

Influence of age and perceptual training on cortical auditory processing

Zaida Escila Martínez Moreno

Integrated Program in Neuroscience
McGill University
Montréal, Québec, Canada



Supervised by: Étienne de Villers-Sidani, MD, FRCP(C)
and Sylvain Baillet, Ph.D.

August 2025

First published on January 11, 2026

A thesis submitted to McGill University in partial fulfillment of the
requirements of the degree of Doctor of Philosophy.

The problem of neurology is to understand man himself and to analyze the means by which man, the creator of science, has done what he has done.

— Wilder Penfield, as quoted in [Feindel \(1977\)](#)

When I first arrived at the Montreal Neurological Institute, I was greeted by a wall bearing a section of this quote. It captured the essence of what I hoped to pursue by coming to McGill University, and it has lived in my mind ever since. I hope this work contributes to our understanding of auditory perception, and in doing so, adds one more small piece in the vast and intricate puzzle of human experience.

Table of contents

List of Figures	v
List of Tables	vii
List of Abbreviations	x
Abstract	xiii
Résumé	xv
Resumen	xvii
Acknowledgements	xix
Funding Sources	xxv
Contribution to original knowledge	xxvi
Contribution of authors	xxvii
1 Introduction	1
1.1 Aging and cognitive decline: challenges and interventions	1
1.1.1 The interplay between hearing loss and cognitive decline	3
1.2 Understanding brain aging: methods and hypotheses	7
1.2.1 Functional neuroimaging techniques in human brain research	7
1.2.2 Cognitive aging: neural changes and theoretical models	12
1.3 Auditory perception in the aging brain	18
1.3.1 Auditory perception system	18
1.3.2 Electrophysiological responses to auditory stimuli	24
1.4 Auditory perceptual learning as an intervention against cognitive decline	37
1.4.1 Neurological impact of auditory perceptual training	38

1.4.2	Auditory perceptual training in an aging paradigm	39
2	Methodology	45
2.1	Participants	45
2.2	Audiometric evaluation	47
2.3	Auditory perceptual training task	51
2.4	Stimuli description and staircase procedure	51
2.5	Evaluation of task performance	54
2.6	Longitudinal training paradigm	54
2.7	Cognitive assessments	56
2.8	Magnetic Resonance Imaging	59
2.9	Magnetoencephalography	60
2.9.1	MEG acquisition and stimuli presentation	60
2.9.2	MEG pre-processing	61
2.9.3	MEG Source Mapping	61
2.9.4	ROI definition	63
2.9.5	Time-domain analysis	64
2.9.6	Time-frequency analysis	65
2.9.7	Connectivity	66
2.10	Statistical analysis	67
2.10.1	Regressions and correlations	68
2.10.2	Mediation	68
2.11	Visualization	69
3	Results	70
3.1	Age-related differences in performance and learning transfer of an auditory perceptual training task	71
3.1.1	Overview and rationale	71
3.1.2	Perceptual task performance improves with training	72
3.1.3	Experimental setting influences behavioral performance	73
3.1.4	Gains in performance generalize to untrained memory and inhibition tasks	73
3.1.5	Summary	77

3.2	Age-dependent activation of right auditory cortex during perceptual auditory training	78
3.2.1	Overview and rationale	78
3.2.2	Age-related amplitude differences of the M100 auditory response across training	79
3.2.3	Response to the cue is not affected by auditory training	83
3.2.4	Age-specific effects of auditory training on baseline activation . . .	83
3.2.5	Later auditory responses exhibit hemispheric lateralization but no training effects	85
3.2.6	Relationships between training-related auditory and behavioral measures	86
3.2.7	Summary	87
3.3	Dorsal attention network age-dependent modulation of auditory perceptual response	89
3.3.1	Overview and rationale	89
3.3.2	Training and aging shape pre-stimulus right dorsal attention network activity	91
3.3.3	Dorsal attention network fully mediates training-related changes in the auditory response of older adults	94
3.3.4	Widespread training-related increase of alpha power in younger adults, but not older adults	97
3.3.5	Training-related modulation of theta power differs across time windows and age groups	101
3.3.6	Training-related increase of pre-stimulus connectivity in older adults	104
3.3.7	Increased activation of bilateral ventral attention network with training in older adults not predictive of auditory response	105
3.3.8	Summary	107
3.4	Influence of individual differences on behavioral and neural plasticity . .	110
3.4.1	Overview and rationale	110
3.4.2	Hearing ability predicts individual variability in older adults but does not account for training-related effects	110
3.4.3	Summary	116
4	Discussion	118
4.1	Overview of the results and key findings	119

4.2	Learning gains and generalization of training across age groups	121
4.3	Auditory gains and attention engagement as neural signatures of learning in older adults	125
4.4	Increased alpha power and reduced neural responses: a signature of efficiency in younger adults?	130
4.5	Divergent neural pathways support learning across age	134
4.6	The role of hearing and other demographic factors in learning variability	136
4.7	Limitations	139
4.8	Implications and future directions	141
5	Conclusion	143
	Supplementary Materials	146
S.1	Statistical Tables	146
	References	201

List of Figures

Introduction

1.1	Population pyramid projections under low- and high-growth scenarios in Canada	2
1.2	Comparison of neuroimaging techniques by spatial and temporal resolution, and relative invasiveness	8
1.3	Dipoles in different orientations relative to the skull and their contributions to M/EEG signals	10
1.4	Modified version of the Scaffolding Theory of Aging and Cognition-revised (STAC-r)	17
1.5	Anatomy of the human auditory cortex	20
1.6	Parcellation of the human brain into seven functional networks	23
1.7	Comparison across evoked potentials at different latencies	26
1.8	Comparison of auditory evoked responses as measured by M/EEG in response to pure tones	28

Methodology

2.1	Audiometric thresholds averages across age groups with normal hearing reference	48
2.2	Structure of a single trial of the auditory task	52
2.3	Description of the stimulus and its staircase difficulty progression	53
2.4	Task performance evaluation measures	55
2.5	Study schedule	55
2.6	Description of the cognitive tests used to evaluate generalization to untrained tasks	56
2.7	Regions of interest	63
2.8	Time sections selected for the time-frequency analysis	66

Results

3.1	Performance improves across training days	72
3.2	Performances are affected by experimental settings	74

3.3	Learning transfer effects on RAVLT, SCWT and AFLT measures	75
3.4	Age-related differences in the M100 component of the right auditory event-related response	80
3.5	Auditory hemispheric differences in M100 amplitude during auditory training	81
3.6	Visual cortex does not exhibit the M100 changes observed in the auditory cortex	82
3.7	Changes in auditory activation during the Cue, Baseline, preM100 and Later Component periods	84
3.8	Age-related differences in right dorsal attention network activity during preM100 period	92
3.9	Training-related changes in preM100 laterality in dorsal attention network depend on age	93
3.10	Right preM100 dorsal attention network activity predicts right auditory M100 amplitude in older adults	95
3.11	Right DAN fully mediates training-related changes in right auditory cortex M100 response in older adults	96
3.12	Training-related changes in spectral power in the auditory cortex and dorsal attention network by response type and age group	98
3.13	Training-related changes in pre-stimulus alpha and theta power in the auditory cortex and DAN	100
3.14	Age- and training-related changes in alpha and theta during the post-stimulus period in auditory cortex and dorsal attention network . .	102
3.15	Training-related increase in DAN-auditory coherence in older adults . . .	104
3.16	Age-related differences in ventral attention network activity during preM100 period	106
3.17	Effect of hearing thresholds on task performance and post-stimulus alpha power in older adults	113
3.18	Effects of education and language proficiency in neural training-related changes	115

List of Tables

Introduction

- 1.1 Overview of literature on neural effects of auditory training in older adults 43

Methodology

- 2.1 Equivalence of education levels to years of education 46
- 2.2 Summarized demographic and audiometric data of trained participants
divided by age group 49
- 2.3 Score calculation and interpretation of RAVLT performance 58
- 2.4 *Brainstorm* “scouts” used to create each ROI 62
- 2.5 Overview of selected event-related fields components and their related
measures 65

Results

- 3.1 Demographic predictors and selected outcome measures with significant
training-related effects 111
- 3.2 Significant associations between demographic variables and
training-related outcome changes 112

Supplementary Materials

Age-related differences in performance and learning transfer of an auditory perceptual training task

- S.1 Statistical models of training task performance 146
- S.2 Statistical models of the effect of environmental setting on task
performance 147
- S.3 Statistical models of RAVLT performance 148
- S.4 Statistical models of Stroop task performance 150
- S.5 Statistical models of AFLT performance 151
- S.6 Correlation between cognitive measures and training performance . . . 152

Age-dependent activation of right auditory cortex during perceptual auditory training

S.7	Statistical models of auditory M100 peak amplitude	153
S.8	Statistical models of laterality and hemispheric differences in auditory M100 amplitude	155
S.9	Statistical models of auditory Cue peak amplitude	157
S.10	Statistical models of auditory baseline average amplitude	159
S.11	Statistical models of auditory preM100 average amplitude	161
S.12	Statistical models of auditory later component average amplitude	162
S.13	Regressions and correlations between auditory measures and behavior performance	164
<i>Dorsal attention network age-dependent modulation of auditory perceptual response</i>		
S.14	Statistical models of dorsal attention network average preM100 activity	166
S.15	Regressions between auditory M100 amplitude and preM100 DAN activity	168
S.16	Mediation analysis of training effects on auditory M100 amplitude via preM100 DAN activity in older adults	171
S.17	Statistical models of baseline alpha oscillations in auditory cortex and DAN	173
S.18	Statistical analysis of pre-stimulus alpha and theta power dynamics in auditory cortex and DAN	174
S.19	Statistical analysis of task-related post-stimulus alpha and theta oscillatory activity in auditory cortex and DAN	177
S.20	Statistical models of DAN-auditory coherence and its relationship to training-related changes	181
S.21	Statistical models of ventral attention network average preM100 activity and its relationship to auditory cortex and training	182
<i>Influence of individual differences on behavioral and neural plasticity</i>		
S.22	Demographic predictors of task performance	185
S.23	Demographic predictors of training-related changes in cognitive tests . .	187
S.24	Demographic predictors of training-related changes in auditory processing	188
S.25	Demographic predictors of training-related changes in the dorsal attention network	190
S.26	Demographic predictors of training-related changes in pre-stimulus oscillations	192
S.27	Demographic predictors of training-related changes in post-stimulus oscillatory activity	194

S.28 Demographic predictors of training-related changes in ventral attention network	199
--	-----

List of Abbreviations

μ	mean
A1, PAC	primary auditory cortex
AC	auditory cortex
ACC	anterior cingulate cortex
ACME	average causal mediation effect
ADE	average direct effect
AEP	auditory evoked potential
AFLT	Aggie Figure Learning Test
aFO	anterior frontal operculum
AI	anterior insula
AIC	Akaike information criterion
ARHL	age-related hearing loss
AWP	average weekly practice
BOLD	blood oxygen level dependent
CI	confidence interval
CRUNCH	compensation-related utilization of neural circuits hypothesis
DAN	dorsal attention network
dB	decibel
dBHL	decibel hearing level
dSPM	dynamic statistical parametric mapping
ECG	electrocardiography
EEG	electroencephalography
EOG	electrooculography
ERF	event related field
ERP	event related potential
Est.	statistical estimate

(Continued)

FDR	false discovery rate
FEF	frontal eye fields
FFT	fast Fourier transform
fMRI	functional magnetic resonance imaging
FP	false positive
GLM	general linear model
GM	gray matter
HAROLD	hemispheric asymmetry reduction in older adults
HG	Heschl's gyrus
Hz	Hertz
IFG	inferior frontal gyrus
IFJ	inferior frontal junction
IPS	intraparietal sulcus
ITI	inter-trial interval
LMM	linear mixed model
LPI	language proficiency index
M/EEG	magnetoencephalography/electroencephalography
Mdn	median
ME	musical education
MEG	magnetoencephalography
MFG	middle frontal gyrus
MI	musicality index
MRI	magnetic resonance imaging
MT+	middle temporal area
Prev	prevalence
PSD	power spectral density
PT	planum temporale
PTA	pure tone average
RAVLT	Rey Auditory Verbal Learning Test
ROI	region of interest
SCWT	Stroop Color and Word Test
SD	standard deviation

(Continued)

SMA	supplementary motor area
SMG	supramarginal gyrus
SNR	signal-to-noise ratio
SPL	superior parietal lobule
SSP	signal source projection
STG	superior temporal gyrus
VAN	ventral attention network
WH	withhold
WM	white matter

Abstract

As we age, our brains undergo biological changes that negatively affect cognitive processes such as selective attention and working memory. Perceptual learning, defined as the improvement in sensory discrimination through training, offers a promising avenue to mitigate these age-related declines by inducing behavioral and cognitive improvements in older adults. While prior studies have documented changes in neurological activity during perceptual training, how these changes dynamically evolve over the learning process, and how they differ between younger and older adults remains unclear. This thesis addresses this knowledge gap by investigating the age- and training-related effects of auditory perceptual learning. Across twelve days of training and four magnetoencephalography sessions, we examined longitudinal changes in behavioral performance and neural responses in sixteen participants divided into younger and older adults, focusing on cortical regions involved in auditory perception and attentional control.

Behavioral analyses revealed significant performance improvements in both age groups, with learning transfer to untrained tasks. Older adults showed gains in auditory attention and memory, while both groups improved in inhibitory control. Neurophysiological results highlighted different age-related patterns in the auditory cortex (AC) and in the dorsal (DAN) and ventral (VAN) attention networks. In younger adults, training was associated with reduced baseline activity in the left AC and increase alpha power in auditory and attention-related regions both before and after stimulus presentation. In contrast, older adults exhibited heightened right AC responses alongside a progressive increase in pre-stimulus activity within the right DAN and bilateral VAN. The dorsal preparatory attentional engagement, which was not observed

in younger adults or other brain regions, fully accounted for training-related increases in right AC responses in older adults. Additionally, functional connectivity between right AC and right DAN increased during the pre-stimulus period. These findings highlight the role of attentional modulation in supporting auditory processing in older adults, and underscore the distinct neural strategies employed by each group during the same adaptive auditory training.

In summary, this work provides new insights into the neural mechanisms underlying perceptual learning across the lifespan. Our results suggest that younger adults adapted by increasing processing efficiency and requiring fewer neural resources, while older adults relied on compensatory, hemisphere-specific strategies, particularly within the right DAN and AC. These findings emphasize the importance of tailoring training paradigms to age-specific neural dynamics and hold implications for designing interventions to address cognitive decline in aging populations.

Résumé

Avec l'âge, le cerveau subit des transformations biologiques qui peuvent nuire aux fonctions cognitives telles que l'attention sélective et la mémoire de travail. L'apprentissage perceptif, qui consiste à renforcer la discrimination sensorielle par l'entraînement, représente une stratégie prometteuse pour atténuer ces déclinis liés à l'âge, en induisant des bénéfices tant comportementaux que cognitifs chez les adultes plus âgés. Bien que des études antérieures aient documenté des modifications de l'activité neurologique au cours de l'apprentissage perceptif, leur évolution dynamique tout au long du processus d'apprentissage et leurs différences selon l'âge restent encore mal comprises. Cette thèse a pour objectif de pallier cette lacune en explorant les effets de l'apprentissage auditif en fonction de l'âge et de l'entraînement. Sur une période de douze jours d'entraînement, comprenant quatre séances de magnétoencéphalographie, nous avons étudié les changements longitudinaux de la performance comportementale et des réponses cérébrales de seize participants, répartis en deux groupes d'âge, en nous intéressant aux régions corticales impliquées dans la perception auditive et le contrôle attentionnel.

