corticospinal, corticostriatal, as well as dentatorubrothalamic tracts, medial lemnisci, and thalamic radiations). Separate analyses addressing potential sources along the full age range (21–88 years) showed a significant effect for posterior parts of the CC in each age-specific subgroup (young, middle-aged, older). Other effects were largely driven by young adults, while effects in the right corticospinal tract remained significant in middle-aged adults as well. Age-selective effects appeared in older adults only, in whom choir singing duration was linked to higher QA in the fornix bilaterally. Choir singing duration showed no negative associations with QA, and the frequency measures (hours/week) for the present and lifetime maximal activity in choir singing were not associated with QA. Results from white matter connectometry are presented in Table 13 and Figure 9.

Table 13 Number of tracts showing increased QA as a function of the duration of lifetime choir singing experience. Analyses corrected for multiple comparisons at FDR < .0125 (Bonferroni). No decreasing trends for QA were found. Reproduced from Moisseinen et al. (2024), CC BY-NC-ND 4.0.

Abbreviations: AC, anterior commissure; AF, arcuate fasciculus; CC, corpus callosum; CPT, corticopontine tract; CST, corticospinal tract; CStrT, corticostriatal tract; DRTT, dentatorubrothalamic tract; EC, extreme capsule; IFOF, inferior fronto-occipital fasciculus; ILF, inferior longitudinal fasciculus; ML, medial lemniscus; ThR, thalamic radiation; UF, uncinate fasciculus.

Tract	Left / Right	All	Young	Middle-aged	Older
Association tracts					
AF	R	-	38	-	-
	L	201	36	-	-
Cingulum	R	15	-	-	-
	L	74	13	-	-
EC	R	6	-	-	-
	L	-	-	-	-
ILF	R	8	-	-	-
	L	11	-	-	-
IFOF	R	568	-	-	-
	L	386	20	-	-
UF	R	-	5	-	-
	L	-	32	-	-
Commissural tracts					
AC	R/L	7	-	-	-
CC	R/L	7481	3164	52	20
Projection tracts					
CPT	R	365	20	-	-
	L	264	205	-	-
CST	R	3275	1539	56	-
	L	445	630	-	-
CStrT	R	101	18	-	-
	L	98	9	-	-

Tract	Left / Right	All	Young	Middle-aged	Older
Projection tracts (continued)					
DRTT	R	446	25	-	-
	L	5	-	-	-
ML	R	664	132	-	-
	L	48	41	-	-
Fornix	R	-	-	-	5
	L	-	-	-	7
ThR	R	115	-	-	-
	L	14	-	-	-
Cerebellar tracts					
Cerebellum	R	-	59	-	-
	L	-	-	-	-

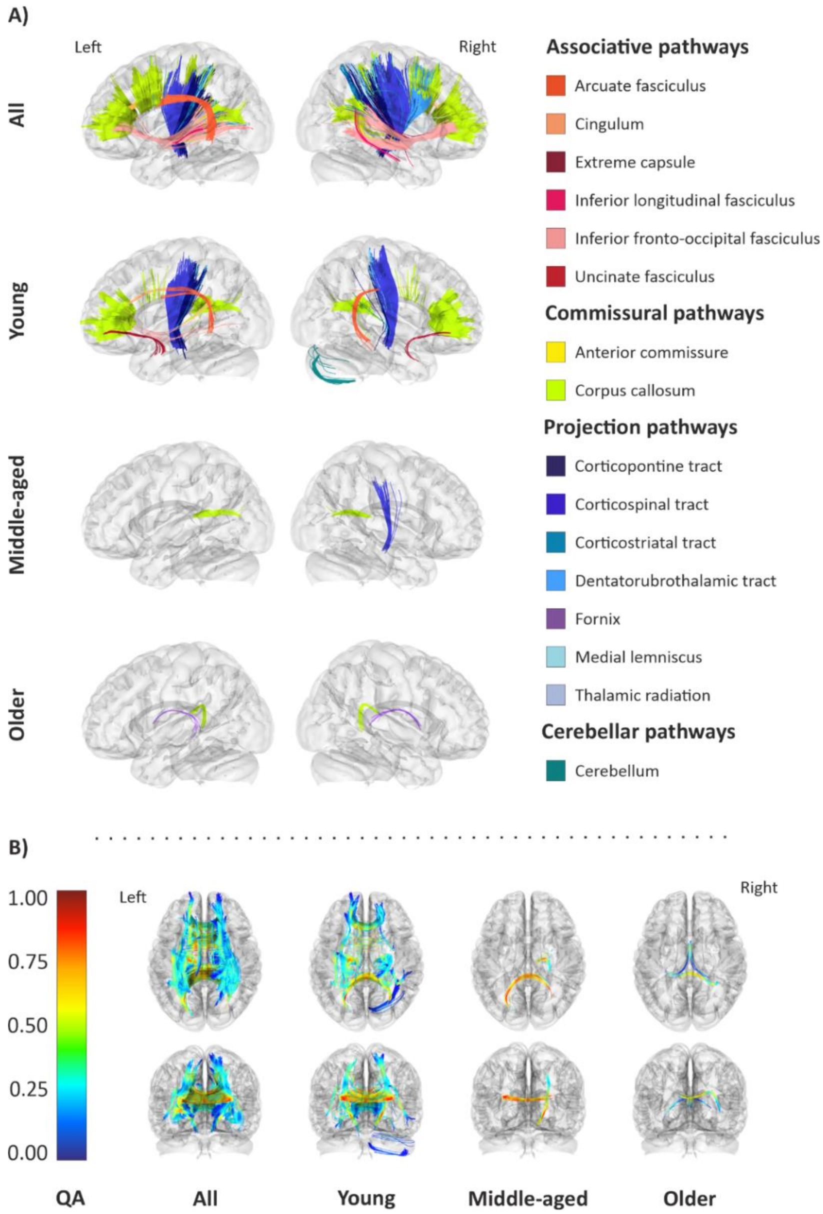

Figure 9 Positive associations between white-matter QA and the duration of lifetime choir singing experience, with (A) WM pathways showing a positive association between QA and choir singing experience regardless of age as well as within each age group, and (B) the respective local indices for QA. All results were corrected for multiple comparisons (Bonferroni). Reproduced from Moisseinen et al. (2024), CC BY-NC-ND 4.0.

4.2.1.2 Grey matter volume

Choir singing duration or frequency measures were not associated with GM volume in the whole-brain models. Secondary analyses with more lenient significance thresholds (whole-brain $p < .001$ uncorrected at the voxel-level, FWE-corrected $p < .0125$ at the cluster-level) validated these null results.

4.2.2 Cognitive performance

4.2.2.1 Direct effects

Regression models with raw scores from neuropsychological assessments showed a positive association between choir singing duration (% of age) and episodic memory as well as verbal fluency; details on the results are outlined in Table 14. Choir singing duration predicted both immediate and delayed recall in the subgroup of choir singers [F (2, 50) = 15.598, adjusted R^2 = .360, $p < .001$; F (3, 49) = 12.023, adjusted R^2 = .389, $p < .001$] as well as in the full sample [F (2, 92) = 28.717, adjusted R^2 =.371, $p < .001$; F (3, 91) = 22.150, R^2 = .403, $p < .001$], together with age and education years, respectively. Subsequent post hoc tests within the three age groups showed no clear source for these effects.

Table 14 Results from stepwise multiple regression for verbal fluency (semantic + phonological) and episodic memory (immediate recall, delayed recall) in the full sample and in the subgroup of choir singers. No significant associations were found for choir singing and other neuropsychological test scores (processing speed, working memory, and executive function; not reported). Significance levels corrected for multiple comparisons at $\alpha = .010$ (Bonferroni). Adapted from Moisseinen et al. (2025), CC BY 4.0.

[1] Phonemic (letter S) + semantic (animals); unique items produced in 60 seconds in each.

[2] Lifetime experience in choir singing (% of age).

[3] WMS Logical memory story A + B (1.) + B (2.) immediate + WMS Word lists immediate.

[4] WMS Logical memory story A + B delayed + WMS Word lists delayed.

	Model				Coefficient(s)		
	df	Adj. R^2	*F*	*p*	Std. β	t	*p*
VERBAL FLUENCY[1]							
Full sample							
Choir singing duration[2]	2, 92	.174	10.900	< .001	.198	2.112	.037
Age					-.403	-4.291	< .001
Choir singers							
Choir singing duration	2, 50	.335	14.102	< .001	.260	2.298	.026
Age					-.533	-4.715	< .001
EPISODIC MEMORY (IMMEDIATE)[3]							
Full sample							
Choir singing duration	2, 92	.371	28.717	< .001	.222	2.713	.008
Age					-.593	-7.235	< .001
Choir singers							
Choir singing duration	2, 50	.360	15.598	< .001	.248	2.230	.030
Age					-.561	-5.049	< .001
EPISODIC MEMORY (DELAYED)[4]							
Full sample							
Choir singing duration	3, 91	.403	22.150	< .001	.257	3.222	.002
Age					-.460	-5.325	< .001
Education (years)					.265	3.076	.003
Choir singers							
Choir singing duration	3, 49	.389	12.023	< .001	.282	2.591	.013
Age					-.398	-3.252	.002
Education (years)					.288	2.350	.023

4.2.2.2 Mediation effects

Following previous evidence, the significance of mediation with the initial regression effects was tested for episodic memory via verbal fluency. As previous evidence (Folia et al., 2023; Gustavson et al., 2020) suggests differential associations of episodic memory with phonemic versus semantic fluency with respect to advancing age, the mediation analyses were carried out for the initial composite score (phonemic + semantic) as well as separately for each of its subcomponents. Details on the mediation results are provided in Table 15 and Figure 10. The composite score and phonemic verbal fluency showed no significant mediation from choir singing duration onto episodic memory. Semantic fluency, however, was a significant mediator for the effect of choir singing duration on both immediate (Figure 10: A) and delayed (Figure 10: B) episodic memory scores in both choir singers and, with smaller indirect effects, in the full sample.

Table 15 Mediation results for choir singing (*X*; present frequency as hours/week, lifetime duration as % of age) and cognitive factors (*Y*) via respective mediators (*M*), in the full sample and in choir singers using 10 000 bootstrapped samples. Results where 0 does not fall within the *CI* (95 %) are considered statistically significant. Adapted from Moisseinen et al. (2025), CC BY 4.0.

[1] WMS Logical memory story A + B (1.) + B (2.) immediate + WMS Word lists immediate.

[2] Composite score represents phonemic (letter S) + semantic (animals); unique items produced in 60 seconds in each task.

[3] Lifetime experience in choir singing (% of age).

[4] WMS Logical memory story A + B delayed + WMS Word lists delayed.

[5] Exact value: .0001.

Y, *X*	*M*	Indirect	*SE*	*CI* (95 %)
EPISODIC MEMORY (IMMEDIATE)[1]	VERBAL FLUENCY[2]			
Full sample				
Choir singing duration[3]	Composite	.024	.018	-.001 – .069
Choir singing duration	Phonemic (letter S)	.005	.001	-.001 – .029
Choir singing duration	Semantic (animals)	.027	.018	.003 – .071
Choir singers				
Choir singing duration	Composite	.044	.034	-.001 – .127
Choir singing duration	Phonemic (letter S)	.005	.015	-.018 – .043
Choir singing duration	Semantic (animals)	.060	.041	.002 – .159
EPISODIC MEMORY (DELAYED)[5]	VERBAL FLUENCY[2]			
Full sample				
Choir singing duration	Composite	.013	.011	-.001 – .039
Choir singing duration	Phonemic (letter S)	.001	.001	-.001 – .012
Choir singing duration	Semantic (animals)	.016	.012	.000[5] – .044
Choir singers				
Choir singing duration	Composite	.029	.023	-.001 – .087
Choir singing duration	Phonemic (letter S)	.003	.001	-.013 – .027
Choir singing duration	Semantic (animals)	.042	.026	.004 – .103

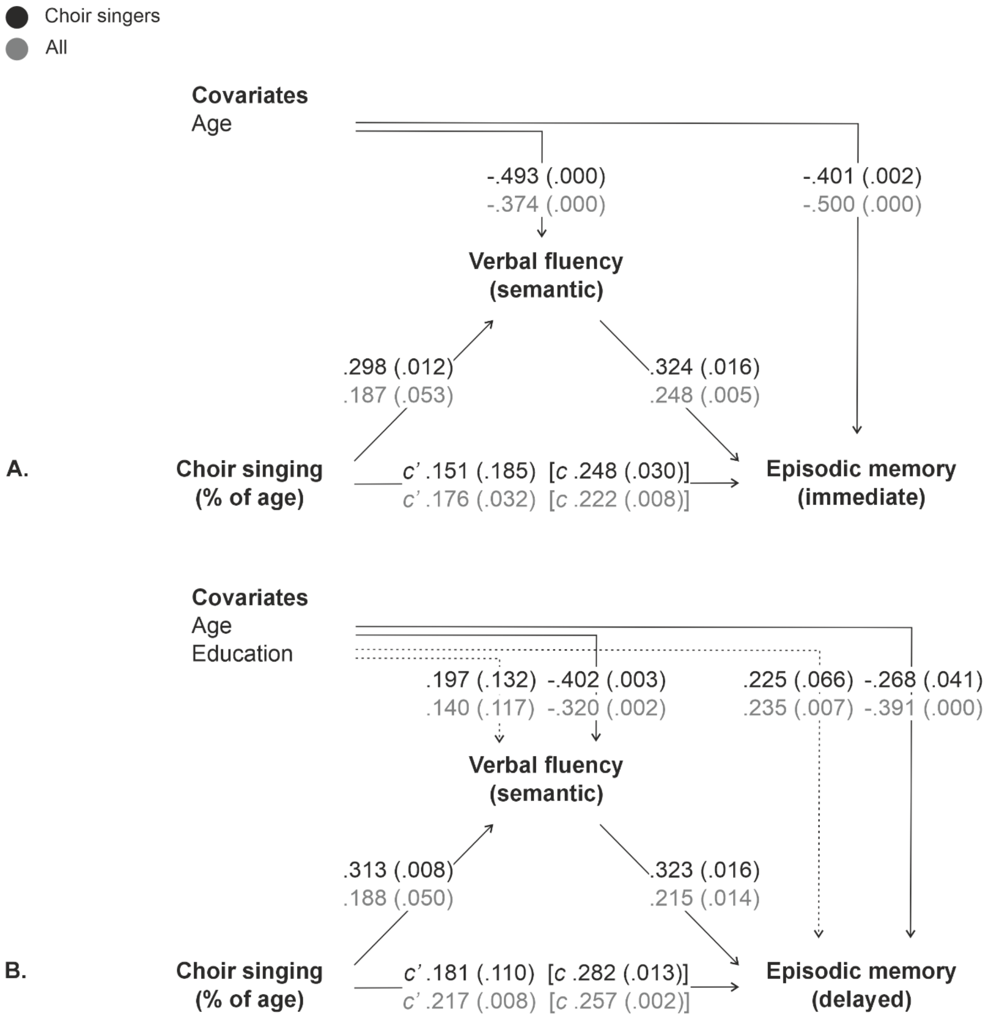

Figure 10 Mediation results for the lifetime duration of choir singing (% of age) and episodic memory (A. immediate recall; B. delayed recall) through semantic verbal fluency (animals), with the direct effects of choir singing (*c'*), using 10 000 bootstrapped samples. Total effects of choir singing (*c*) provided for comparison. Results for choir singers and the full sample displayed in black and grey, respectively. Each result reported as the standardised coefficient (*p* value). Reproduced from Moisseinen et al. (2025), CC BY 4.0.