Les analyses comportementales ont montré des améliorations significatives des performances dans les deux groupes d'âge, ainsi qu'une généralisation de l'apprentissage à des tâches non entraînées. Les adultes plus âgés ont démontré des progrès en attention et mémoire auditives, tandis que les capacités de contrôle inhibiteur des deux groupes ont vu une amélioration significative. Les résultats neurophysiologiques ont révélé l'existence de dynamiques distinctes selon l'âge dans le cortex auditif, ainsi que dans les réseaux d'attention dorsal (RAD) et ventral. Chez les jeunes adultes, l'entraînement a été associé à une diminution de l'activité de base

dans le cortex auditif gauche et à une augmentation de la puissance alpha dans les régions auditives et attentionnelles, aussi bien avant qu'après la présentation du stimulus. En revanche, les adultes plus âgés ont présenté des réponses accrues du cortex auditif droit, accompagnées d'une élévation progressive de l'activité pré-stimulus dans le réseau d'attention dorsal droit et ventral bilatéral. L'engagement attentionnel préparatoire dorsal, absent chez les jeunes adultes et dans les autres régions cérébrales, explique entièrement l'intensification des réponses du cortex auditif droit chez les personnes âgées. En outre, la connectivité fonctionnelle entre le cortex auditif droit et le RAD droit a augmenté avant la présentation du stimulus. L'ensemble de ces résultats met en exergue le rôle de la modulation attentionnelle dans le soutien du traitement auditif chez les personnes âgées, et indique que chaque groupe recourt à des stratégies neurologiques distinctes pour s'adapter à un même entraînement auditif adaptatif.

En somme, ce travail propose un nouvel éclairage sur les mécanismes cérébraux qui sous-tendent l'apprentissage perceptif tout au long de la vie. Les résultats suggèrent que l'entraînement des jeunes adultes s'est traduite par une amélioration de l'efficacité du traitement et une réduction de la demande en ressources cérébrales, tandis que les adultes plus âgés ont recours à des stratégies compensatoires latéralisées, observées dans le RAD et le cortex auditif droits. Ces observations soulignent la nécessité d'adapter les protocoles d'entraînement à la dynamique cérébrale spécifique à chaque groupe d'âge, et ouvrent des perspectives pour la conception d'interventions visant à atténuer le déclin cognitif dans les populations vieillissantes.

Resumen

A medida que envejecemos, nuestro cerebro sufre cambios biológicos que afectan de forma negativa a funciones cognitivas como la atención selectiva y la memoria de trabajo. El aprendizaje perceptivo, definido como la mejora en la discriminación de estímulos sensoriales mediante la práctica sistemática de tareas específicas, representa una herramienta prometedora para contrarrestar estos déficits asociados con el envejecimiento, al favorecer mejoras cognitivas en las personas mayores. Aunque investigaciones previas han documentado cambios en la actividad neurológica durante este tipo de intervenciones, aún se desconoce cómo evoluciona a lo largo del proceso de aprendizaje y en qué medida difieren entre adultos jóvenes y mayores. Esta tesis tiene como objetivo estudiar el impacto de la edad sobre la plasticidad sensorial promovida por la práctica de una tarea auditiva. A lo largo de doce días de entrenamiento auditivo y cuatro sesiones de magnetoencefalografía, examinamos los cambios longitudinales en el rendimiento conductual y en la actividad cerebral de dieciséis participantes distribuidos en dos grupos según la edad, enfocándonos en las regiones corticales implicadas en la percepción auditiva y el control de la atención.

Los análisis conductuales mostraron mejoras significativas en el rendimiento de ambos grupos de edad, con evidencia de transferencia del aprendizaje a otras habilidades. Los adultos mayores mejoraron en atención y memoria auditivas, mientras que ambos grupos incrementaron su capacidad de control inhibitorio. Los resultados neurofisiológicos revelaron patrones diferenciados según la edad en la corteza auditiva y en las redes de atención dorsal y ventral. En los adultos jóvenes, el entrenamiento se asoció con una disminución de la actividad basal en la corteza auditiva izquierda, así como un aumento de la potencia de alfa en regiones auditivas y atencionales, tanto

antes como después de la presentación del estímulo. En cambio, los adultos mayores mostraron una mayor respuesta auditiva en el hemisferio derecho, acompañada de un incremento progresivo de la actividad previa al estímulo en las redes de atención dorsal derecha y ventral bilateral. El aumento en la actividad auditiva derecha observado tras el entrenamiento en este grupo fue completamente explicado por el reclutamiento anticipado de la red atencional dorsal, mientras que este efecto no se observó en adultos jóvenes ni en otras regiones corticales. Además, la conectividad funcional entre la corteza auditiva derecha y el sistema de atención dorsal derecho aumentó antes de la presentación del estímulo. Estos resultados destacan el papel clave de la modulación atencional en el procesamiento auditivo de adultos mayores y sugieren que cada grupo recurre a mecanismos neurológicos distintos frente a un mismo entrenamiento auditivo adaptativo.

En conjunto, esta investigación amplía nuestra comprensión de los procesos cerebrales implicados en el aprendizaje perceptivo a lo largo de la vida. Los resultados sugieren que los adultos jóvenes se adaptaron al entrenamiento mediante una mayor eficiencia en el procesamiento de la información auditiva y, por ende, una menor demanda de recursos cognitivos, mientras que los adultos mayores recurrieron a estrategias compensatorias lateralizadas, especialmente en la red atencional dorsal y la corteza auditiva del hemisferio derecho. Estos hallazgos recalcan la necesidad de adaptar los programas de entrenamiento a las particularidades cerebrales propias de cada etapa de la vida, y ofrecen una base valiosa para el diseño de intervenciones orientadas a mitigar el deterioro cognitivo en la vejez.

Acknowledgements

We live by each other and for each other.

Alone we can do so little.

Together we can do so much.

— Helen Keller, as quoted in [Brown \(1984\)](#)

This project was a long and arduous journey, and it would not have been possible without the support (academic or otherwise) of so many people. This is my attempt to acknowledge every one of you with a list that, while long, is by no means exhaustive. If I forgot to mention you, please forgive me, and know that I am truly grateful.

First and foremost, I would like to thank my supervisors, Étienne and Sylvain, for their support and guidance across the many stages of this project:

Étienne, thank you for trusting me with this project and for giving me complete freedom to develop, explore and apply my own ideas, even when it felt daunting. That level of independence helped me grow into the scientist that I am today. Your belief in me, especially during uncertain times, and the leaps of faith you took on my behalf pushed me to believe in myself too. Your support, empathy, understanding and encouragement really helped me when it mattered the most. Your continuous emphasis on the potential impact of my results on people's lives motivated me throughout this process. And, above all, your frequent but gentle reminders that perfection is not necessary in order to move forward have challenged and grounded me in equal measure—this thesis is, in many ways, the result of me finally taking that step.

Sylvain, thank you for your guidance, your steady support and openness at every stage of this project. Your thoughtful feedback, your readiness to always make time for meetings and respond without delay, and your willingness to adapt when I needed more structure helped me find my way forward at a time when continuing didn't feel possible. Your decision to connect me with Alex, whose guidance became fundamental in this project, and all the regular meetings that followed, were pivotal in helping me make real progress and take the reins of this project. Your calm and curious approach to science (including your beautifully written blog posts, *that one* presentation on your scientific journey, and your infectious enthusiasm for collaboration and open science) has been grounding, motivating, and truly inspiring.

To Alex Wiesman, there are truly no words to describe how much your guidance and encouragement over the last four years meant to me, or how deeply grateful I am. Your continuous support, enthusiasm for science (and cats), and above all, your candor about the struggles and joys of science (and life) helped me realize that difficulty is a natural part of the process, not a personal failing. When the path felt most uncertain, you reminded me what I was working toward and helped me keep the end goal in sight. Your clear explanations, helpful tutorials, and judgement-free answers, even to my most basic questions, eased the overwhelming pressure of learning so much, so quickly, in a field I was unfamiliar with. I am especially grateful for your encouragement to think beyond the PhD and use those future goals to shape my path, and for listening not just to the science, but to me as a person. That *Espresso Patronum* mug was a reminder that I was seen, and that mattered more than you probably know. I truly would not have finished this thesis without your support, thank you for everything.

To my supervisory committee, Robert Zatorre and Julien Doyon, thank you for your invaluable feedback and for the thoughtful discussions that felt less like evaluations and more like shared scientific exploration. In those moments, I began to feel not just like a student, but a fellow scientist, and that made all the difference. Special thanks to Robert for checking in during conferences, and for the rotation in your lab.

To my thesis examiners, Denise Klein and Mickael Deroche, for their constructive feedback and thoughtful questions that enriched this work and inspired new ideas.

To all the participants in this project: thank you for your time, patience, and generous contribution of brain data. This work would not have been possible without you.

To Elizabeth Bock, Marc Lalancette, Martin Cousineau and Raymundo Cassani, your invaluable technical support with the intricacies of MEG acquisition and analysis, troubleshooting in *Brainstorm*, and the challenges of MATLAB programming, made this research possible. Thank you not only for your help, but also for all the good moments we shared between MEG sessions and coding concerns.

To Josephine Nalbantoglu—since that first conversation we had in Mexico, thank you for seeing my potential from the start, for encouraging and supporting my path into the program, and for helping me navigate the many logistics that followed.

To Ed Ruthazer and Carl Ernst, for the opportunity to join the rotation program, through which I began to explore the world of neuroscience. Special thanks to Ed Ruthazer, who, as my mentor, offered guidance and support during difficult times.

To Philippe Albouy—our brief collaboration on that *small project* solidified my choice of human neuroscience. Your curiosity and optimism, even in the face of null results, showed me that every finding is a step forward and can lead to better questions and more interesting answers.

To all the members of the EVS and NeuroSpeed labs: Alex, Mike, Jason, Ellie, Jonathan Côté, Pat, Maryse, Conor, Veronica, Ana, Katie, Hannah, Niloofar, Jeremy, Jie, Jonathan G., Luc, Peter, Mathieu, Xiaobo, Olivia, Max, and all the other wonderful people I had the pleasure to work with. Thank you for the lunches we shared, the venting and brainstorming sessions, lab meetings, shared frustrations, and good ol' teamwork. We went through the pandemic and the helium shortage, and we survived! Special thanks to Mike, for supporting me since my arrival in Canada, and to Pat, for all the time we spent outside the MEG room.

To the social butterflies of my labs: Beth, Jason, Jeremy, Jonathan, Veronica, Ellie and Niloofar. Thank you for taking the lab's social life into your hands. From Friday dinners, ping pong games, movie nights, and that one DnD session and cake competition, to the yearly Secret Santa and *cabane à sucre*—you made my time here so much more enjoyable, helping me open up and let go of my shyness, even if just for those brief moments. A special thank you to Jason, for always being there, making sure I felt included; I hope to visit you soon in London. And to Ellie, for helping with packing: not a single thing broke; if all else fails, we could always be professional movers.

To Irwin, thank you for all your support over the years, for your kind words of encouragement, and for welcoming me as part of your family in a place that once felt unfamiliar. Your generosity, warmth and love for plants made a big difference.

To Serena, thank you for talking to me at *that* meeting, which *somehow* turned into a transcontinental friendship. You made my first year in Montreal so much less overwhelming, and the pandemic far less lonely. I will be forever grateful for your friendship and for all the times you have reminded me of the things I have overcome.

To Bizzy, thank you for showing me that online friendships can be just as meaningful, for deepening my love of DnD with your eccentric and hilarious characters (Dismas...), and for letting me be part of your wedding—it was such an honor to be there.

To Sergei, thank you for being there at the beginning and the end, for your help with moving, and for making it easier to navigate neurodivergence through your understanding, honesty and humour.

To Paty, Aya and Flor, thank you for adopting me into your lab family. I enjoyed those poutine dinners and holiday celebrations, and I will never forget the New Year's Eve when we participated in a gigantic snowball fight in downtown Montreal.

A todos mis amigos en Montreal: Rafa, Alice, Andrea, Alejandra, Aline y Jorge. Gracias por todas las memorias que hemos creado: cenas, piñatas, fiestas, juegos de mesa y clases de francés. Ustedes me ayudaron a sentirme en casa en este nuevo país.

A todos mis amigos en México, que me llenan de energía y amor cada vez que los veo: Migue, Dianita, Eugene, Andy, Joaco, Andreita, Pao, Gustavo, Marcos, Lalito, Aitana y tantos más... Gracias por recibirme siempre como si nunca me hubiera ido.

Ameyalli, soy muy afortunada de tenerte en mi vida y de compartir contigo esta experiencia maravillosa (y aterradora) de hacer un doctorado en el extranjero. Gracias por estar a mi lado en cada dificultad y cada celebración de este proceso.

Manu, ya van más de 15 años de amistad y, de ellos, casi 12 viviendo en diferentes ciudades, países y continentes, pero cada vez que nos vemos es como si el tiempo no hubiera pasado. Gracias por hacer que la distancia nunca se sienta tan grande y por estar siempre presente en los momentos importantes de mi vida.

To all my friends who have been touched by conflict, war, and senseless violence. I may never fully understand what you have gone through, and I do not know the right words to say, so I have almost always remained silent, but I think of you and wish every day for a world that is better, kinder, safer, more tolerant, just and peaceful, so that you and your families would never have to endure such pain.

To those no longer by my side, I know you would have shared this moment with me, and I wish I could have shared this with you. Abuelita, no pude estar contigo en el final; pero sé que estarías orgullosa de mí. Te agradezco por tus palabras y por tu ejemplo de cómo ser una mujer fuerte, independiente, resiliente y perseverante. Siempre estarás conmigo, en lo que soy, y en la huella que veo reflejado en mi mamá. Gracias.

To Whisky and "Noams", my sometimes diabolical cats, you don't know how to read, but you deserve this space nonetheless. You have been my companions through all those days (mainly nights) at my desk, distracting me or supporting me, helping me to take breaks and keeping me company. Thank you, you little things.

Josué, hermanito, gracias por acompañarme toda la vida. Aunque la distancia crezca y se acorte cada lustro, sé que en el momento en el que nos juntemos, no importará el paso del tiempo, será como siempre y bailaremos como pingüinos.

Papá y mamá, gracias por todo su apoyo incondicional. Esas llamadas largas siempre me llenaron el corazón y me dieron fuerzas para llegar hasta aquí. Papito, aunque las palabras a veces sean escasas, tu mano en el corazón siempre me llenó de alegría. Mamita, tu comprensión y tu presencia, incluso en la distancia, han sido mis cimientos. Gracias por su amor, por sus enseñanzas y por siempre creer en mí.

Jorge, no hay palabras para agradecerte ni para describir todos los momentos que hemos vivido juntos. Pero si aun así lo intento, gracias por los viajes, las fotos, las memorias, los rompecabezas, los nuevos comienzos, las series juntos, One Piece, las enseñanzas y tu increíble paciencia. Este logro es tanto tuyo como mío, y no podría haberlo hecho sin tu apoyo, tu amor, tus abrazos, tu cocina (¡las pizzas!), tu inquebrantable fé en mí y todos esos momentos en los que me has motivado, consolado y distraído para que pudiera seguir. Tu “¡No te rindas!” lleva motivándome por más de 4 años, ya es casi un mantra. Así que te agradezco desde el alma por todo lo que me has dado. Te amo hasta el infinito y más allá. Gracias por todo.

I also want to acknowledge the effort behind this journey: the many hours spent in front of the computer, the moments of doubt and exhaustion, the immense resilience and perseverance it took to keep going. There were tears, setbacks, and internal struggles, but also joy and so much learning. To myself: be proud, ¡lo lograste ♡!