4.2.3 Well-being

4.2.3.1 Direct effects

Regression models on self-reported well-being showed significant associations between present frequency of choir singing (hours/week) and depressive symptoms (CES-D) as well as QOL scores; details on the results are outlined in Table 16. Choir singers showed a negative association between present frequency of singing and self-reported depressive symptoms [$F(1, 51) = 10.955$, adjusted $R^2 = .161$, $p < .002$]. The full sample showed a similar trend; however, the model did not survive correction for multiple comparisons at $\alpha = .01$ ($p = .025$) and it violated the independence of errors. The effect was not significant in the age-specific subgroups.

Choir singers showed trends towards positive associations between present frequency of singing and psychological and overall QOL ($p = .019$; $p = .031$, respectively). The latter also approached significance in the full sample ($p = .018$), yet the result showed a violation of the normality assumption and should thus be interpreted with caution. Crucially, none of the QOL models survived correction for multiple comparisons at $\alpha = .01$, nor were they significant in the age-specific subgroups.

Table 16 Results from stepwise multiple regression for depressive symptoms and QOL in the full sample and in choir singers. Stepwise models found no significant associations for choir singing and other domains of QOL (not reported). Significance levels corrected for multiple comparisons at α = .010 (Bonferroni). Adapted from Moisseinen et al. (2025), CC BY 4.0.

[1] Center for Epidemiological Studies: Depression (CES-D).

[2] Present frequency of choir singing (hours / week).

[3] WHOQOL-BREF.

				Model		Coefficient(s)	
	df	Adj. R^2	*F*	*p*	Std. β	*t*	*p*
DEPRESSIVE SYMPTOMS[1]							
Full sample							
Choir singing frequency[2]	1, 93	.053	5.192	.025	-.230	-2.278	.025
Choir singers							
Choir singing frequency	1, 51	.161	10.955	.002	-.421	-3.310	.002
QOL (WHOQOL OVERALL)[2]							
Full sample							
Choir singing frequency	1, 93	.059	5.824	.018	.243	2.413	.018
Choir singers							
Choir singing frequency	1, 51	.070	4.894	.031	.296	2.212	.031
QOL (WHOQOL PSYCHOLOGICAL)[3]							
Choir singers							
Choir singing frequency	1, 51	.086	5.881	.019	.322	2.425	.019

4.2.3.2 Mediation effects

As depressive symptoms can predict QOL (Tang & Thomas, 2020; see also da Rocha et al., 2009), mediation models from the present frequency of choir singing were carried out onto QOL scores with depressive symptoms as the mediator; details on the results can be found in Table 17 and Figure 11. Reduced depressive symptoms significantly mediated the positive associations between present frequency of choir singing and psychological QOL (Figure 11: A) as well as overall QOL (Figure 11: B). Supplementary analyses suggested weaker mediation effects in the full sample for both psychological and overall QOL. Given the violations of assumptions described above, however, the full-sample mediation results should be interpreted with caution.

Table 17 Mediation results for choir singing (*X*; present frequency as hours/week, lifetime duration as % of age) and well-being factors (*Y*) via respective mediators (*M*), in the full sample and in choir singers using 10 000 bootstrapped samples. Results where 0 does not fall within the *CI* (95 %) are considered statistically significant. Adapted from Moisseinen et al. (2025), CC BY 4.0.

[1] WHOQOL-BREF.

[2] Center for Epidemiological Studies: Depression (CES-D).

[3] Present frequency of choir singing (hours / week).

Y, *X*	*M*	Indirect	*SE*	*CI* (95 %)
QOL (OVERALL)[1]	DEPRESSIVE SYMPTOMS[2]			
Full sample				
Choir singing frequency[3]	CES-D (total)	.128	.058	.013 – .241
Choir singers				
Choir singing frequency	CES-D (total)	.230	.089	.084 – .437
QOL (PSYCHOLOGICAL)[1]				
Full sample				
Choir singing frequency	CES-D (total)	.166	.073	.018 – .310
Choir singers				
Choir singing frequency	CES-D (total)	.354	.119	.153 – .630

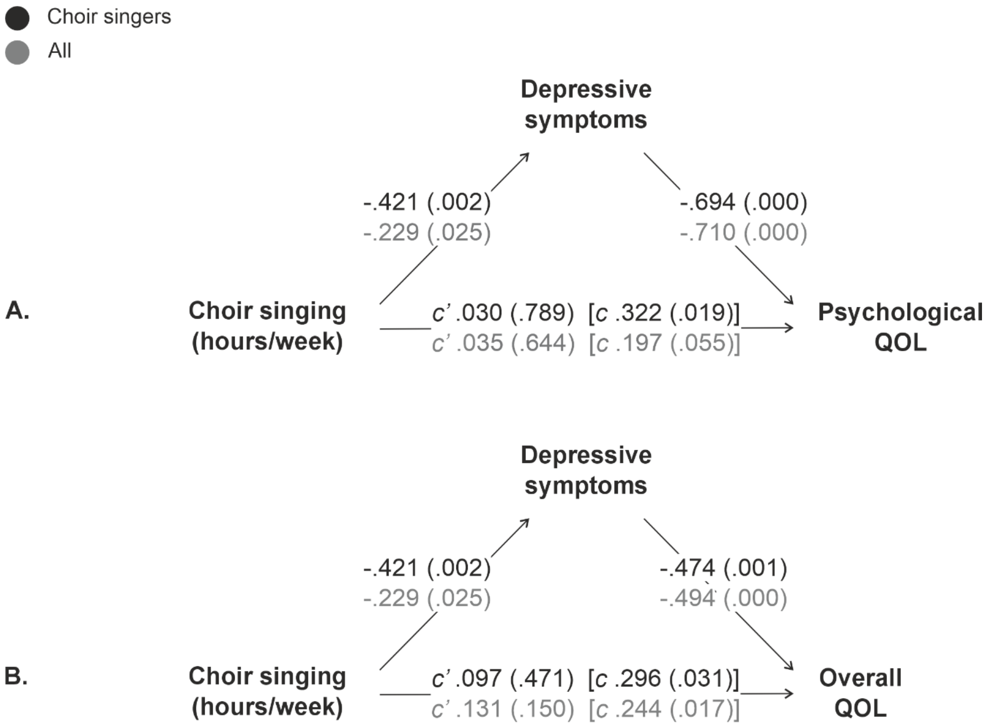

Figure 11 Mediation results for the present frequency of choir singing (hours/week) and QOL (A. psychological QOL; B. overall QOL) via self-reported depressive symptoms, with the direct effects of choir singing (*c'*), using 10 000 bootstrapped samples**.** Total effects of choir singing (*c*) provided for comparison. Results for choir singers and the full sample displayed in black and grey, respectively. Each result reported as the standardised coefficient (*p* value). Reproduced from Moisseinen et al. (2025), CC BY 4.0.