And thanks to you, dear reader, for taking the time to read this thesis (or at least this part of it). I hope you find it useful, inspiring, or at least entertaining. If you have any questions, comments or requests, feel free to reach out to me at zaida.mtz93@gmail.com or zaida.martinezmoreno@mail.mcgill.ca

*Au milieu de l'hiver, j'ai découvert en
moi un invincible été.*

— Albert Camus, «Retour à Tipasa», *L'Été* (1953)

Funding Sources

This work was supported by the following funding sources:

- 2017–2018** Mitacs Globalink Graduate Fellowship Award (Intern ID GLF364), awarded to Zaida Escila Martínez Moreno.
- 2017–2021** McGill University, Integrated Program in Neuroscience Rotation program Graduate Excellence Award in Neurology and Neurosurgery (no. M159875C51), awarded to Zaida Escila Martínez Moreno.
- 2018–2022** Consejo Nacional de Ciencia y Tecnología (CONACYT) PhD scholarship (Reference no. 2018-000009-01EXTF-00082), awarded to Zaida Escila Martínez Moreno.
- 2018–2022** Natural Sciences and Engineering Research Council of Canada (NSERC, No. I238911C0G), awarded to Etienne de Villers-Sidani.
- 2021–2023** Fonds de recherche du Québec – Nature et technologies (FRQNT) Doctoral research scholarship (Aplication no. 307777, DOI: [10.69777/307777](https://doi.org/10.69777/307777)), awarded to Zaida Escila Martínez Moreno.
- 2022–2025** Canadian Institutes of Health Research (CIHR, No. I256267C0G), awarded to Etienne de Villers-Sidani.
- 2025** McGill University (No. M120473C0G), awarded to Etienne de Villers-Sidani.

Contribution to original knowledge

The present thesis makes original contributions to the field of auditory neuroscience and aging. Through behavioral, cognitive, and neurophysiological measures, this work demonstrates that younger and older adults benefit from auditory perceptual training via distinctive neural mechanisms. While both groups improved on the trained task and generalized gains to untrained cognitive functions, including inhibitory control and memory, the associated brain activity patterns diverged. Training in younger adults was linked to increased alpha power and reduced baseline activation in auditory and attentional regions, consistent with greater neural efficiency. In contrast, older adults showed heightened right auditory responses and increased preparatory activity in the right dorsal attention network, which fully mediated the observed auditory changes. These results suggest that aging alters the neurophysiological pathways that support learning, shifting from efficient internal modulation to reliance on compensatory attentional engagement.

To the best of our knowledge, this thesis presents the first longitudinal study to compare both behavioral and neural changes induced by auditory perceptual training in younger and older adults using magnetoencephalography. By characterizing time-resolved changes in both event-related and spectral activity within auditory and attentional networks, this work advances the current understanding of how perceptual learning unfolds across the lifespan. The evidence presented here reinforces the need to better understand how auditory training shapes neural function differently across age groups, and how such insights can inform age-appropriate interventions aimed at supporting perceptual and cognitive health.

Contribution of authors

This doctoral thesis reflects work conducted under my primary responsibility, with the assistance of collaborators whose specific contributions are detailed below. The roles are described using the Contributor Roles Taxonomy (CRediT; Allen *et al.*, 2014; Brand *et al.*, 2015) and visualized using the LaTeX template provided by Rieck and Born (v709a62b; 2023). My contributions span all chapters and include conceptualization, data curation, formal analysis, investigation, methodology, project administration, software, validation, visualization, and writing.

	Conceptualization	Data curation	Formal analysis	Funding acquisition	Investigation	Methodology	Project administration	Resources	Software	Supervision	Validation	Visualization	Writing – original draft	Writing – review & editing
Zaida Escila Martínez Moreno														
Alex I. Wiesman														
Jonathan Côté														
Lucy Karp														
Erica Woodruff														
Patrice Voss														
Sylvain Baillet														
Etienne de Villers-Sidani														

For more information on the CRediT taxonomy, refer to the CRediT website (<https://credit.niso.org/>). The definitions of the contributor roles are summarized in Table 1 in the original publication by Brand *et al.* (2015).

Every one knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought.

— William James, *The Principles of Psychology* (1890)

No one knows what attention is.

— Hommel *et al.* (2019)



Introduction

1.1 Aging and cognitive decline: challenges and interventions

The world is experiencing a major demographic shift, with a growing number of older adults and increasing health challenges associated with aging. In 2022, 10% of the global population was aged 65 and over, and this proportion is predicted to increase to almost 16% by 2050 (UN, 2022). This trend is even more pronounced in Canada, where 19% of the population is currently over 65 (Statistics Canada, 2024), and this figure is expected to reach up to 32% by 2074 (Figure 1.1; Statistics Canada, 2025). While advancements in medicine have contributed to longer lifespans, improvements in healthy life expectancy (i.e., number of years lived in good health) have not kept the same pace (Kyu *et al.*, 2018). As a result, preserving cognitive and functional abilities in older adults has become a critical public health priority.

Dementia is one of the most pressing health concerns associated with an aging population, given its increasing global prevalence and substantial economic burden

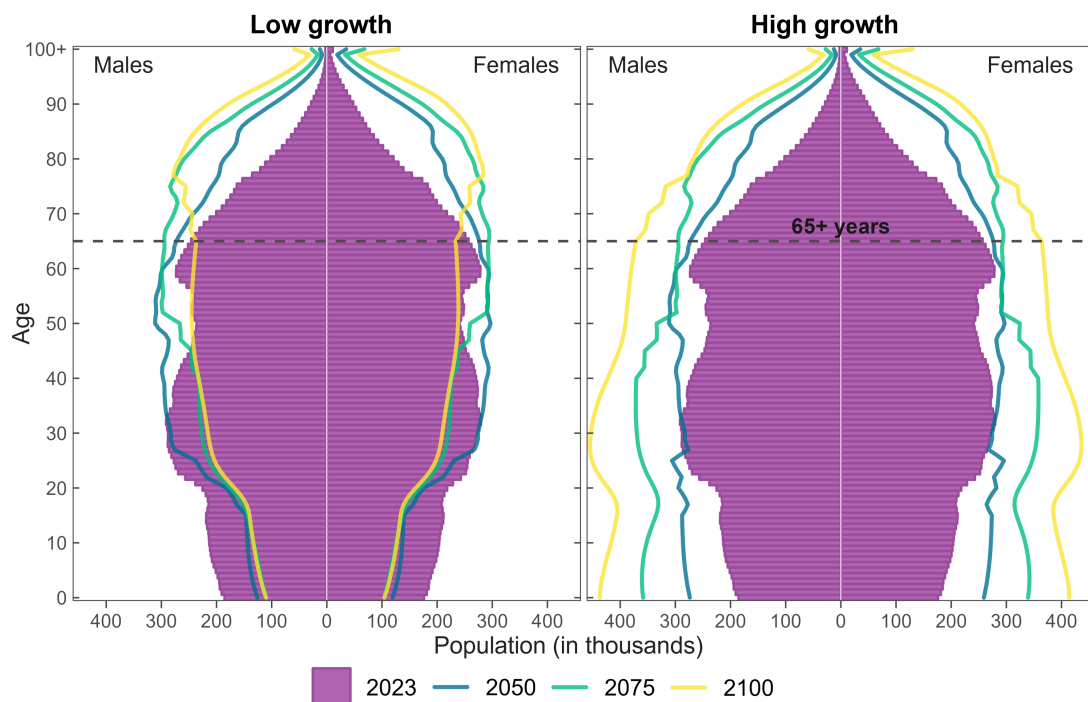


Figure 1.1: Population pyramid projections under low- and high-growth scenarios in Canada. Bars represent Canadian population estimates by single year of age for 2023, while lines show projections under low- (left) and high-growth (right) scenarios for 2050 (blue), 2075 (green), and 2100 (yellow). Each pyramid separates the population by sex (males: left; females: right). Growth scenarios are based on low- and high-fertility variants from UN projections (2024a; 2024b).

(WHO, 2012). In Canada, an estimated 7.1% of adults aged 65 and older live with dementia, following a 20% increase in prevalence between 2003 and 2013 (PHAC, 2017). Nevertheless, mounting evidence suggests that dementia is not an inevitable consequence of aging and that it may be delayed or prevented through targeted interventions (Qiu and Fratiglioni, 2018). Among the modifiable risk factors identified, hearing loss stands out as one of the most consistently associated with dementia, with estimates suggesting it may contribute to around 7% of cases (Livingston *et al.*, 2024, 2020, 2017). Consequently, the relationship between hearing loss and cognitive decline has emerged as a key area of investigation, given its potential as a modifiable target for the prevention of dementias.

1.1.1 The interplay between hearing loss and cognitive decline

Sensory impairments, indicative of a decline in the quality of sensory inputs, increase significantly with age (Dillon *et al.*, 2010; Paraskevoudi *et al.*, 2018; Schubert *et al.*, 2017), with hearing loss being among the most prevalent and underrecognized conditions in older adults (Mick *et al.*, 2021). Age-related hearing loss (ARHL), also known as presbycusis, is characterized as a bilaterally symmetric sensorineural hearing impairment, resulting from damage to the inner ear or auditory nerve (CAA, 2017; Cheslock and Jesus, 2023; Pearlman, 1982). Its severity is typically determined using pure tone averages (PTA), which are a measure of hearing thresholds across key frequencies expressed in decibels hearing level (dBHL), with normal hearing defined as below 25 dBHL, mild hearing loss as 26–40 dBHL, moderate as 41–60 dBHL, and severe as greater than 60 dBHL (Mick *et al.*, 2021; Olusanya *et al.*, 2019; WHO, 1991). In Canada, 54% of adults aged 40 to 79 exhibit mild hearing loss; however, 77% are unaware of their condition (Ramage-Morin *et al.*, 2019). Furthermore, its prevalence increases with age, with more severe forms affecting nearly one-third of adults aged 71 and older (Reed *et al.*, 2023). Beyond the challenges associated with communication, ARHL has been associated with lower quality of life and increased risks of cognitive decline and dementia (Brenowitz *et al.*, 2019; Brewster *et al.*, 2021; Fischer *et al.*, 2016; Maruta *et al.*, 2020; Slade *et al.*, 2020; Uchida *et al.*, 2019). These findings suggest a close relationship between age-related declines in auditory and cognitive processing (Peelle and Wingfield, 2016), emphasizing the need to understand the neurobiological effects of aging on both hearing and cognition.

Several hypotheses have been postulated to explain the observed association between hearing loss and cognitive decline. The *common cause hypothesis* proposes that both sensory and cognitive declines are manifestations of a shared underlying factor, such as widespread neural degeneration, microcirculatory insufficiency, general physical health, genetics, and oxidative stress among others (Roberts and Allen, 2016; Slade *et al.*, 2020; Uchida *et al.*, 2019; Wayne and Johnsrude, 2015). Alternatively,

the *cognitive load on perception hypothesis* reverses the typical direction of causality, proposing that cognitive decline may cause hearing loss by limiting the mental resources available for auditory perception, although empirical support for this view is limited (Roberts and Allen, 2016; Wayne and Johnsrude, 2015). Furthermore, the *overdiagnosis or harbinger hypothesis* raises a methodological concern, suggesting that hearing impairment may compromise performance on cognitive assessments involving verbal materials, leading to an apparent cognitive decline that actually stems from reduced auditory acuity (Uchida *et al.*, 2019). However, these explanations describe indirect pathways connecting hearing loss to cognitive decline, and may account for only part of the association, particularly in light of the many contributing factors identified in the development of dementia (Livingston *et al.*, 2024).

Conversely, other hypotheses suggest a direct causal pathway from hearing loss to cognitive decline. The *perceptual hypothesis*, which encompasses both the *information degradation* and *sensory deprivation* hypotheses, postulates that degraded auditory input increases reliance on cognitive resources such as memory and attention to support perception (Roberts and Allen, 2016; Slade *et al.*, 2020; Wayne and Johnsrude, 2015). This chronic reallocation of mental effort, described in the Framework for Understanding Effortful Listening (FUEL) and supported by the *information degradation hypothesis*, may interfere with processes like encoding and memory consolidation, and over time, contribute to measurable declines in cognitive performance (Pichora-Fuller *et al.*, 2016; Wayne and Johnsrude, 2015). The *sensory deprivation perspective* further emphasizes how long-term auditory deprivation and resources relocation can lead to structural and functional changes in the auditory cortex, including cortical atrophy and reorganization (Slade *et al.*, 2020; Wayne and Johnsrude, 2015). The *cascade hypothesis* builds on this idea, proposing that peripheral hearing loss initiates a sequence of changes, beginning with altered auditory processing and extending to reduced social interaction, loneliness, and depression—all of which may accelerate cognitive decline (Uchida *et al.*, 2019). Collectively, these perspectives imply that early intervention to preserve or improve auditory perception may offer a protective effect against later

cognitive decline.

Adult aural rehabilitation refers to a comprehensive approach aimed at reducing the functional, social, and quality-of-life impacts of hearing loss through a combination of sensory management, education, perceptual training, and counseling (Boothroyd, 2007; Ferguson *et al.*, 2019). Within this framework, the predominant strategy to address presbycusis is the use of hearing aids (Gates and Mills, 2005; NIDCD, 2023), which enhance the quality of auditory input and can partially compensate for peripheral deficits. Their use has been associated with a range of cognitive and psychosocial benefits in individuals with ARHL, including stabilization of cognitive decline, reductions in depression and anxiety, and improvements in speech perception, memory, executive function, attention, and quality of life (Amieva *et al.*, 2015; Castiglione *et al.*, 2016; Glick and Sharma, 2020; Maharani *et al.*, 2018; Manrique-Huarte *et al.*, 2016; Nkyekyer *et al.*, 2019; Sarant *et al.*, 2020). Despite these benefits and the high prevalence of hearing loss, the use of hearing aids remains low: only 18% of adults with mild to severe impairment (PTA > 25 dBHL) and 29% of those over 70 report using hearing devices (Mick *et al.*, 2021; Reed *et al.*, 2023). This limited uptake may reflect a range of factors, including stigma, discomfort, high cost, lack of awareness, and limited insurance coverage (BCBS FEP, 2024, 2025; Jenstad and Moon, 2011; McKee *et al.*, 2019). Given the limitations on the use of hearing devices, it is imperative to investigate complementary or alternative strategies to promote auditory and cognitive health in older adults.

Perceptual learning has emerged as a promising approach to mitigate the effects of age-related hearing loss through targeted auditory training (Boothroyd, 2007; Ferguson *et al.*, 2019; Livingston *et al.*, 2017; Stropahl *et al.*, 2020). It is defined as a long-term change in stimulus perception resulting from repeated experience or practice with that stimulus (Irvine, 2018). Such changes are typically reflected as improved perceptual discrimination and may involve modifications in subjective experience, task performance, neural processing, and cognitive or motor responses (Prettyman, 2019).

As a form of perceptual learning, auditory training offers a non-invasive and accessible strategy to potentially support auditory and cognitive functioning in older adults (Stropahl *et al.*, 2020). Indeed, evidence suggests that auditory perceptual training can lead to functional benefits across a range of auditory and cognitive domains in older adults, including those with and without hearing loss (Fostick *et al.*, 2020; Heidari *et al.*, 2020; Mishra *et al.*, 2014; Nkyekyer *et al.*, 2019; O'Brien *et al.*, 2017), and that extended training may even enable older adults to match the performance of younger individuals on cognitive tasks (Das and Steyvers, 2023). Findings from both human and animal studies further indicate that such training may help counteract age-related changes in auditory structure and function (Cheng *et al.*, 2017; de Villers-Sidani *et al.*, 2010; Voss *et al.*, 2016; Zatorre *et al.*, 2012), and may also promote broader improvements in attention and cognitive control through learning transfer (Adcock *et al.*, 2009; Fisher *et al.*, 2009; Tremblay, 2007; Vinogradov *et al.*, 2012). Consequently, auditory perceptual training has emerged as a compelling intervention for promoting healthy cognitive aging and potentially reducing the risk of cognitive decline by targeting both sensory deficits and their cognitive consequences (Holman and de Villers-Sidani, 2014).