5 Discussion

The present study aimed to (i) map the functional neural overlap and differences of speech and singing production and (ii) explore the effects of ageing on the neural substrates of speech and singing production with various cognitive task demands (Study I). Further, the present study aimed to (iii) explore the associations of the duration and frequency of singing with white matter connectivity and grey matter volume (Study II) as well as cognitive performance and subjective well-being across adulthood (Study III). To address these aims, a cross-sectional sample ($N = 100$) of healthy Finnish-speaking volunteers (aged 21–88 years) with variable amateur-level choir singing experience (46 non-singers) participated in the set of Studies I–III involving functional and structural MRI, a neuropsychological test battery assessing verbal fluency, episodic memory, working memory, processing speed and executive function, and questionnaires assessing demographic and musical background factors as well as subjective socioemotional well-being. The results showed, first, differential ageing effects for speech and singing despite substantial overlap in age-independent main effects. Second, the results suggested that the duration of choir singing is associated with extensive enhancements in white matter connectivity as well as performance in episodic memory and verbal fluency, while the frequency of singing was associated with mood and QOL. The subsequent sections discuss these findings and their theoretical implications in more detail.

5.1 Neural processing of speech and singing production across adulthood

This study aimed to systematically map the overlap and differences as well as the effects of age in neural processing underlying speech and singing production with respect to variable cognitive task demands. Study I addressed these aims using a set of overt production tasks targeting (i) short-term verbal working memory and simple motor production (Repetition task; repetition of familiar phrases) with additional components of (ii) retrieval from long-term memory (Completion task; completion of familiar phrases) and (iii) cognitive flexibility and fluency (Improvisation task; completion of new phrases by improvising).

Corroborating and extending previous evidence, the results suggested extensive overlap of speech and singing production, with mainly focal differences across the three task types. With respect to effects of age, however, the results suggested no overlap between speech and singing production. Speech tasks systematically showed reduced activation with ageing in pre- and postcentral regions, also reflected in contrasts between speech and singing, along with reduced hemispheric asymmetry in the lateral prefrontal regions as well as overactivation in bilateral angular and right inferior temporal and fusiform activation in the Improvisation task. By contrast, age effects in singing were limited to medial prefrontal and medial and lateral parietal overactivation in recall from memory (Completion task).

5.1.1 Overlap and differences

The main effects of speech and singing showed extensive overlap across the brain. Corroborating previous findings, all speech and singing production tasks elicited widespread activation across frontal, temporal, parietal, and cerebellar regions falling under the bihemispheric networks for cognitive and auditory-motor feedback control (Peretz et al., 2015; Zarate, 2013) and somatosensory integration in vocal production (Zarate, 2013). This pattern involved highly similar cluster peaks in the left PoCG corresponding to the somatosensory representation of the mouth area (Grabski et al., 2012) along the left-lateralised dorsal streams of speech (Hickok & Poeppel, 2004, 2007) and singing production (Loui, 2015; Musso et al., 2015).

Compared to speech production, singing production tasks elicited stronger activation in auditory (STG, HG), associative (SMA, Rolandic operculum), and cerebellar regions bilaterally. In line with the present findings, regional specialisation towards the acoustic features of music (rather than speech) has been associated with anterior STG and lateral HG bilaterally (Fedorenko et al., 2012; Leaver & Rauschecker, 2010), with PrCG, PoCG and SMA feeding to the dorsal processing stream of singing (Loui, 2015). Crucially, the Rolandic operculum lies adjacent to the IFG, joining PrCG and PoCG at their inferior ends at the proximity of the representation areas for tongue and larynx. It is thought to support articulatory functions, yet its vast connectivity with temporal and subcortical regions associates it with several complex functions from sensory integration to bodily self-awareness (for a review, see Triarhou, 2021).

While replicating classical findings of a stronger bilateral engagement in production tasks involving repetition (Özdemir et al., 2006) and recall (Callan et al., 2006; Jeffries et al., 2003), the present results extend these effects to cued improvisation, thus providing further validation for the widely assumed difference between speech and singing networks. Further, it should be noted that the activation patterns across the three task types appeared highly similar: this is shown when viewing results from speech and singing production side by side (Figure 3) and by their overlap and differences (Figure 4). While direct contrasts between the intentionally diverse task types were outside the scope of this study, this trend encourages the design of tasks with more systematic manipulation of cognitive demands could diversify results from these comparisons (cf. Liu et al., 2012).

In contrast to classical findings, the present results also suggested greater focal activity in speech compared to singing in the Repetition and Completion tasks. These clusters centred in the IPL and SPL regions (AG, precuneus), previously associated with episodic memory and semantic cognition (Humphreys et al., 2021) as well as attentional control in information retrieval (Emch et al., 2019) and, in the Repetition task, also in the right crus 2 of the cerebellum, a region involved in linguistic processing, particularly in the prediction and error detection of phonological content (Callan et al., 2007; Lesage et al., 2017). While advances in MRI methods and a larger sample size may partially explain the contrast to the classical studies, factors associated with the auditory items used are also likely to contribute. First, the classical studies were conducted in English and Japanese, and the present one in Finnish. In Finnish language, meaning is characteristically conveyed via phonological length with intonation carrying remarkably less semantic value. Considering that intonation is often directly assimilated with the melodic properties of song (e.g., Özdemir et al., 2006; Zatorre & Baum, 2012), low variability in speech intonation may introduce an exceptionally great gap between speech and singing as forms of auditory information. Second, earlier studies have matched sung and spoken items by using spoken versions of song lyrics for the speech conditions. By design, the present study used proverbs instead of song lyrics to prevent potential inference from the unintentional activation of associated melodic information during speech production, presumably introducing a greater difference between speech- and singing-associated activation.

5.1.2 Ageing and singing production

While the influence of ageing on singing has remained largely unknown, the asymmetries of singing and speech networks in the young adult brain, as discussed above (section 1.4), seem to predict differential ageing mechanisms for the two vocal domains. Consistent with this notion, the present study showed dissimilar ageing effects in singing and speech production, with no systematic ageing effects across the singing tasks. Specifically, the sole ageing effect in singing was observed for Completion of song phrases from memory: as increased activation in the medial frontal and parietal default mode network (DMN) regions, including ACC/MedFG and AG, centrally involved in supporting the internal narrative, such as retrieval of episodic information (Menon, 2023; Smallwood et al., 2021), including musical memories and pleasure (Hennessy et al., 2025; Jacobsen et al., 2015; Janata, 2009).

Consistent with the present findings, coordinated co-activation of DLPFC (MFG) has been found to support cued recall from autobiographical memory, presumably through the coordination of the various processes associated with this task (e.g., Nawa & Ando, 2020), along with left posterior temporal semantic processing regions (MTG/ITG) subserving semantic control (Hodgson et al., 2024; Noonan et al., 2013). Another control mechanism coupling retrieval, right cerebellum (crus 2) is involved in the prediction and error detection of phonological content (Callan et al., 2007; Lesage et al., 2017).

Cohering with the task demands requiring the identification and retrieval of the correct target response as well as its accurate production, the elicited ageing effect thus appears to reflect a coactivation pattern of regions centrally involved in episodic retrieval, musical memories included, and control processes subserving search performance and online monitoring of phonological content. In favour of this interpretation, mere repetition of familiar phrases (Repetition of song phrases) did not elicit an ageing effect, thus suggesting an effect associated with retrieving the correct response from memory.

Prevailing models of neurocognitive ageing attribute overactivation to increasing compensatory effort with increasing task demands (e.g., Reuter-Lorenz & Cappell, 2008; Reuter-Lorenz & Park, 2014), thus suggesting increasing effort and need for compensation in recall. Interestingly, such a pattern did not reach significance in the spoken counterpart of this task (Completion of proverbs). Considering that music has well established mnemonic effects on the retrieval of verbal material (for a review, Derks-Dijkman et al., 2024) involving reductions rather than increases of effort compared to speech, however, a modality-specific compensation effect in singing seems unlikely. Indeed, the direct contrast between the sung and spoken conditions (Completion of song phrases > Completion of proverbs), showing no significant difference between the two modalities, suggested that this effect was not fully unique to singing. It should be noted, however, that single phrases belonging to the larger context of a song may be less efficiently automated or ‘chunked’ than proverbs, which are complete lexical entities on their own. Thus, the present task design, involving naturalistic items, may carry partially differential demands for retrieval in the two vocal modalities. Further, the retrieval of a song phrase may also elicit musical memories associated with the song and require inhibition of retrieving consecutive phrases from the song. Consistent with the present results, the cues for recall, selected from traditional seasonal songs and evergreens, for instance, are indeed likely to induce more reminiscing in older participants.

To summarise, the present ageing effects in the recall of familiar song phrases suggest increased effort in retrieval, potentially owing to the choice to use naturalistic items and associated inhibitory processing in part. Crucially, the present results extend previous evidence by illustrating an interplay of neurocognitive ageing and vocal production outside the speech domain. Based on the present evidence, it is thus recommended that future studies on vocal production and ageing pay particular attention to the cognitive task demands involved in the production task (see also Davis et al., 2014).

5.1.3 Ageing and somatosensory processing in speech production

All speech production tasks showed reduced activation in the left PoCG as a function of age; this effect also appeared contralaterally in Repetition and Completion tasks. Despite the remarkable overlap of main effects in left ventral PoCG across all speech and singing production tasks discussed above, these reductions appeared also in the speech minus singing contrasts, suggesting that this effect was unique to speech. Considering the overlap of these effects with somatosensory processing in articulatory control (cf. Bouchard et al., 2013; Segawa et al., 2015; Shuster & Lemieux, 2005), this finding might reflect decreased efficiency or precision in sensorimotor integration as predicted by behavioural evidence on speech production and ageing (Mefferd & Corder, 2014; Tremblay et al., 2018, 2019).

As age-induced declines are characterised by focal accelerations, it seems likely that the initial differences between networks underlying speech and singing production would also indicate differential needs for adaptation in later life. Specifically, structural neuroimaging evidence suggests that the somatosensory regions along PoCG and adjacent regions show accelerated GM loss, often with a bias towards the left hemisphere (Minkova et al., 2017). While both singing and speech recruit left-hemisphere networks, recent evidence on post-stroke aphasia (Pitkäniemi et al., 2023) suggests that singing relies less heavily on the dorsal pathway flowing across the somatomotor regions. Another study (Grube et al., 2016) also suggested that processing along the dorsal stream might explain the dissociated speech and singing ability in different subtypes of primary progressive aphasia (PPA; e.g., Polk & Kertesz, 1993; see also Baird & Thompson, 2019).

Placed in this context, the present results suggest that heavier reliance on the left dorsal stream in speech production can lead to a greater need to adapt somatosensory feedback processing. The systematicity of this effect across the present speech tasks corroborates and extends previous evidence showing the impact of cognitive demands on speech processing in the ageing brain (e.g., Davis et al., 2014; Tremblay et al., 2017). Considering the relatively low level of cognitive demands in the present tasks (cf. Tremblay et al., 2017), however, these findings argue for further investigations where also the level of associated demands is varied by increasing the length of individual items, for instance (cf. Liu et al., 2012).

5.1.4 Ageing and cued improvisation in speech production

Age was associated with changes in laterality, as indicated by LI, in the Improvisation task in speech but not in singing production, showing minor rightward shifts across the whole brain and in the prefrontal regions. Likely driven by an age-associated trend towards increased activation in the right IFG (opercularis, triangularis), this pattern of results aligns well with previous examples from speech production studies showing compensatory overactivation effects (Cabeza, 2002; Reuter-Lorenz & Park, 2014) in right prefrontal regions (Hoyau et al., 2017; Wierenga et al., 2008). This effect was accompanied by increased right-dominant temporo-parietal activity, including right FG, posterior ITG and bilateral AG. These regions align contralaterally with the left-dominant (auditory) semantic control and broader semantic cognition regions (Jackson, 2021; see also Noonan et al., 2013) typically involved in tasks requiring the manipulation of semantically meaningful stimuli (Hodgson et al., 2024), such as the present one (i.e., cued improvisation).

As the present data did not show rightward shifts in the laterality of activation outside the frontal lobes, however, compensatory overactivation of right-hemisphere homologues seems a less likely source for the present effect but might be better explained by age-associated regional overactivation (Cabeza et al., 2018). Interestingly, also bilateral IFG has been implicated in semantic control in young adults (Jackson, 2021). Consistent with the present findings, a recent fMRI study (Becker et al., 2020) found joint involvement of right IFG and AG as well as FG in a modified, semantically primed version of the compound remote associates (CRA) task mapping verbal creative problem solving, while another study (Hodgson et al., 2024) suggested selective involvement of right posterior ITG in non-semantic stimulus manipulation tasks.

Although the present results showed no age effects for the sung version of the Improvisation task, it should be noted that the temporo-parietal effects of age in speech did not survive when directly contrasted against singing. Two conclusions can be drawn from this. First, prefrontal hemispheric asymmetry reduction, although observed in demanding speech tasks such as the present one, does not emerge in singing under similar task demands. A tentative explanation for this is that singing engages vocal production networks more bilaterally already in early adulthood. Second, the observed overactivation of right IFG could stem from a combination of age-associated hemispheric asymmetry reduction (speech only) and more generic age effects in right-hemisphere semantic and other control processing (speech only or predominantly). Given that the adaptive advantages of singing over speech are traditionally attributed to the greater involvement of right-hemisphere regions in singing (for a review on clinical evidence, see Schlaug et al., 2010), this pattern of results argues for a more detailed mapping of age effects in speech versus singing within the right hemisphere specifically. Ideally, this would also provide confirmation on whether the absence of hemispheric asymmetry reduction is due to less lateralised networks of singing.

5.2 Neurocognitive and well-being effects of choir singing across adulthood

The present study mapped the associations of choir singing experience [age-adjusted duration (% of age in years), lifetime maximal frequency and present frequency (hours/week)] with grey matter volume and structural connectivity (Study II), self-reported well-being measures in depressive symptoms and QOL as well as neuropsychological test scores in verbal fluency, processing speed, working memory, episodic memory, and executive function (Study III), while controlling for the effects of age, education, and other musical hobbies.

First, results from Study II suggested positive associations between choir singing duration and QA of commissural (AC and CC) pathways and of associative (left AF and bilateral cingulum, ILF, and IFOF) and motor pathways (bilateral medial lemnisci, thalamic radiations, and corticostriatal, corticospinal, corticopontine, and dentatrorubrothalamic tracts). The whole-sample results were largely driven by effects in young adults, possibly relating to higher intensity of musical activities following earlier starting age (see Gaser & Schlaug, 2003; Hutchinson, 2003). The integrity of the posterior CC showed experience-dependent increase in all age groups (young, middle-aged, and older adults). In addition, older adults showed positive effects of choir singing experience in the bilateral fornix, which was not observed in the other age groups. Neither negative effects on WM integrity nor associations with GM volume were found in relation to lifetime choir singing experience.

Second, results from Study III suggested that the duration of choir singing experience was positively associated with immediate and delayed episodic memory performance, together with age and education years, and with enhanced verbal fluency together with age. Enhancements in semantic verbal fluency mediated the effects in both episodic memory scores. In addition, questionnaire results from Study III suggested that the present frequency of choir singing was associated with reduced depressive symptoms as well as enhanced psychological and total QOL. Here, reduced depressive symptoms mediated effects in both domains of QOL.