1.2 Understanding brain aging: methods and hypotheses

Behavioral and cognitive studies have long established that aging is associated with declines in processing speed, working memory, executive function, inhibition, and attentional control (Daigneault *et al.*, 1992; Harada *et al.*, 2013; Murman, 2015; Park and Reuter-Lorenz, 2009; Wecker *et al.*, 2000). While these findings have shaped our understanding of cognitive aging, behavioral measures alone provide a limited view of the underlying neural mechanisms. Since the early 2000s, advances in neuroimaging techniques have enabled researchers to examine brain activity during task performance (Bigler, 2017; Hall *et al.*, 2014; Roalf and Gur, 2017). These tools have significantly deepened our understanding of how the aging brain supports cognition and have revealed complex functional differences between younger and older adults that are not always evident at the behavioral level (Holman and de Villers-Sidani, 2014; Murman, 2015; Reuter-Lorenz, 2002). The following subsections outline the principles and applications of these techniques in cognitive aging research, as well as the main structural and functional brain changes observed in aging and the theoretical models proposed to explain them.

1.2.1 Functional neuroimaging techniques in human brain research

A wide range of neuroimaging techniques are currently used to assess brain activity, each differing in spatial and temporal resolution, their physiological basis and the types of neural processes they best capture (Figure 1.2; Bandettini, 2009; Minati, 2006). Among these, only functional magnetic resonance imaging (fMRI), functional near-infrared spectroscopy (fNIRS), electroencephalography (EEG) and magnetoencephalography (MEG) offer the temporal precision necessary to examine changes in brain activity during task performance, while avoiding the invasiveness of intracranial recordings (Baillet, 2017; Yang and Wang, 2025). Understanding the

strengths and limitations of each technique is essential for interpreting findings and selecting appropriate methods for investigating specific research questions.

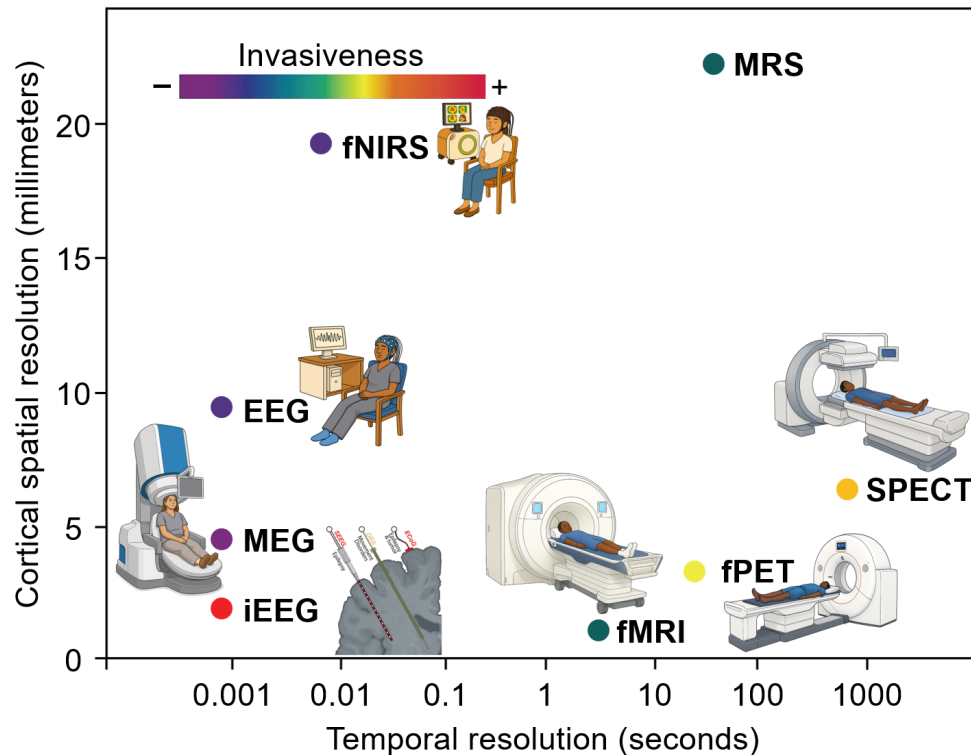


Figure 1.2: Comparison of neuroimaging techniques by spatial and temporal resolution, and relative invasiveness. Color bar indicates relative invasiveness. General layout adapted from Zamrini *et al.* (2011). Techniques: magnetoencephalography (MEG)^{a,h}, electroencephalography (EEG)^{a,b}, intracranial electroencephalography (iEEG)^c, magnetic resonance spectroscopy (MRS)^d, functional magnetic resonance imaging (fMRI)^{a,h}, single-photon emission computerized tomography (SPECT)^{e,h}, functional positron emission tomography (PET)^{f,h}, and functional near-infrared spectroscopy (fNIRS)^{g,h}. **Sources:** Resolution: ^a(Hall *et al.*, 2014; Savoy, 2001; Singh, 2014), ^c(Mercier *et al.*, 2022), ^d(Stanley and Raz, 2018), ^e(Cheng *et al.*, 2025; Pellico *et al.*, 2021), ^f(Hahn *et al.*, 2023; Werner *et al.*, 2015), ^h(Yang and Wang, 2025). Adapted images: ^b(Nagel and Spüler, 2019), ^c(Mercier *et al.*, 2022), ^h(OpenAI, 2025).

Functional magnetic resonance imaging

Functional magnetic resonance imaging (fMRI) has played a central role in advancing neuroscience by uncovering patterns of brain activity that reflect how different regions are involved in perception, cognition, and behavior (Roalf and Gur, 2017). MRI was first commercialized in 1980, with systematic studies linking its findings to neuropsychological outcomes emerging by 1988, and the first human fMRI studies conducted in 1992 (Bandettini *et al.*, 1992; Bigler, 2017; Minati, 2006; Wilson *et al.*,

1988). Since then, fMRI has rapidly evolved into a robust, noninvasive tool that has contributed to a methodological and conceptual shift in neuroscience by facilitating the dynamic mapping of neural activity and revealing the brain's functional organization with unprecedented detail (Bandettini, 2012; Chen and Glover, 2015).

In order to accurately interpret fMRI research, it is important to understand that this technique does not directly measure neural activity, but instead captures changes in blood flow and oxygenation that occur as a consequence of neuronal activation (Minati, 2006). When neurons become active, their metabolic demand for oxygen and glucose increases, prompting a rise in local arterial blood flow to meet these needs (Roalf and Gur, 2017). This results in a higher concentration of oxygenated hemoglobin relative to deoxygenated hemoglobin, which differ in their magnetic properties, and generate measurable changes in the magnetic resonance signal that can be detected over time (Hall *et al.*, 2014). The resulting blood oxygenation level-dependent (BOLD) response is closely associated with the spatial location of neuronal activity, providing high spatial resolution in the order of millimeters. However, because the physiological response underlying the BOLD signal unfolds over several seconds, the temporal resolution of the fMRI remains limited (Hall *et al.*, 2014; Roalf and Gur, 2017). This poses a particular challenge for studying auditory processing, as many neural responses in the auditory system occur on the order of milliseconds (Coffey *et al.*, 2016; Shahin *et al.*, 2007), far faster than what fMRI can reliably resolve. Furthermore, the acoustic noise produced by MRI scanners during image acquisition interferes with stimulus presentation and perception, preventing continuous data acquisition in auditory paradigms (Brummett *et al.*, 1988).

Electrophysiology: electroencephalography and magnetoencephalography

To overcome the temporal and acoustic limitations of fMRI, electrophysiological techniques such as electroencephalography (EEG) and magnetoencephalography (MEG) are used to investigate the timing of neural responses with millisecond precision (Savoy, 2001). The first study of electric fields generated by the brain was conducted

by Pravdich-Neminsky in 1913, laying the foundation for EEG (Minati, 2006). Several decades later, David Cohen (1968) successfully measured the magnetic fields produced by intracranial currents using a Superconducting-Quantum-Interference-Device (SQUID), establishing the basis for MEG.

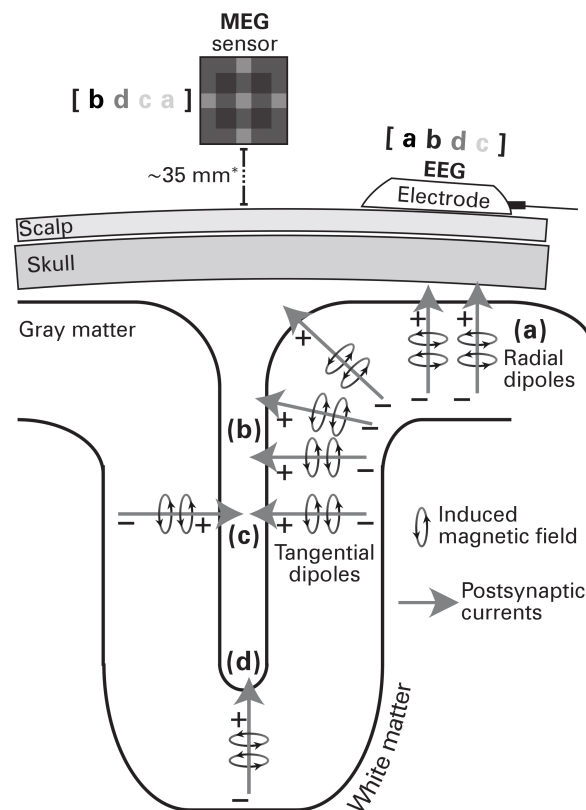


Figure 1.3: Dipoles in different orientations relative to the skull and their contributions to M/EEG signals. The main sources of measurable electric and magnetic signals are the postsynaptic currents generated by layers of pyramidal neurons in the cortex. EEG can detect dipoles in all orientations but is especially sensitive to radial sources (a). MEG is largely insensitive to radial signals but is highly sensitive to tangential sources (b). Dipoles on opposite walls of a sulcus (c) tend to generate opposing fields that can partially cancel, making them less likely to be detected. Dipoles located deeper within the cortex (d) contribute less to the overall signal due to their distance from the sensors. Modified from Cohen (2014) with permission from The MIT Press. *Source: Tanaka *et al.* (2025); Matsubara *et al.* (2022).

© 2017 Massachusetts Institute of Technology. All rights reserved.

Both techniques detect neural dynamics generated by coordinated activity across populations of cortical neurons, from localized clusters spanning a few millimeters to large-scale brain regions (Cohen, 2014). The main sources of electric signals measured by EEG and their resultant magnetic fields detected by MEG are postsynaptic currents

generated by layers of pyramidal neurons located in the cerebral cortex (Figure 1.3; Buzsáki *et al.*, 2012; Murakami and Okada, 2006). In particular, EEG can detect activity from neurons with different orientations relative to the scalp, but it is especially sensitive to those located at the top of cortical folds (gyri), where neurons are oriented perpendicular (radial) to the scalp surface (Tivadar and Murray, 2019). In contrast, MEG is most sensitive to activity from neurons located in the walls of cortical folds (sulci), where the orientation is parallel (tangential) to the scalp, and has low sensitivity to radial activity (Ahlfors *et al.*, 2010; Baillet, 2017; Singh, 2014). Although both techniques capture fundamentally similar neural signals (Buzsáki *et al.*, 2012), these differences in source sensitivity can lead to changes in the properties and detectability of specific brain responses (see Section 1.3.2; Shahin *et al.*, 2007; Srinivasan *et al.*, 2006).

Both EEG and MEG detect neural activity generated in the cortex, but identifying the precise location of these signals within the brain relies on source localization techniques. Because both methods rely on extracranial recordings, spatial information must be inferred by mathematically projecting the measured signals back onto the brain (Hall *et al.*, 2014; Minati, 2006). This inverse modeling process is inherently ill-posed, as multiple source configurations can produce the same sensor data, thereby requiring assumptions to constrain the solution and ultimately limiting the spatial precision of both techniques (Baillet, 2010; Baillet *et al.*, 2001; Barnes *et al.*, 2006). MEG, however, holds a key advantage over EEG in this regard, as magnetic fields are less affected by the differences in conductivity of the cerebrospinal fluid, skull and scalp, allowing for potentially more accurate forward models (Hall *et al.*, 2014; Lopes da Silva, 2013). Furthermore, MEG systems typically include a larger number of sensors positioned around the head, yielding higher signal-to-noise ratios and greater sensitivity (Cohen, 2014). While EEG and MEG may achieve comparable spatial resolutions under similar sensor configurations (Baillet, 2017; Hedrich *et al.*, 2017; Klamer *et al.*, 2015), preparing high-density EEG setups (e.g., with over 150 electrodes) is considerably more time-consuming than standard MEG procedures, significantly extending the duration of each recording session (Criscuolo and Brattico, 2023).

1.2.2 Cognitive aging: neural changes and theoretical models

Neuroimaging studies of the aging brain have revealed consistent patterns of anatomical and functional changes that include widespread reductions in gray matter volume and decreased integrity of white matter tracts (Murman, 2015). These structural declines are most pronounced in the prefrontal cortex and medial temporal lobe structures, such as the hippocampus and amygdala, and have been linked to poorer memory performance and executive control (Harada *et al.*, 2013; Hedden and Gabrieli, 2004). In parallel, functional imaging has shown both increased and decreased activation across brain regions, reflecting processes of neural redistribution or reorganization that may support compensatory mechanisms in older adults (Brehmer *et al.*, 2014). Among these functional alterations, declines in prefrontal structure and function have been associated with reduced top-down attentional control over sensory processing, explaining broader deficits in attention, inhibition, and processing speed observed in cognitive aging (Zanto and Gazzaley, 2016). To interpret this complex set of observations, several theoretical frameworks have been proposed, offering complementary explanations for how the aging brain adapts to cognitive demands and helping clarify the interplay between neural decline, compensatory mechanisms, and interindividual variability.

HAROLD model

The Hemispheric Asymmetry Reduction in Old Adults (HAROLD) model, proposed in 2002 by Roberto Cabeza, suggests that neural activity, particularly in the prefrontal cortex, exhibits reduced lateralization in older adults than in younger adults, a notion primarily supported by studies on memory, perception and inhibitory control. The auditory cortex is highly lateralized, showing hemispheric differences in activation that depend on sound characteristics: the right hemisphere is more involved in processing spectral features, while the left is more specialized for temporal features (Albouy *et al.*, 2020; Zatorre and Belin, 2001; Zatorre *et al.*, 2002). In accordance with the

HAROLD model, studies have reported reduced hemispheric asymmetry in auditory processing with advancing age, which may reflect compensatory mechanisms but could also disrupt the specialized functions of each hemisphere (Angenstein, 2024; Bellis *et al.*, 2000). Similar patterns of reduced lateralization have also been observed in attention-related networks, further supporting the relevance of the HAROLD model beyond memory and perception domains (Learmonth *et al.*, 2017). However, some have proposed that the HAROLD pattern may not be a standalone model, but rather an instance of broader age-related compensatory mechanisms described by more general frameworks (Berlingeri *et al.*, 2013).