5.2.1 Emotion and well-being

Musical expression, including singing, can trigger strong emotional responses, engaging cingulate and insular regions as well as the dopaminergic mesolimbic reward system (Koelsch et al., 2021; for reviews, see also Koelsch, 2014; Menon & Levitin, 2005; Pando-Naude et al., 2021). Qualitative evidence suggests that choir singing promotes psychological well-being with frequent participation (Coulton et al., 2015; Galinha et al., 2023; Skingley et al., 2016), the added social dimension potentially enhancing the influence on mood as compared to solo singing (Stewart & Lonsdale, 2016). Corroborating and extending these findings, the present results (Study III) suggested that the present frequency and not the duration of choir singing experience was associated with reduced depressive symptoms and higher scores on psychological and overall QOL, with depression mediating the effects with both QOL measures.

These effects concerned the full age range (21–88 years) with no significant contribution from the age covariate, suggesting that such effects, although previously studied in older adults primarily, can extend throughout adulthood. The overall predictive outcomes of choir singing frequency, especially with respect to QOL, remained modest, however, appearing even reduced in the full sample compared to the subsample of choir singers. This suggests that the present well-being effects (Study III), although well aligned with previous findings, are not highly unique but instead comparable to the various sources of well-being present in the general population, including other group activities such as team sports (Lonsdale & Day, 2021; Maury & Rickard, 2022).

Lifetime duration of choir singing, on the other hand, was associated with microstructural enhancements to the anterior medial parts of the cingulum (Study II). Here, the most proximal cingulate projection sites are involved in the processing of emotion, reward, and pain (Bubb et al., 2018; Kollenburg et al., 2024), including musical emotions (Koelsch, 2014; Koelsch et al., 2021; Pando-Naude et al., 2021) and, potentially, a modulatory influence on the analgesic effects of music (Antioch et al., 2020). Hypothesising on the anatomical proximity within the network, the present results tentatively suggest training-induced enhancements on the directly underlying associative pathways of the cingulum.

While it is important to bear in mind that the cingulum bundle, comprising major associative pathways between cortical and limbic regions, for instance, is involved in various functions from goal-directed behaviour to learning (Bubb et al., 2018; Kollenburg et al., 2024), the strong relationship of music with emotional processing argues for further investigations on how the microstructural integrity of the anterior medial cingulum may influence musical emotion and closely associated phenomena, such as musical memories. Further, the effects found along cingulum were coupled with enhanced QA in the extreme capsule (EmC), with selective effects in the uncinate fasciculus (UF) in young adults. Both EmC and UF microstructure (FA) have been associated with happiness and emotional reactivity in real-world settings (Kim et al., 2023), raising the question of whether musical experience would add sensitivity to musical emotions or emotional reactivity through enhanced structural connectivity in the underlying networks (e.g., Sharp et al., 2019) and, further, how training versus individual traits would contribute to such effects (see also Carraturo et al., 2022). Crucially, aberrations of UF microstructure are often found in mood disorders, such as depression (for a meta-analysis, see Xu et al., 2023). Building on the substantial reductions of UF FA after adolescence, some studies (e.g., Lebel et al., 2012) have suggested that UF microstructure might indeed play a role in early adulthood mental health. Within the framework of the present findings, this idea motivates future investigations on the mood-enhancing effects of choir singing in younger adults in particular.

5.2.2 Memory

Classical findings in music neuroscience suggest that sustained engagement in musical activities can reduce the risk of dementia (Arafa et al., 2022; Verghese et al., 2003) and improve episodic memory performance in normal ageing (Galinha et al., 2021; Hanna-Pladdy & MacKay, 2011; Mansens et al., 2018) as well as in early stages of dementia (Lyu et al., 2018; Särkämö et al., 2014). The present behavioural results (Study III) corroborate the well-established association between music and episodic memory, suggesting that longer durations of choir singing are associated with better episodic memory performance across adulthood.

Episodic memory performance typically echoes earlier performance in the long continuum of ageing (see Nyberg, 2017). In the clinical context, semantic verbal fluency can be used as an independent predictor of episodic memory performance and of progression from normal ageing to mild cognitive impairment (Folia et al., 2023; Gustavson et al., 2020) and to Alzheimer's type dementia (Benjamin et al., 2015; Folia et al., 2023). A recent singing intervention study (Lyu et al., 2018) also reported parallel enhancements in semantic fluency and episodic memory in mild Alzheimer's disease, albeit not testing for mediation effects. Consistent with these findings, the present results suggested a mediating effect for semantic fluency in singing-associated benefits on episodic memory. Based on a cross-sectional sample, the present data does not allow for direct investigations on whether this mediation effect stems from the same origin as the predictive association between semantic fluency and episodic memory described above.

Within the context of music studies, however, it should be noted that the well-established benefits of musical practice on episodic memory can be driven by more than one mechanism. For instance, emerging evidence suggests that positive effects on episodic memory can occur without parallel enhancements in semantic fluency in ageing instrumentalists (Hanna-Pladdy & MacKay, 2011; Strong, 2022). Instead, instrumental activities may enhance performance in phonemic fluency tasks without parallel benefits on episodic memory (Fauvel et al., 2014; Hanna-Pladdy & MacKay, 2011). Given the integral component of lexical-semantic processing in singing and its typical absence in instrumental practice, it seems possible that episodic memory benefits associated with singing (Fu et al., 2018; Galinha et al., 2021; Lyu et al., 2018) versus instrumental activities are linked to partially different mechanisms.

Furthermore, assuming that singing-associated benefits on episodic memory, observed in Study III, indeed stem from a joint effect linking to semantic fluency, it is possible to demarcate candidates for underlying mechanisms using their mutual substrates in the brain. While both functions are eminently complex by nature, they are both vulnerable to relatively early declines in normal ageing, as discussed above; this tentatively suggests that the shared neural mechanisms would show early declines too.

Parallel WM connectometry evidence from the same sample (Study II) showed singing-associated enhancements of QA across CC, with a more focal effect in the posterior parts in middle-aged and older adults, and selective effects in the fornices in older adults. CC forms the largest commissural pathways in the human brain, its microstructure correlating with general cognition (Coelho et al., 2021; Raghavan et al., 2020; see also Shafer et al., 2022). Its anterior parts are subject to faster degradation in normal ageing (Fan et al., 2019), while older populations with MCI and AD show accelerated degradation in its posterior parts, including posterior body, splenium, and forceps major (Qiu et al., 2016; Xiao et al., 2022; for a review, see also Teipel et al., 2016), with the disrupted functional connectivity potentially mediating episodic memory performance in these groups (Qiu et al., 2016). Like posterior CC, structural disintegration of the adjacent fornices—main pathways of the hippocampi—have been linked to memory decline (see R. Li et al., 2022; Senova et al., 2020) as well as semantic fluency (Biesbroek et al., 2021). The fornices typically mature and decline among the first WM tracts in the brain (Jang et al., 2011; Korbmacher et al., 2023; Lebel et al., 2012; Yap et al., 2013), which may explain why the observed singing-related QA enhancements were seen exclusively in older adults. Disruptions in fornix microstructure also typically precede those seen in posterior CC in AD and may already appear at the pre-clinical stage (Teipel et al., 2016).