CRUNCH

Expanding the concept of compensatory recruitment, the Compensation-Related Utilization of Neural Circuits Hypothesis (CRUNCH) offers a broader framework for understanding how the aging brain maintains cognitive performance by engaging supplementary brain regions that are not typically recruited by their younger counterparts under the same task demands (Reuter-Lorenz and Mikels, 2006). This compensatory activity can take the form of increased activation within task-relevant brain regions, engaging more neural resources from the same functional system, or the recruitment of additional, task-atypical regions that support performance through alternative strategies when primary pathways are no longer sufficient (Reuter-Lorenz and Cappell, 2008). Moreover, this compensation is not limitless, as older adults may reach a ceiling in neural recruitment at higher levels of cognitive demand (the “CRUNCH point”), leading to a decline in performance (Zahodne and Reuter-Lorenz, 2019). Moreover, not all increased activation is adaptive: overactivation may also reflect maladaptive processes such as dedifferentiation, where regions lose functional specificity and respond to a wider range of neural processes, or inhibition deficits, where normally suppressed areas become active, potentially interfering with task performance (Reuter-Lorenz and Lustig, 2005).

The CRUNCH framework has been widely supported by cognitive neuroscience

research in aging paradigms (Cappell *et al.*, 2010; Kang *et al.*, 2022; Schneider-Garces *et al.*, 2010), although the “CRUNCH point” is not always observed (Jamadar, 2020). Importantly, this model also implies that compensatory mechanisms can be modified, as maladaptive activation patterns may be corrected and neural capacity strengthened through interventions such as cognitive or perceptual training (Reuter-Lorenz and Cappell, 2008; Reuter-Lorenz and Lustig, 2005; Reuter-Lorenz and Mikels, 2006). Building on this framework, more recent findings have shown that older adults often exhibit delayed activation in frontal regions across various cognitive tasks (Jimura and Braver, 2010; Martins *et al.*, 2012; Paxton *et al.*, 2008; Velanova *et al.*, 2007; Wingfield and Grossman, 2006). These observations contributed to the development of the Dual Mechanisms of Cognitive Control (DMC) account, which proposes an age-related shift from proactive (anticipatory) to reactive (on-demand) control strategies (Braver *et al.*, 2007, 2009). The Temporal Hypothesis for Compensation (THC) integrates these findings and expands the CRUNCH model further, suggesting that delayed (later onset of activation) and sequential (step-by-step rather than parallel) neural engagement allows older adults to preserve performance by trading processing speed for accuracy and by postponing the use of cognitively expensive processes until task demands explicitly require them (Martins *et al.*, 2015).

Complementary theories of cognitive aging

In addition to the HAROLD and CRUNCH models, several other theories have been proposed to explain for age-related changes in brain activity and their functional implications. These include the dedifferentiation hypothesis, the Posterior-Anterior Shift in Aging (PASA), and the Cognitive Reserve hypothesis. Each of these models offers a different perspective on how the brain adapts or fails to adapt to the challenges of aging.

The dedifferentiation hypothesis proposes that aging leads to a loss of functional specificity, such that brain regions that were once selectively engaged for specific tasks become more broadly activated. This decline in neural precision is thought to

result from reduced dopaminergic modulation, which increases neural noise and degrades the distinctiveness of cortical representations (Goh, 2011; Koen and Rugg, 2019; Rajah and D'Esposito, 2005). Dedifferentiation can be viewed as the reversal of the developmental trajectory observed in childhood, where distinct cognitive abilities become increasingly specialized. In aging, that specialization diminishes, and different cognitive functions come to rely on overlapping neural resources (Cabeza, 2002).

Complementing this view, the Posterior-Anterior Shift in Aging hypothesis, first reported by Grady *et al.* in 1994, describes a common neuroimaging pattern in which reduced activity in posterior sensory regions is accompanied by increased activation in anterior areas, particularly the prefrontal cortex. This anterior recruitment is often interpreted as a compensatory mechanism, with prefrontal areas supporting cognitive performance when sensory processing becomes less efficient with age (Davis *et al.*, 2008). PASA has been linked to visual attention demands and altered functional connectivity, and is amplified in the context of neurological conditions such as Alzheimer's disease (Ansado *et al.*, 2012; McCarthy *et al.*, 2014). However, other studies argue that this frontal increase may reflect dedifferentiation rather than compensation, underscoring the complex and sometimes overlapping interpretations of age-related neural reorganization (Morcom and Henson, 2018; Myrum, 2019).

Extending beyond task-specific reorganization, the Cognitive Reserve hypothesis, proposes that lifelong experiences, such as education, multilingualism, and intellectually stimulating activities, build resilience to age-related neural decline or pathology (Christensen *et al.*, 2008; Reuter-Lorenz and Park, 2014; Stern, 2009, 2012). According to this framework, individuals vary in their ability to cope with neural changes, which helps explain the heterogeneity in cognitive aging outcomes. Stern differentiates between *brain reserve*, reflecting passive structural attributes such as brain size or synaptic density, and *cognitive reserve*, which involves the active use of pre-existing cognitive strategies (*neural reserve*) or the recruitment of alternative networks (*neural compensation*) that help maintain cognitive function despite underlying damage (Stern,

2009, 2012).

STAC and STAC-r models

While previous models concentrate on particular aspects of neural aging, the Scaffolding Theory of Aging and Cognition (STAC) presents a more comprehensive framework. It synthesizes findings on compensation, dedifferentiation, and, in its revised form (STAC-r, [Figure 1.4](#)), incorporates cognitive reserve and life-course influences to explain how the aging brain adjusts to structural and functional decline through the recruitment of alternative circuits ([Park and Reuter-Lorenz, 2009](#); [Reuter-Lorenz and Park, 2014](#)). STAC-r posits that changes in brain integrity may be indicative of both positive and negative outcomes, influenced by a dynamic interplay between plasticity, development, and accumulated experiences. The model emphasizes that cognitive aging is modifiable, as neural scaffolding can be either reinforced or weakened by long-term enrichment or depletion of cognitive resources. This adaptive neural support may also be sustained later in life through targeted interventions such as physical activity, cognitive training, or other cognitively engaging activities ([Figure 1.4](#); [Reuter-Lorenz and Park, 2014](#)). For example, the auditory training program used in the present study may contribute to this scaffolding process by enhancing perceptual processing and facilitating the recruitment of compensatory neural resources. These changes could help mitigate age-related decline in auditory and attentional functions and may also promote improvements in cognitive function. However, the extent of these benefits likely depends on each participant's prior experiences and cognitive reserve, highlighting the importance of accounting for individual differences.

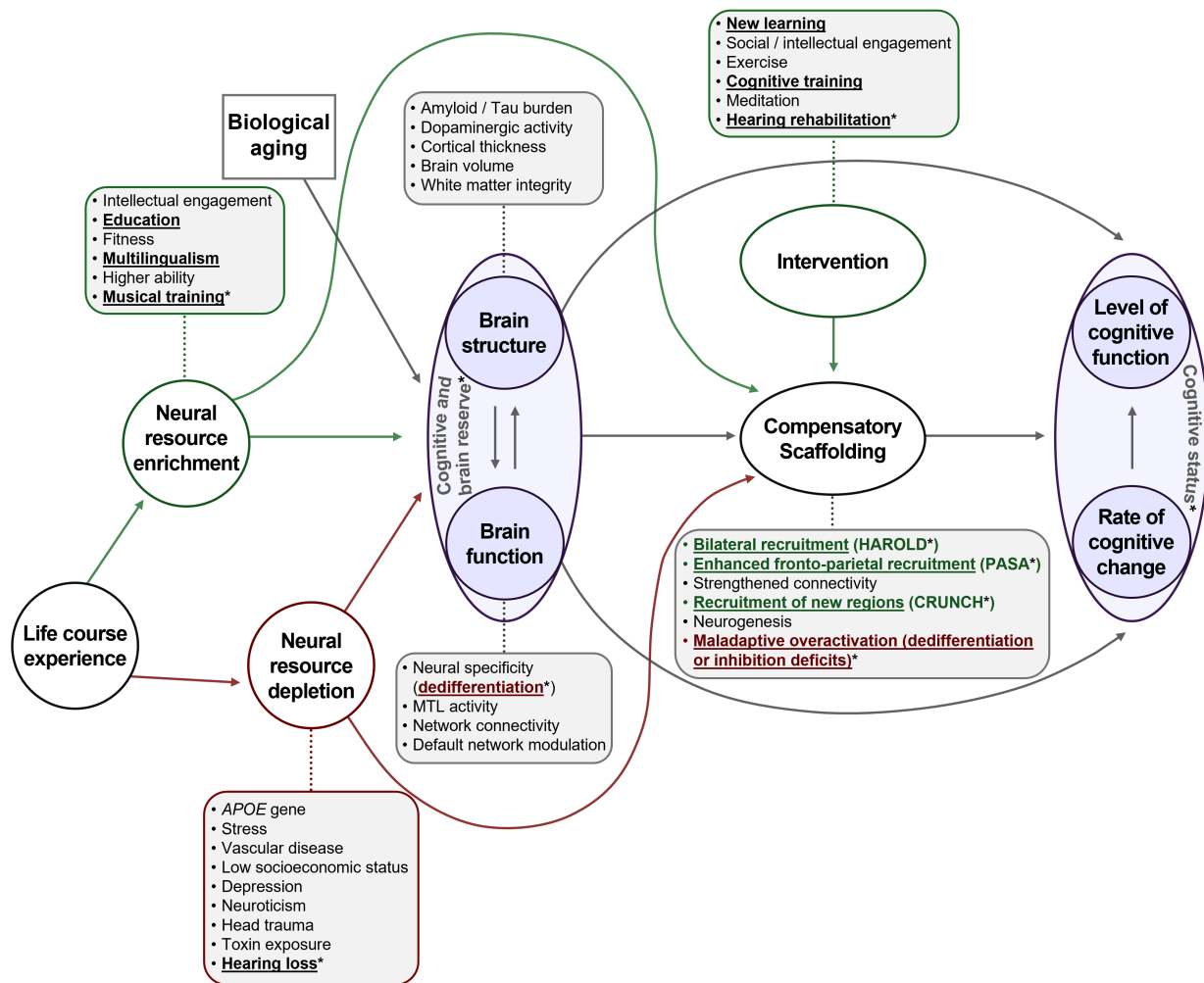


Figure 1.4: Modified version of the Scaffolding Theory of Aging and Cognition-revised (STAC-r).

This figure, adapted from Reuter-Lorenz and Park (2014), incorporates theoretical constructs relevant to the present study, including the Hemispheric Asymmetry Reduction in Old Adults (HAROLD; Cabeza, 2002), Posterior–Anterior Shift in Aging (PASA; Davis *et al.*, 2008), Compensation-Related Utilization of Neural Circuits Hypothesis (CRUNCH; Reuter-Lorenz and Mikels, 2006), dedifferentiation hypothesis (see Section 1.2.2), and Cognitive Reserve hypothesis (Stern, 2009, 2012). Positive influences on cognitive function through compensatory scaffolding are indicated in green, and negative influences in red. Asterisks (*) denote variables added or modified from the original model, and terms relevant to the present project are bolded and underlined.

1.3 Auditory perception in the aging brain

Hearing loss and aging are closely linked, with ARHL affecting more than 65% of adults over the age of 70 (Reed *et al.*, 2023; see Section 1.1.1). While age-related declines in hearing ability are commonly attributed to peripheral degeneration, due to the loss of hair cells and structural deterioration within the cochlea, they also entail widespread effects throughout the auditory pathway, including cortical regions involved in auditory processing (Peelle and Wingfield, 2016; Uchida *et al.*, 2019). These central changes are reflected in structural and functional alterations in the auditory cortex, thereby affecting auditory perception (Campbell and Sharma, 2013; Eckert *et al.*, 2012; Rigters *et al.*, 2017). Additionally, non-auditory regions such as attention-related networks are also impacted by hearing loss, likely reflecting compensatory recruitment aimed at maintaining perceptual performance in the face of sensory decline (Slade *et al.*, 2020). The following subsections describe the neural systems that support auditory perception, as well as the electrophysiological responses that reflect their activity, to better understand how aging influences auditory function.

1.3.1 Auditory perception system

While auditory perception relies on activation of the auditory cortex, it also engages additional regions such as attention networks, particularly in environments where sound is degraded or masked by background noise (Jäncke *et al.*, 1999; Peelle, 2019; Price and Moncrieff, 2021; Wong *et al.*, 2009). Functional MRI studies show that these attention networks undergo reconfiguration during challenging listening tasks, suggesting flexible coordination between sensory and attentional systems in support of perception (Alavash and Obleser, 2024). Auditory perceptual learning further extends this recruitment, engaging not only sensory representations and attention networks, but also systems involved in decision-making and reward processing to promote adaptive changes in perception (Doshier and Lu, 2017; Irvine, 2018).

This interaction between sensory and attentional systems can be interpreted through the lens of predictive coding. According to this framework, perception arises from a continuous comparison between sensory input and top-down predictions based on prior experience, with the brain aiming to minimize the mismatch between the two (Rao and Ballard, 1999). Within this framework, the interaction between attention and auditory regions may reflect how attention modulates the precision of prediction errors by adjusting the gain of bottom-up signals, while prediction provides top-down expectations that guide interpretation (Chennu *et al.*, 2013; Schröger *et al.*, 2015). In the context of aging, declines in sensory fidelity may lead the brain to rely more heavily on internal predictions and to increasingly engage attention networks to regulate the precision of degraded auditory input (Chan *et al.*, 2021; Hsu *et al.*, 2021).

Therefore, there is substantial evidence supporting the interaction between these two systems to enable accurate auditory perception. Exploring their structure and function provides insight into the neural mechanisms through which aging, training and sensory decline reshape auditory perception.

Auditory cortex

The auditory cortex is located in Heschl's gyrus (HG), also known as the transverse temporal gyrus, on the dorsal surface of the superior temporal gyrus (STG; Henderson *et al.*, 2023). The primary auditory cortex (PAC), also referred to as A1 or the core area, occupies the medial two-thirds of HG and corresponds to Brodmann area 41 (Figure 1.5; Khalil, 2018). Regions surrounding A1, including the posterior part of STG and the planum temporale (PT), are thought to form the auditory association cortex, also referred to as secondary auditory cortex, and are typically linked to Brodmann area 42, although their precise boundaries remain under debate (Henderson *et al.*, 2023; Smiley, 2009; Trébuchon *et al.*, 2021). Substantial variability has been observed in both HG and A1 across individuals and between hemispheres, making consistent anatomical definitions across participants difficult (Abdul-Kareem and Sluming, 2008).

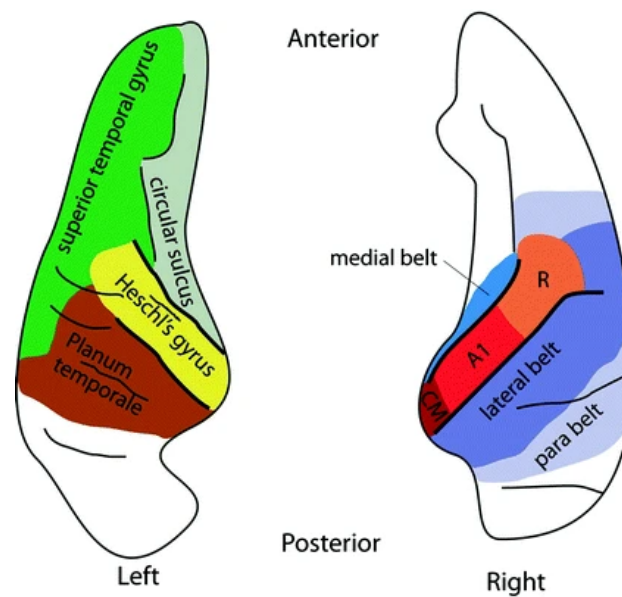


Figure 1.5: Anatomy of the human auditory cortex. Top view of the auditory cortex located on the superior temporal plane and buried within the Sylvian fissure. Left hemisphere displays the large-scale anatomical organization, while the right shows histological auditory cortex subdivisions. Primary auditory cortex (A1) lies within Heschl's gyrus and may also include the core medial (CM) and rostral (R) fields. A1 is surrounded by secondary, or association auditory cortex, which includes medial and lateral belt regions that extend into the planum temporale and circular sulcus, as well as the parabelt that continues into the superior temporal gyrus. Reproduced with permission from Springer Nature (Gutschalk, 2014).

Hemispheric specialization within the auditory cortex plays a key role in auditory perception. While A1 in both hemispheres responds to temporal variation, sensitivity to rapid temporal features such as those found in speech is typically greater in the left hemisphere (Zatorre and Belin, 2001). In contrast, spectral aspects of sound, like those found in music, are primarily processed in the secondary auditory cortex and show a dominance in the right hemisphere (Albouy *et al.*, 2020; Tervaniemi and Hugdahl, 2003; Zatorre *et al.*, 2002). However, this functional asymmetry tends to decrease with age, as older adults show reduced hemispheric specialization in response to both speech and tonal stimuli (Bellis *et al.*, 2000; Chen *et al.*, 2013; Côté, 2022). This reduction in lateralization may be influenced by age-related declines in the efficiency of auditory information transfer between hemispheres (Martin and Jerger, 2005).

The age-related decline in functional asymmetry is accompanied by structural changes in the auditory cortex, including reduced gray matter (GM) volume in HG and

PT, as well as decreased white matter (WM) integrity in HG, that are further exacerbated by hearing loss (Eckert *et al.*, 2012; Ouda *et al.*, 2015; Profant *et al.*, 2014). Even modest elevations in PTA thresholds within the range typically classified as normal hearing (≤ 25 dBHL) are associated with reduced brain activity in STG during speech processing, lower GM volume in the right auditory cortex and decreased WM volume across the brain (Peelle *et al.*, 2011; Peelle and Wingfield, 2016; Rigters *et al.*, 2017). The intricate relationship between age and hearing loss poses significant challenges in disentangling their respective contributions to brain changes (Ouda *et al.*, 2015; Slade *et al.*, 2020). This underscores the necessity of accounting for hearing acuity when investigating the neural substrates of auditory perception and brain aging.

Attention networks

The concept of attention has been rightly criticized for its ambiguity and conceptual overuse (Anderson, 2011; Hommel *et al.*, 2019). Still, a recent and integrative definition describes attention as *"the set of evolved brain processes that leads to adaptive and effective behavioral selection"* (Krauzlis *et al.*, 2023). Despite the broad nature of the label, decades of research have enabled the identification of specific brain networks involved in the selection of relevant information from the environment. This prioritization process is guided by endogenous or top-down signals, which reflect internal goals and expectations; by exogenous or bottom-up signals, triggered by novel or unexpected stimulus features; and by additional factors such as prior experience (Awh *et al.*, 2012; Vossel *et al.*, 2014). Based on converging evidence from neuroimaging and lesion studies, Corbetta and Shulman (2002) proposed two distinct attentional systems: the dorsal attention network (DAN), or dorsal frontoparietal network (dFPN), which modulates top-down or voluntary attention, and the ventral attention network (VAN), or ventral frontoparietal network (vFPN), which supports bottom-up or involuntary attention.

Although the specific brain regions comprising the attentional networks vary across studies, several core areas are consistently identified. The dorsal attention

network typically includes the frontal eye fields (FEF), superior parietal lobule (SPL), and intraparietal sulcus (IPS; Corbetta and Shulman, 2002; Vossel *et al.*, 2014), with some studies also reporting involvement of the inferior frontal junction (IFJ) and middle temporal area (MT+; Kim, 2014; Yeo *et al.*, 2011). While the DAN is generally described as bilaterally organized, especially in visual paradigms, evidence points to functional asymmetries, with the right hemisphere exerting a dominant role by controlling attention across both hemifields, whereas the left hemisphere is limited to contralateral space (Bartolomeo and Seidel Malkinson, 2019; Mengotti *et al.*, 2020).

In contrast, the ventral attention network is largely right-lateralized, less studied, and shows greater variability in its anatomical definition across studies. It is commonly described as comprising ventral frontal regions, such as the middle frontal gyrus (MFG) and inferior frontal gyrus (IFG), as well as the temporoparietal junction (TPJ; Bartolomeo and Seidel Malkinson, 2019; Corbetta and Shulman, 2002; Vossel *et al.*, 2014). Additional regions sometimes reported as part of the VAN are the supplementary motor area (SMA), supramarginal gyrus (SMG), anterior insula (AI), anterior cingulate cortex (ACC), and adjacent frontal operculum (aFO; Kim, 2014; Yeo *et al.*, 2011). Several of these regions, particularly SMA, AI, ACC, and aFO, have also been associated with the cingulo-opercular network (CON), a distinct executive attention network implicated in alertness maintenance, task performance and error monitoring (Coste and Kleinschmidt, 2016; Freedman *et al.*, 2020; Peelle, 2019). The CON is also recruited during speech-in-noise tasks and is engaged differently in individuals with ARHL, with evidence of increased connectivity to right HG that may reflect a compensatory role in auditory attention (Fitzhugh *et al.*, 2019; Peelle, 2019; Slade *et al.*, 2020).

Large-scale network parcellations using resting-state fMRI have sought to establish the boundaries between multiple functional systems in the brain, including attentional networks. Both Yeo *et al.* (2011) and Schaefer *et al.* (2018) divided the brain into seven networks that included the DAN and VAN, with the latter encompassing regions commonly associated with the salience and cingulo-opercular networks (Figure 1.6).

While these parcellations offer a valuable framework for distinguishing and studying attentional systems, growing evidence suggests that DAN and VAN interact and may not be as functionally segregated as originally assumed. Rather than operating in isolation, these networks are interconnected both structurally and functionally (Cazzoli *et al.*, 2021; Katsuki and Constantinidis, 2014; Vossel *et al.*, 2014), with anatomical projections linking their frontal and parietal regions (Catani *et al.*, 2017; de Schotten *et al.*, 2011) and coordinated activity supporting behavioral performance (Wen *et al.*, 2012).

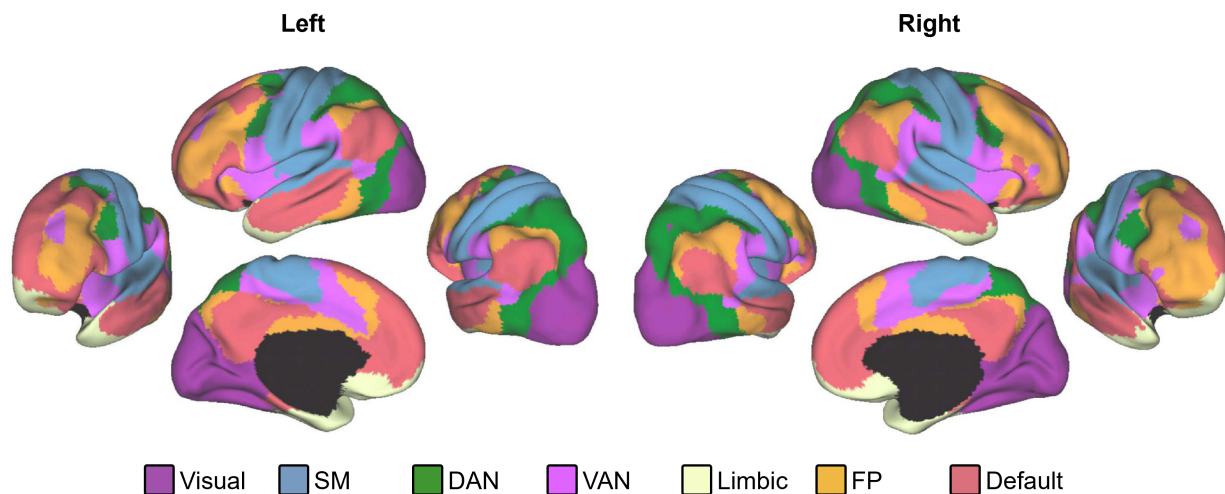


Figure 1.6: Parcellation of the human brain into seven functional networks. Adapted from Yeo *et al.* (2011). SM: somatomotor network; DAN: dorsal attention network; VAN: ventral attention network; FP: fronto-parietal network.

Most of the evidence characterizing DAN and VAN comes from the visual domain (Katsuki and Constantinidis, 2014), but studies in auditory attention have revealed similar patterns of functional organization (Kim, 2014; Krumbholz *et al.*, 2009; Mamashli *et al.*, 2020; Rossi *et al.*, 2014; Salmi *et al.*, 2009). The presence of both top-down modulation and bottom-up feedback in auditory processing has been documented in numerous studies (Henderson *et al.*, 2023; Jääskeläinen and Ahveninen, 2014; Kuchibhotla and Bathellier, 2018; Schönwiesner *et al.*, 2007; Shamma and Micheyl, 2010). In addition, anatomical evidence indicates that HG projects to frontoparietal regions involved in attentional control, including the inferior parietal lobule and frontal

cortex (Behrmann *et al.*, 2004; Maffei *et al.*, 2015; Peers *et al.*, 2005; Szczepanski *et al.*, 2010). In auditory contexts, however, the functional boundaries between endogenous and exogenous attention appear less rigid, as regions typically associated with either the DAN or VAN can be flexibly recruited by both attention types (Alho *et al.*, 2015; Salmi *et al.*, 2009). This functional versatility underscores the intricate coordination between the auditory system and both attention networks necessary to support successful auditory perception.

1.3.2 Electrophysiological responses to auditory stimuli

Understanding how the brain responds to auditory stimuli requires examining not only the regions involved in perception and attention, but also the neural dynamics underlying these processes. In this work, we focus on three complementary analytical approaches commonly applied to electrophysiological methods such as M/EEG:

- Time-domain analysis, through event-related potentials (ERPs) in EEG or event-related fields (ERFs) in MEG, reflects activity that is both time- and phase-locked to a stimulus or task.
- Time-frequency analysis characterizes how features of neural activity vary across frequency bands and evolve over time.
- Connectivity analysis evaluates functional interactions within or between brain regions.

Together, these methods offer a comprehensive examination of the neural dynamics that support auditory perception and are described individually in the subsections that follow.

Time-domain responses

The evoked responses captured by EEG or MEG reflect small changes in voltage or magnetic field that are time- and phase-locked to an event, whether external, internal,

or omitted (Parviainen and Kujala, 2023; Tivadar and Murray, 2019). Although their precise neurophysiological origins remain debated (Cohen, 2014; Helfrich and Knight, 2019), ERP/Fs are thought to result from phase resetting of ongoing neural activity (*phase reset* model) or from responses specifically elicited by events (*additive* model), and they are often considered to involve a combination of both mechanisms (Parviainen and Kujala, 2023; Tivadar and Murray, 2019).

To study these responses, they are often classified into three categories based on their latency (Figure 1.7), although the naming conventions and specific components vary between studies (Eggermont, 2019; Pratt, 2011; Price and Moncrieff, 2021):

- a) Early-latency responses, or auditory brainstem responses (ABRs), occur within the first 8 ms after stimulus onset. They are not generated in the cortex, but along subcortical structures of the auditory pathway, up to and including the brainstem (Eggermont, 2019; Gutschalk, 2019).
- b) Middle-latency responses occur within 10–50 ms following stimulus onset. Neural generators of these responses include the ascending pathway beyond the brainstem, thalamocortical projections, and cortical activity in Heschl's gyrus, particularly in A1 (Pratt, 2011). They are best elicited by chirps and clicks, though pure tones can also evoke them with lower amplitude and altered morphology (Gutschalk, 2019; Winkler *et al.*, 2022).
- c) Long-latency components refer to responses occurring after 50 ms and exhibit larger amplitudes due to the increase in cortical recruitment as auditory processing progresses (Figure 1.7; Pratt, 2011). These components have been studied extensively and are particularly sensitive to attentional modulation (Jääskeläinen and Ahveninen, 2014; Price and Moncrieff, 2021; Winkler *et al.*, 2022); therefore, they constitute the primary focus of the analysis presented in this thesis.

The nomenclature of auditory long latency components, referred to as ERP/Fs

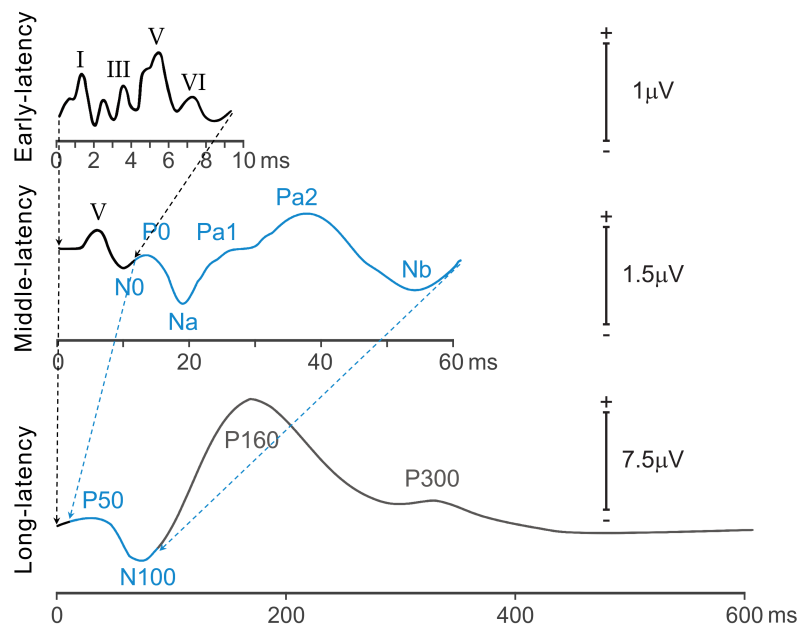


Figure 1.7: Comparison across evoked potentials at different latencies. Early- (top), middle- and long-latency (bottom) evoked potentials are shown, highlighting differences in timing and amplitude (μV). As signals ascend the auditory pathway, increased neural recruitment leads to larger amplitudes, but also to reduced synchrony that results in slower waveform oscillations and longer latencies per each component. Adapted from Pratt (2011).

from herein, varies according to the polarity of the waveform observed in EEG (P for positive and N for negative), the order of appearance, the typical peak latency, and the recording modality (Winkler *et al.*, 2022). For example, the first positive component is referred to as P1 or P50 in EEG, reflecting its positive polarity and approximate 50 ms latency, and P1m or M50 in MEG. Under these conventions, ERP/Fs are typically identified as P1, N1, P2 and N2 in EEG, or M50, M100 and M200 in MEG (Eggermont, 2019).

The P1 component is the earliest auditory ERP, peaking around 50 ms after stimulus onset and typically exhibiting the smallest amplitude among these responses. While its primary generators are located in A1, additional sources in the hippocampus, PT and lateral temporal cortex have been reported (Parviainen and Kujala, 2023; Pratt, 2011). P1 is the first auditory response reliably modulated by attention (Price and Moncrieff, 2021; Winkler *et al.*, 2022). However, its amplitude declines with age and may become

undetectable in adults (Key *et al.*, 2005), where the response is instead dominated by N1 and P2 due to their temporal overlap (Eggermont, 2019).