While the present effects were associated with long-sustained practice, previous RCTs have reported microstructural enhancements (as shown by TOI-based FA) in the fornices already after six months of dancing (Burzynska et al., 2017) and instrumental training (Jünemann et al., 2022), the latter involving a positive association to episodic memory in healthy, musically naïve older adults. Considering that both dancing and instrument playing have also been associated with a reduced risk of dementia (Verghese et al., 2003) and improved cognitive and memory functioning in older persons with mild cognitive impairment (Doi et al., 2017), choir singing would seem another promising leisure activity to protect structures supporting memory function. As singing is currently underrepresented in neurocognitive research literature, however, with partially mixed evidence on its effects on episodic memory (Johnson et al., 2020; Lyu et al., 2018; Pentikäinen et al., 2021, 2023), well controlled longitudinal evidence comparing various musical activities is needed to test this idea. Further, the question of sufficient duration and frequency needs to be addressed, including whether anatomically pre-confined short-term effects would be strengthened with sustained practice.

To summarise, the positive association of lifetime choir singing duration with episodic memory and (semantic) verbal fluency as well as the structural integrity of posterior CC and the fornices, showing mutually associated declines in normal ageing, provides a testable framework for advancing our knowledge on the positive impact of musical practice on memory. While the direct association between cognitive function and structural connectivity effects were outside the scope of the present exploratory mapping study, it is recommended that future works aiming to establish such a connection would consider methodological choices of previous studies, including the duration and frequency of practicing, typical ageing patterns of the structures of interest (Korbmacher et al., 2023), as well as individual variability, including the contribution of unique lifetime factors (Chan et al., 2018). Further, cognitive processes underlying behavioural outcome measures should be considered. For instance, the use of semantic versus episodic strategies may differ between fluency tests (Cheke & Clayton, 2013), potentially influencing the scores with respect to episodic memory.

5.2.3 Speech

The functional networks underlying speech and singing overlap largely, with speech showing stronger left-hemisphere bias, as also shown in the present study sample (Study I). Further, previous evidence suggests beneficial transfer effects from music to language skills, including auditory-acoustic processing (Asaridou & McQueen, 2013; Kraus & Chandrasekaran, 2010), articulatory accuracy (Tremblay et al., 2023), and phonemic (Fauvel et al., 2014; Hanna-Pladdy & Gajewski, 2012; Pentikäinen et al., 2023) and semantic fluency (Fu et al., 2018; Lyu et al., 2018), and supporting speech production also in non-fluent aphasia (Schlaug et al., 2008). Corroborating previous findings, the present results suggested that, across the full age range (21–88 years), the duration of choir singing was positively associated with verbal fluency (Study III) along with enhanced QA in the left AF and bilateral IFOF (Study II), key pathways of the dorsal and ventral streams of the language network, respectively (Friederici & Gierhan, 2013; see also Conner et al., 2018).

According to the traditional view, transfer effects from singing to speech stem from the functional overlap of the two networks (Peretz et al., 2015), where the more extensive use of right hemisphere in singing compared to speech, also shown in the present data (Study I), can enable functional reorganization (Schlaug et al., 2010). Later examples from professional (Cheng et al., 2023; X. Li et al., 2021) and amateur musicians (Perron et al., 2021) and aphasic non-musicians (Sihvonen et al., 2024) have since challenged this view, suggesting that the transfer effects from singing to speech may have a more bilateral origin. Cheng et al. (2023) reported that singing can increase structural network density within the left hemisphere in professional singers but not instrumentalists, suggesting a more direct transfer effect from singing to speech. Similarly, a study with aphasic non-musicians (Sihvonen et al., 2024) showed that singing-induced enhancements in the microstructural integrity of the left AF (also shown in the present data, Study II; Andrews et al., 2021; Halwani et al., 2011; Perron et al., 2021), a key pathway supporting speech production through phonological processing and the mapping of sound to motor output (Shekari & Nozari, 2023), can support speech production in chronic aphasia.

In line with the bilateral account, the present results (Study II) also suggested singing-associated increases of QA in IFOF in both hemispheres. Branching along the ventral stream of the language-dominant hemisphere, the IFOF serves various lexical-semantic functions, including semantic verbal fluency (Houston et al., 2019; for a review on IFOF in speech and language, see Shekari & Nozari, 2023). While the present findings indeed suggest parallel enhancements in verbal fluency (Study III), previous evidence with respect to the function of right IFOF remains less consistent. Connecting several networks across the brain (Sarubbo et al., 2013), previous evidence suggests that right IFOF can contribute to various functions ranging from emotional processing to nonlinguistic semantics and mentalisation (H. Li et al., 2020; Matyi & Spielberg, 2023; Roux et al., 2021). Sihvonen et al. (2022) also reported that damage to right IFOF predicted both prosodic deficits and amusia in stroke patients, hypothesising that the resulting disruptions of information flow along the right ventral stream may lead to inefficient rhythmic-melodic integration. In their recent review, Shekari & Nozari (2023) also point out the need to consider the various IFOF functions with respect to control functions; enhancements in the bilateral IFOF have also been suggested to benefit language functions more broadly (Houston et al., 2019). This notion aligns well with evidence on the bilateral mechanisms of music-induced beneficial transfer effects on language functions.

To summarise, the present results corroborate previous evidence, suggesting significant associations between singing experience and speech in both behavioural (Study III) and structural network measures (Study II). While enhancements in right-hemisphere QA (Study II) provide indirect support for the traditional account that transfer effects from singing to speech, stemming from the more extensive engagement of the right hemisphere in singing compared to speech (also shown in Study I), enhancements of QA along the left dorsal and ventral streams (Study II) as well as verbal fluency (Study III) provide parallel evidence for left-lateralised mechanisms, suggesting that the overlap of singing and speech in the left hemisphere (Study I) could benefit speech processing at larger volumes of training.

Corroborating previous findings, the present results thus support bilateral rather than right-reliant mechanisms.

5.2.4 Vocal-motor production

Vocal production is a cognitively engaging, yet also highly specialised and complex motor activity involving precise control of posture and breathing as well as facial muscles, lips, tongue, soft palate, and pharynx. Study I showed remarkable overlap of speech and singing production, particularly in precentral and postcentral regions corresponding to the somatomotor representations of these areas. In Study II, choir singers showed extensive QA increases along the somatomotor control circuitry, including the corticospinal tracts, thus suggesting that sustained training of singing-associated motor control can also enhance structural connectivity of the somatomotor systems.

Evidence from chronic aphasics (Dresang et al., 2021) suggests the involvement of corticostriatal pathway and corticospinal tract in verb retrieval, rendering their importance for voluntary motor control in vocal production. Further, while conveying motor signals, the pathways are primed by emotional stimuli, such as facial expressions and music (Baumgartner et al., 2007; Borgomaneri et al., 2021; Haber, 2016; see also Pisner et al., 2017). Interestingly, similar neuroplastic effects on descending motor tracts have also been documented for instrumental musical practice (Engel et al., 2014; Imfeld et al., 2009; Rüber et al., 2015), i.e., outside the vocal production context. Considering the brains' strong sensory-motor (Vuust et al., 2022) and emotional-motor response integration in music (Putkinen et al., 2021; see also Matthews et al., 2020), it seems plausible that music could enhance the effects of sustained training in motor control, ultimately leading to an extensive influence on these pathways as suggested by the present data.