The N1 component (also referred to as N100, N1m and M100) was the first auditory ERP described over 80 years ago (Davis *et al.*, 1939) and remains the most extensively studied, likely due to its prominence in auditory responses. It peaks between 100–150 ms and is primarily generated in the superior temporal cortex, including Heschl's gyrus and planum temporale, with additional contributions from other auditory association areas and even motor and premotor cortices (Gutschalk, 2019; Key *et al.*, 2005; Parviainen and Kujala, 2023). N1 characteristics are modulated by stimulus properties such as pitch, by presentation rate and by attention, with the latter increasing its amplitude when sounds are attended (Key *et al.*, 2005; Price and Moncrieff, 2021; Schröger *et al.*, 2015; Winkler *et al.*, 2022). Functionally, it has been associated with the detection of changes in the external auditory scene, the extraction of auditory features and the retention of sensory information (Pratt, 2011; Winkler *et al.*, 2022). Although this stage of processing is not sensitive to linguistic information (Parviainen and Kujala, 2023), it supports the integration of spectral features of the sound (Jenkins *et al.*, 2010). Within predictive coding theories, the N1, along with the earlier P1, is proposed to reflect the evaluation of the internal representation of auditory environment (Joos *et al.*, 2014). Supporting this view, N1-like responses have also been elicited by the omission of predicted sounds (Bendixen *et al.*, 2009; Schröger *et al.*, 2015).

Following N1, a positive waveform known as P2 (also P175, P200, P2m or M200) emerges between 150–250 ms post-stimulus. Its sources are located anterior to those of the N1 and include both primary and secondary cortices (Gutschalk, 2019; Winkler *et al.*, 2022). This component has been associated with selective attention, stimulus change, feature detection, and short-term memory, and may represent the attentional modulation of non-target stimuli (Key *et al.*, 2005; Winkler *et al.*, 2022). Due to their temporal proximity and functional overlap, P2 is often studied together with P1 and N1 as part of P1–N1–P2 or N1–P2 complexes, though evidence suggests that these

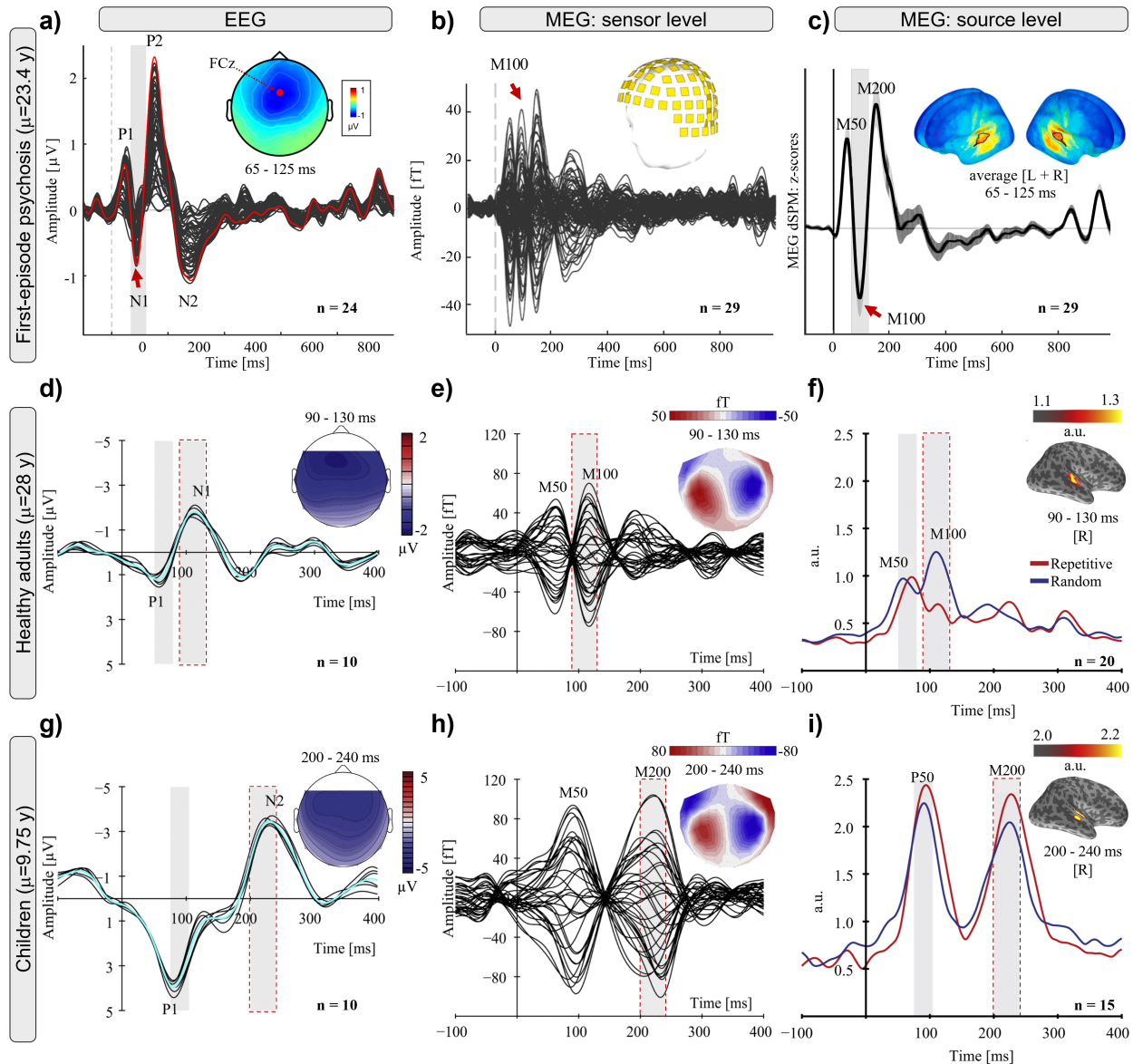


Figure 1.8: Comparison of auditory evoked responses as measured by M/EEG in response to pure tones. Adapted from López-Caballero *et al.* (2025, panels a–c) and Ruhna *et al.* (2011, panels d–i). EEG (60 electrodes in a; 23 in d, g) and MEG (102 magnetometers) were recorded in adults with first-episode psychosis (a–c), healthy adults (d–f), and children (g–i). Stimuli consisted of 50 ms 1kHz tones in panels a–c, and 200 ms 500 Hz tones in panels d–i. (a, d, g) EEG butterfly plots showing responses across all electrodes (a) or a fronto-central cluster (d, g), with FCz highlighted in red (a) and mean activity overlaid in cyan (d, g). Shaded regions indicate specific ERP components, and scalp topographies show their spatial distribution over the indicated time windows. (b, e, h) MEG sensor-level butterfly plots showing responses across magnetometers. Insets show corresponding topographical field maps for the component highlighted in red. (c, f, i) Source-reconstructed MEG responses averaged across bilateral (c) or right hemisphere (f, i) auditory cortex. Cortical maps display the distribution of the selected component projected onto an MNI template (L: left, R: right).

components arise from distinct neural mechanisms (Eggermont, 2019; Parviainen and Kujala, 2023). In conjunction, the N1–P2 complex has been linked to early perceptual filtering processes that are sensitive to attentional state and show atypical patterns in language-related disorders (Parviainen and Kujala, 2023; Price and Moncrieff, 2021).

While earlier event-related components are primarily generated within the auditory cortex, later responses involve broader networks, including frontal and parietal regions. One of the last major components frequently described in ERPs is the N2 (N200), a complex waveform occurring between 150 and 350 ms post-stimulus and encompassing several subcomponents (Winkler *et al.*, 2022). Its generators are located in medial frontal regions, such as the ACC and the right ventral and dorsolateral prefrontal cortex (Eggermont, 2019), and it has been linked to cognitive control, inhibition, and initial decoding of phonemic information (Parviainen and Kujala, 2023). The mismatch negativity (MMN), or mismatch field in MEG (MMF), is a subcomponent of N2 elicited by deviant or unexpected sounds in oddball paradigms, typically observed between 100 and 250 ms, even in the absence of attention (Key *et al.*, 2005; Winkler *et al.*, 2022). N2 responses are also sensitive to aging, with increased inter-individual variability, amplitude reductions or even absence in older adults, and often co-occur with later components such as the P3 under active listening conditions (Eggermont, 2019; Hsiao *et al.*, 2014).

Unlike earlier auditory components, the P3 (or P300) emerges only during tasks that require active attention and behavioral engagement (Price and Moncrieff, 2021). Its latency (250–700 ms) and amplitude vary according to task demands, with more complex tasks eliciting later and larger responses (Bertoli and Bodmer, 2016; Criscuolo and Brattico, 2023). As such, P3 engages a distributed network that includes not only the auditory cortex, but also frontal regions, hippocampus, and centro-parietal areas (Eggermont, 2019). Its frontal activity has been associated with bottom-up attention and the processing of novel information, while parietal components are thought to reflect top-down attentional control and memory-related functions (Helfrich and Knight,

2019). Within the framework of predictive coding, P3 is thought to refine internal models of the sensory environment, functioning alongside earlier components such as the MMN (Chennu *et al.*, 2013; Schröger *et al.*, 2015).

Aging is associated with several changes in auditory event-related potentials that reflect both sensory and cognitive alterations. Early components such as P1 and N1 show increased amplitudes in older adults in response to pure tones and auditory speech (Müller *et al.*, 2009), accompanied by reduced or absent N2 responses and enhanced P3 to deviant stimuli, reflecting inhibitory deficits in sensory gating and heightened attentional capture by irrelevant stimuli (Stothart and Kazanina, 2016). However, reduced amplitudes have also been reported in older adults in response to increased task demands, particularly in later components such as P3, alongside increases in subsequent responses that may serve to compensate for these deficits (Bertoli and Bodmer, 2016). Additionally, P2 responses tend to be both increased and delayed in older adults, particularly those with hearing loss, and are accompanied by reduced activation in auditory regions and compensatory increases in frontal areas (Campbell and Sharma, 2013).

Auditory evoked responses recorded with EEG and MEG are similar in their overall shape (Figure 1.8; Virtanen *et al.*, 1998), but differences in the source orientations that each method detects result in some component-specific distinctions. For example, the T-complex, a subcomponent of N1, as well as certain frontal generators involved in P1, N1, MMN, and P2, are less visible in MEG due to their predominantly radial orientation (see Figure 1.3; Eggermont, 2019; Key *et al.*, 2005; Pratt, 2011; Shahin *et al.*, 2007). These modality-related effects are evident in findings by Ruhnau *et al.* (2011), who reported modulations in the N1 response of children using EEG that were not detected in MEG recordings, likely due to differences in source sensitivity, sensor distance, or signal cancellation. Moreover, most ERP studies have been conducted at the sensor level, where the resulting waveforms reflect the combined activity of multiple neural sources (Cohen, 2014). In contrast, source-localized MEG signals offer

greater anatomical specificity, as the resulting ERFs primarily reflect activity from the selected cortical region and reduce the influence of distant sources.

Time-frequency domain responses

While time-domain analyses have contributed meaningfully to the characterization of auditory responses, they are limited in detecting neural activity with low amplitude, widespread cortical distribution, or not strictly phase-locked to the stimulus (Winkler *et al.*, 2022). Time-frequency approaches address these limitations by capturing both rhythmic and arrhythmic changes in brain activity, thereby enabling the characterization of dynamic processes in M/EEG signals that may remain undetected in traditional time-domain analyses (Cohen, 2014). While the precise physiological origin of these spectral dynamics remains under investigation, they are thought to reflect cyclical fluctuations in the balance of excitatory and inhibitory activity within neuronal populations (Cohen and Gulbinaite, 2014; Jensen *et al.*, 2014; Lopes da Silva, 2013).

The classification of spectral activity into frequency bands is based on historically defined boundaries that are not firmly rooted in neurophysiological mechanisms. As a result, their precise limits may vary across studies, but a common classification includes delta (1–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), beta (15–30 Hz), and gamma (30–90 Hz; Lopes da Silva, 2013; Tavano *et al.*, 2023). Of particular interest in this study are the alpha and theta frequency bands, as they have been recently associated with task engagement, top-down attentional modulation and working memory in auditory contexts (Albouy *et al.*, 2017; Fontolan *et al.*, 2014; Frey *et al.*, 2014; Gourévitch *et al.*, 2020; Keller *et al.*, 2017; López-Madróna *et al.*, 2024; Yordanova *et al.*, 1998), and encompass the spectral content of long-latency auditory responses such as M100, which lie primarily within the 3–10 Hz range (Gutschalk, 2019; Hari and Puce, 2023; Zhang *et al.*, 2024).

Alpha activity has traditionally been interpreted as a marker of inhibition due to its presence when irrelevant or distracting stimuli are encountered (Foxe and Snyder,

2011). Supporting this view, increased posterior alpha power is associated with reduced BOLD activity, indicative of decreased neural activation (Laufs *et al.*, 2006; Scheeringa *et al.*, 2009). In auditory paradigms, alpha activity exhibits dynamic spatial and temporal modulations that vary with task demands and behavioral goals, and that are linked to attentional control and memory maintenance (Bonnefond and Jensen, 2012). Spatially, lateralized alpha reflects the distribution of attention, increasing on the ipsilateral side to suppress processing in the contralateral hemisphere during focused listening (Ahveninen *et al.*, 2013; Deng *et al.*, 2020; Wöstmann *et al.*, 2021). Temporally, higher alpha power has been observed before and after auditory stimulation (López-Madrona *et al.*, 2024; Wöstmann *et al.*, 2019), and is more pronounced under challenging listening conditions, including reduced signal quality and hearing impairment (Herrmann *et al.*, 2023; Obleser *et al.*, 2012; Petersen *et al.*, 2015). In cases of mild-to-moderate hearing loss, elevated alpha may reflect a compensatory strategy to support auditory processing; however, this mechanism fails in more severe impairment (>50 dB HL), where alpha activity is instead diminished (Petersen *et al.*, 2015). While these findings align with an inhibitory role, recent evidence has also shown alpha power reductions, even in the presence of distractors (Brilliant *et al.*, 2024; Strunk and Duarte, 2019; Weisz *et al.*, 2020; Zhou *et al.*, 2023), suggesting an alternative role for alpha in prioritizing task-relevant information. These opposing dynamics, through which alpha activity balances inhibition or prioritization depending on task demands, may operate in parallel across hemispheres to facilitate target perception while suppressing irrelevant input (Wöstmann *et al.*, 2019).

The spatial localization of alpha activity spans multiple cortical regions, including the supratemporal auditory cortex (Frey *et al.*, 2014; López-Madrona *et al.*, 2024), as well as frontal and parietal cortices (Deng *et al.*, 2019; Wöstmann *et al.*, 2019). Notably, some of these sources overlap with regions of the dorsal and ventral attention networks (Kasten *et al.*, 2024), underscoring the close relationship between alpha modulation and attentional control. Moreover, the anatomical distribution of alpha sources is also influenced by age: while younger adults show prominent modulations in superior

parietal regions, older adults display stronger activity in posterior temporal areas and reduced parietal engagement (Herrmann *et al.*, 2023). Still, the modulatory properties of alpha seem to be preserved in aging, as older adults retain the ability to engage preparatory neural processes that support memory encoding (Strunk and Duarte, 2019). Finally, although spectral dynamics are typically studied independently from event-related responses, recent evidence indicates that alpha modulations can partially account for the amplitude, shape and localization of the P3 component (Studenova *et al.*, 2023).