5.2.5 Effects of practice across the ageing continuum

Finally, it should be noted that the general effects on structural connectivity (Study II) were largely driven by the subgroup of young adults, suggesting that singing-associated structural specialisation was most pronounced in participants under 40 years of age. Given that the study used an age-adjusted score to allow for comparable results between the age-specific subgroups, this effect is more likely related to an earlier onset of training (Gaser & Schlaug, 2003) rather than age-dependent variability of the duration score (see also Table 1). For highly trained young participants, such early onset of sustained training would coincide with the highly plastic periods from childhood to early adulthood (Altenmüller & Furuya, 2016). Furthermore, while the present analyses considered the influence of other musical hobbies (i.e., solo singing and instrument playing), the possibility of enhancing of effects from the chronological overlap of multiple sources of exposure to music should not be discounted. One example is plain exposure to music; the neural networks supporting the perception of different types of music are likely to overlap, thereby potentially amplifying the plastic effects through increased overall frequency during these developmental periods (Altenmüller & Furuya, 2016; see also Hanna-Pladdy & Gajewski, 2012; Hanna-Pladdy & MacKay, 2011; Mansens et al., 2018).

With respect to the ageing continuum, however, it should be noted that this pattern of results suggests that the present whole-sample effects of choir singing may only have limited significance for structural compensation in ageing (Reuter-Lorenz & Park, 2014; for a review on contemporary models of ageing, see Oosterhuis et al., 2023). Instead, the more selective effects on CC and fornix, potentially delaying the functional and memory declines associated with their deterioration (see Qiu et al., 2016; Senova et al., 2020), suggest that choir singing may offer a form of beneficial enrichment by supporting the development of a healthy ageing trajectory within this context. This motivates future works to assess the effects of choir singing on the long-term changes in these structures as well as associated changes in functional connectivity and memory (see also Jünemann et al., 2022; Liebscher et al., 2024).

By contrast, the present GM data suggested no associations between amateur-level choir singing and GMV. While this pattern of results aligns well with the generally earlier peaks and declines of GMV compared to WM measures (Bethlehem et al., 2022), as well as that volumetric methods show lower sensitivity to the subtle variations in ageing effects (Giorgio et al., 2010), the present null results contradict previous ageing studies on music and GMV. Specifically, various forms of amateur-level musicianship (Chaddock-Heyman et al., 2021) as well as weekly exercise with music (Tabei et al., 2017) suggest music-associated benefits on GMV in the prefrontal regions (see also Espinosa et al., 2025), while evidence from professional musicians, singers included (Kleber et al., 2016), suggest training-induced plasticity also in the auditory cortices, for instance (for reviews on musical training and brain structure, see also Criscuolo et al., 2022; Herholz & Zatorre, 2012; Münte et al., 2002).

Within the context of structural compensation predicted in several prevailing models of ageing (see Oosterhuis et al., 2023, for a review), the contrast between the present null results and previous evidence on music-associated benefits on GMV suggest that amateur-level choir singing may be insufficient to produce changes in GMV in adulthood. Indeed, while the present frequency measures (current hours/week, lifetime max. hours/week) suggested no direct association between choir singing and brain structure, the present results do not rule out the possibility of a moderating effect from training frequency or level. Another potential cause for this discrepancy relates to methodological choices in the analysis of GM data, including variable control for factors shown to influence GMV results, such as education (Arenaza-Urquijo et al., 2013) and TIV (Barnes et al., 2010), as well as the application of a whole-brain versus anatomically confined (ROI-based) approach. With this these limitations considered, it is recommended that future studies assessing the influence of singing (or other types of musical activity) with respect to the level of practice (cf. Kleber et al., 2016) while considering the influence of normative ageing trajectories of the human brain along with confounding factors known to impact GMV.

5.3 Conclusion

This thesis aimed to (i) map the functional neural overlap and differences of speech and singing production and (ii) explore the effects of ageing on the neural underpinnings of speech and singing production, while varying the cognitive demands associated with the production task (Study I). Further, the thesis aimed to (iii) explore the associations of the duration and frequency of singing with local volumes of grey matter as well as white matter connectivity across adulthood (Study II), while (iv) determining the associations of training factors in singing with cognitive performance and subjective well-being across adulthood (Study III).

Focusing on the first two aims with task-based sparse-sampling fMRI, the results from Study I suggested an extensive overlap of activation across speech (Proverb) and singing (Song phrase) tasks involving the Repetition and Completion of familiar items as well as completion of new items by Improvisation, with minimal focal differences from the manipulation of task demands. Despite this overlap, speech tasks showed systematic age-associated reductions of activation in pre- and postcentral regions representing the mouth area, likely attributable to increasing challenges in processing somatosensory feedback control along the left-lateralised dorsal processing stream. Such an effect did not appear in singing, potentially due to lesser dependence of singing on the left dorsal stream, as suggested in previous works. By contrast, a single positive ageing effect, overlapping with regions subserving episodic retrieval and associated control processes, was found in Completion of song phrases from memory. Together, these effects corroborate and extend previous findings showing, for the first time, the differential ageing effects of speech and singing, and that cognitive task demands, previously implicated in ageing literature on speech, can also influence the ageing effects of singing.

With respect to the two latter aims focusing on the associations of choir singing, Studies II and III suggested large-scale enhancements of structural connectivity associated with the lifetime duration of choir singing, along with duration-associated enhancements in immediate and delayed episodic memory and verbal fluency, as well as reduced depressive symptoms and enhanced psychological and total QOL (full age range). Cohering with the behavioural results, microstructural enhancements (QA) were found across commissural and associative pathways, such as CC and the cingulum bundle (full age range) and fornices bilaterally (older adults), as well as AF and IFOF (full age range). For the first time, the evidence from Study III also showed that the positive associations between choir singing duration and episodic memory performance were mediated by performance in a semantic verbal fluency task, which aligns well with previous evidence suggesting a predictive effect of semantic verbal fluency on episodic memory. Corroborating previous findings, the positive association of choir singing frequency and psychological and total QOL was mediated by reduced depressive symptoms. Crucially, all effects on QOL were stronger within choir singers than within the full sample involving non-singers. This suggests that the well-established well-being effects of choir singing are non-unique but likely comparable to those elicited by other leisure activities in the non-singing population.

Although providing converging evidence on the overlap and differences of singing and speech and the beneficial associations of amateur level singing with brain structure, cognitive function, and socioemotional well-being, this dissertation is not without limitations. First, as a longitudinal design was not realistic given the targeted age range, a cross-sectional sample was recruited for convenience. Consequently, the present results do not establish causal evidence for these effects but provide guidance for designing future studies. Second, although Study III considered the potentially differential effects of choir singing experience within choir singers and when generalised across the full sample, the source of singing-associated effects in Studies II–III cannot be determined reliably, specifically, whether they are in fact a result of practice, of natural disposition to music, or a combination of these two.

Third, the sample size (N = 100) was limited, allowing balancing of key demographic features, but leading to lack of power when estimating age-specific effects within subgroups of different ages. Indeed, the present null results, observed across most of the age-specific analyses in Studies II–III, might be due to the small sample sizes and associated heterogeneity within these subgroups. Fourth, previous ageing studies on music addressing both neural and behavioural measures have remained scarce, and associations between these effects largely unknown. Although establishing parallel associations of choir singing duration with enhancements in structural connectivity and cognitive function, mutually associated in previous works, the present studies (II–III) do not establish direct associations. It is encouraged that future works aiming to establish such connections in ageing would consider functions of interest within the larger context of parallel and intertwined declines. For instance, fluent vocal production is largely dependent on age-sensitive cognitive functions, such as episodic memory.

These limitations considered, this thesis corroborates and extends previous evidence by replicating the classical overlap and differences of speech and singing production in a new task context, improvisation, and showing the joint influence of age and cognitive task demands on the neural substrates of vocal production outside the speech context. In addition, this work provides frameworks for mapping the joint influence of age and cognitive task demands in vocal production, as well as potential mechanisms by which sustained regular singing can benefit brain structure, cognitive function, and socioemotional well-being across adulthood and promote the development of a healthy ageing trajectory.

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