Beyond alpha, theta oscillations also play a critical role in auditory processing and cognitive functions such as attention and memory. Modulations of this frequency band have been consistently observed in response to auditory stimulation (Brilliant *et al.*, 2024; Hsiao *et al.*, 2009; Keller *et al.*, 2017; López-Madrona *et al.*, 2024; Mai *et al.*, 2016). However, as with alpha, the direction of the changes varies depending on task demands and stimulus characteristics. Most effects emerge within 0 to 400 ms after stimulus onset and include decreases in theta power following pure tones (López-Madrona *et al.*, 2024), as well as increases in response to auditory tasks that require greater attentional engagement, such as detecting deviant stimuli across modalities or processing speech in challenging conditions (Brilliant *et al.*, 2024; Hsiao *et al.*, 2009; Keller *et al.*, 2017). In addition, theta activity before stimulus onset influences how auditory information is perceived and encoded (Kubetschek and Kayser, 2021; Ostrowski and Rose, 2024), with the auditory system selectively tracking acoustic dynamics at this frequency (Teng *et al.*, 2017). Although the precise role of pre- and post-stimulus theta dynamics remains unclear, both have been linked to memory-related processes. In particular, elevated theta power prior to the stimulus is associated with better memory performance (Ostrowski and Rose, 2024). Similarly, during memory retention, specific features of theta activity reflect the content of memorized auditory items (Weisz *et al.*, 2020), and transcranial magnetic stimulation (TMS) in the theta range applied to parietal DAN regions enhances auditory working memory performance (Albouy *et al.*, 2017).

The specific cortical sources of theta activity in the brain remain poorly defined, as most studies have relied on sensor-level EEG analyses. Evidence from this method typically shows theta activity over central and frontal scalp regions (Keller *et al.*, 2017; Kubetschek and Kayser, 2021; Ostrowski and Rose, 2024). Midfrontal theta in particular is thought to arise primarily from radial dipoles, and is therefore underrepresented in MEG studies (Cohen, 2014). In studies where source localization has been applied, post-stimulus increases in theta power have been identified in the medial frontal cortex and ACC (Ahveninen *et al.*, 2013), with additional sources observed in STG and attention-related regions including IFG and SPL (Brilliant *et al.*, 2024).

Research on age-related differences in theta activity shows mixed findings, with some evidence suggesting increases in older adults (Yordanova *et al.*, 1998) and several other studies observing reductions in theta power with age (De Blasio and Barry, 2018; Cummins and Finnigan, 2007; Müller *et al.*, 2009). In addition to power differences, aging also influences the functional role of theta, with older adults showing greater temporal consistency across trials, primarily in the theta band, and distinct influences of pre-stimulus theta on later ERP components (De Blasio and Barry, 2018; Müller *et al.*, 2009), suggesting compensatory mechanisms that support task performance through alternative neural dynamics.

While alpha and theta are often discussed as distinct frequency bands with some shared functions in attention and memory, they are not always clearly dissociable. These neural signals often emerge together in low-frequency clusters (e.g. 4–15 Hz) before or after auditory stimulation, and may jointly support similar cognitive processes depending on task context (López-Madróna *et al.*, 2024; Ostrowski and Rose, 2024). For example, increases in pre-stimulus power within the theta–alpha range have been associated with more successful memory encoding (Ostrowski and Rose, 2024). Importantly, age-related spectral flattening and broadband power reductions further complicate interpretations (McNair *et al.*, 2019; Müller *et al.*, 2009; Voytek *et al.*, 2015), highlighting the need for caution when attributing narrowly defined or exclusive

cognitive roles to individual frequency bands. A comprehensive understanding of time-frequency dynamics requires consideration of their interdependence, spatial and temporal variability, and age-related changes.

Connectivity

As outlined by [Brookes *et al.* \(2019\)](#), different neuroimaging techniques can be used to measure three types of connectivity: structural, functional, and effective. Structural connectivity describes the anatomical pathways (i.e., white matter tracts) linking different brain regions and is typically measured using diffusion-weighted imaging, an MRI-based technique. In contrast, functional connectivity captures the statistical relationships between neural signals recorded at spatially distinct brain locations. Effective connectivity goes a step further by estimating the causal influence one region exerts on another, often through computational models that infer the directionality of information flow. In electrophysiological studies, functional connectivity is the primary approach available to assess interactions within or between brain regions, using methods such as power correlations, phase locking, and coherence ([Bastos and Schoffelen, 2016](#)). Coherence, in particular, is a widely accepted measure of connectivity ([Fischer *et al.*, 2023](#)), that quantifies the degree of linear dependency between two signals in the frequency domain, incorporating both phase and amplitude information ([Malekpour *et al.*, 2018](#)).

Studies using fMRI have identified functional and structural connections between primary and secondary auditory areas, involving both anterior and posterior pathways ([Upadhyay *et al.*, 2008](#)), and between auditory areas and regions within the dorsal and ventral attention networks, with overlapping engagement during bottom-up and top-down attention ([Maffei *et al.*, 2015](#); [Rossi *et al.*, 2014](#)). Moreover, functional connectivity between auditory cortex and attention-related areas has been shown to increase with higher auditory thresholds ([Fitzhugh *et al.*, 2019](#)). Connectivity research using M/EEG has furthered our understanding of the timing and direction of information exchange between primary and secondary auditory cortices ([Guéguin *et al.*, 2007](#)), as

well as their interactions with attentional networks (Hsiao *et al.*, 2010; Mamashli *et al.*, 2020). In fact, these electrophysiological techniques showed that connectivity patterns vary depending on the timing relative to stimulus onset, the brain regions involved, the frequency bands examined, and the cognitive demands of the task (Mamashli *et al.*, 2020; Polomac *et al.*, 2015; Weisz *et al.*, 2014). Notably, coherence between the inferior parietal lobule, a part of DAN, and STG increases during the anticipatory period following a cue (Weisz *et al.*, 2014), suggesting preparatory attentional modulation of auditory cortex activity prior to stimulus presentation.

Age-related changes in connectivity have been observed primarily through fMRI studies during resting-state and visual paradigms, revealing altered or reduced functional connectivity across most cortical networks in older adults (Damoiseaux, 2017; Geerligs *et al.*, 2014; Onoda *et al.*, 2012; Sala-Llonch *et al.*, 2015). These alterations have been linked to cognitive decline and support the dedifferentiation theory of aging (see Section 1.2.2). In the auditory domain, functional connectivity has been reported to both increase (Müller *et al.*, 2009) and decrease (Hsiao *et al.*, 2014; Moezzi *et al.*, 2019) with age. Although differences in measurement approaches complicates the interpretation of these changes (Brookes *et al.*, 2019), available evidence suggests that older adults tend to exhibit reduced and disrupted connectivity patterns, which may contribute to cognitive decline.

1.4 Auditory perceptual learning as an intervention against cognitive decline

Auditory perceptual training has gained attention as a promising intervention to counteract cognitive decline by promoting generalization of learning to untrained tasks (Kattner *et al.*, 2017; Mahncke *et al.*, 2006; Tremblay *et al.*, 1997; Wright and Zhang, 2009). This transfer of learning is typically categorized in two types: near-transfer, where the trained and untrained tasks rely on similar processes or stimulus features, and far-transfer, where improvements extend to tasks that involve different cognitive abilities (Bürki *et al.*, 2014). Both types of generalization have been explored in auditory training studies. Examples of near-transfer include the transfer of frequency discrimination from a trained ear to the other (Delhommeau *et al.*, 2002), or from a trained frequency to untrained frequency ranges (Amitay *et al.*, 2005; Fitzgerald and Wright, 2011). Other studies have investigated far-transfer effects, based on evidence that degraded sensory representations, such as those observed in age-related hearing loss (Lentz *et al.*, 2022; Ouda *et al.*, 2015), can negatively impact higher-order cognitive processes (Roberts and Allen, 2016; Vinogradov *et al.*, 2012). From this perspective, improving the quality of sensory input through training may in turn support cognitive functions such as attention, memory, and executive control (Vinogradov *et al.*, 2012). Indeed, complex auditory training programs have been shown to generalize to verbal learning and global cognition in individuals with schizophrenia (Adcock *et al.*, 2009; Fisher *et al.*, 2009), and to persist months after the intervention (Fisher *et al.*, 2010; Loewy *et al.*, 2022). Together, these studies suggest that auditory perceptual training may lead to enduring cognitive benefits, potentially driven by changes in brain plasticity that could benefit older adults.

1.4.1 Neurological impact of auditory perceptual training

Behavioral improvements and their generalization to other domains suggest that auditory perceptual training drives plastic changes in auditory and attention-related brain networks. Indeed, a substantial body of research over the past 25 years has documented such neural adaptations in the auditory cortex and associated regions (Irvine, 2018; Stropahl *et al.*, 2020; Tremblay, 2007). Across this literature, oddball paradigms remain the most common approach for auditory training, typically involving frequency or speech contrasts, and consistently eliciting increases in neural responses including the M100, P2, P3, and MMN (Menning *et al.*, 2000; Reinke *et al.*, 2003; Tong *et al.*, 2009; Tremblay *et al.*, 1997). However, the observation of such changes does not necessarily establish a causal link to learning, as certain components such as P2 may instead reflect stimulus exposure or task execution rather than learning-specific plasticity (Tremblay *et al.*, 2014). In contrast to these correlational findings, Matsushita *et al.* (2021) provided causal evidence for the role of the right auditory cortex in pitch learning, demonstrating that its disruption with transcranial direct current stimulation impaired both pitch discrimination and its learning. This result also supports the notion of hemispheric specialization in auditory processing, with the right hemisphere more involved in spectral resolution (Albouy *et al.*, 2020; Zatorre *et al.*, 2002).

Auditory training has been shown to produce both near and far transfer effects, with the extent of generalization depending on task difficulty: more challenging paradigms tend to yield broader cognitive benefits (Flegal *et al.*, 2019; Vinogradov *et al.*, 2012). Further, recent evidence indicates that while behavioral improvements and transfer emerge early in training, corresponding neural changes in sensory perception often require sustained practice to consolidate (Reetzke *et al.*, 2018). These findings align with the Reverse Hierarchy Theory of learning, which proposes that early stages of learning rely on higher-order cognitive systems, such as attention, and that with extended practice, these systems progressively engage and refine lower-level sensory representations (Ahissar *et al.*, 2009; Nahum *et al.*, 2008). Supporting this framework,

complex auditory training tasks have been associated with the recruitment of frontal and parietal regions involved in attentional control, including the inferior frontal gyrus and the inferior parietal lobule (Schneiders *et al.*, 2012; de Souza *et al.*, 2013).

Clinical populations with auditory-related deficits, such as those with dyslexia or schizophrenia, have likewise demonstrated behavioral improvements following auditory training, often accompanied by neurophysiological changes linked to cognitive gains (Dale *et al.*, 2016; Russo *et al.*, 2005). In schizophrenia, for example, auditory training has been found to restore reduced sensory representations in auditory cortex, and this recovery underlies transfer effects to executive function tasks (Dale *et al.*, 2016). Moreover, in recent-onset cases, such training has been linked to reduced cortical thinning, implying a potential neuroprotective effect (Ramsay *et al.*, 2021). Together, these findings highlight the capacity of auditory training to induce meaningful neural adaptations across diverse populations and suggest that similar mechanisms could be leveraged to help counteract the sensory and cognitive declines associated with aging.

1.4.2 Auditory perceptual training in an aging paradigm

Brain plasticity varies across the lifespan, with distinct patterns emerging at different stages of development and aging (Cisneros-Franco *et al.*, 2020; Voss *et al.*, 2017). Evidence from animal models suggests that while older brains can exhibit experience-dependent plasticity, the changes observed following non-adaptive auditory discrimination training tend to be short-lived and decay more rapidly than in younger rats (Cisneros-Franco *et al.*, 2018). In contrast, studies employing adaptive or cognitively demanding auditory regimens have produced more durable effects, including the reversal of age-related functional impairments in auditory cortex (de Villers-Sidani *et al.*, 2010) and improved distractor suppression (Mishra *et al.*, 2014). Moreover, when animals are exposed to attentionally demanding paradigms in young adulthood, the resulting benefits can persist into old age, thereby delaying typical age-related decline (Cheng *et al.*, 2017). These findings suggest that, in humans, auditory training may

serve not only to mitigate cognitive and sensory decline in older adults, but also to delay its onset when implemented earlier in life, particularly through adaptive and cognitively demanding interventions.

Perceptual and cognitive deficits are well documented in older adults, encompassing impairments in auditory functions such as frequency discrimination and inhibitory control (Freigang *et al.*, 2011; Mishra *et al.*, 2014; Moore *et al.*, 2019; Stothart and Kazanina, 2016), as well as declines in attention and memory (Brehmer *et al.*, 2012; Fernández-Rubio *et al.*, 2024; Zanto and Gazzaley, 2016). Nevertheless, learning rates in older adults are often comparable to those of younger individuals (Alain and Snyder, 2008; Brehmer *et al.*, 2016; Colby *et al.*, 2018; Karawani *et al.*, 2016; Kishon-Rabin *et al.*, 2013; Scharenborg and Janse, 2013), suggesting that their capacity for learning remains intact despite overall performance deficits. Behavioral evidence further indicates that auditory training can lead to learning transfer in older adults with and without hearing loss. In normal-hearing older adults, benefits have been observed in domains such as working memory span (Mishra *et al.*, 2014), problem solving (Strenziok *et al.*, 2014), attention (O'Brien *et al.*, 2017), and speech-in-noise perception (Heidari *et al.*, 2020). Similarly, older adults with presbycusis have shown gains in auditory memory, processing speed, neural timing, attention, and speech comprehension following training (Karawani *et al.*, 2016; Stropahl *et al.*, 2020). The coexistence of perceptual and cognitive decline with preserved learning capacity and evidence of transfer across domains suggests that training engages distinct, potentially compensatory neural mechanisms in older adults that may differ from those observed in younger individuals.

Despite extensive behavioral evidence, relatively few studies have examined the neurophysiological changes that underlie auditory training in older adults (see Table 1.1). Using MRI, Strenziok *et al.* (2014) reported that auditory cognitive training induces both functional and structural modifications in attention-related networks, including changes in white matter integrity and network connectivity. Electrophysiological studies have further shown training-related modulations across multiple stages of auditory

processing, from brainstem to cortical and spectral responses. These include restored temporal precision and improved speech envelope encoding, even in older adults with hearing loss where training restored exacerbated responses to levels observed in normal-hearing peers (Anderson *et al.*, 2013a, 2014, 2013b). Additional cortical changes include latency and amplitude shifts in early ERP components (P1, N1, P2), reductions in later components (P3), and increased frontal theta power linked to target detection and distractor suppression (Alain and Snyder, 2008; Mishra *et al.*, 2014; O'Brien *et al.*, 2017; Yang *et al.*, 2018). Increases in alpha power and global functional connectivity have also been reported following auditory and audiovisual training (Ren *et al.*, 2024). Notably, some of these neurophysiological effects have been found to persist for several months after training (Anderson *et al.*, 2014; Bugos *et al.*, 2022).

However, only a limited number of studies have directly compared the neurophysiological effects of auditory training between younger and older adults. Among them, Alain and Snyder (2008) employed a rapid learning paradigm within a single session, while Ren *et al.* (2024) and Yang *et al.* (2018) investigated audiovisual integration. Although these approaches offer valuable insights, isolating auditory processing from multisensory influences is essential to uncover the mechanisms of auditory-specific plasticity available in older adults. Such understanding is critical to evaluate the potential of auditory perceptual learning as a targeted intervention for age-related hearing loss and its associated cognitive decline. Moreover, most studies have examined neural activity only before and after training, overlooking the dynamic changes that unfold across the learning process and that could reveal how brain responses evolve over time and how these trajectories differ by age. Critically, to the best of our knowledge, no prior work has leveraged the temporal and spatial precision of magnetoencephalography to examine region-specific changes in neural activity during auditory training in younger and older adults. In particular, the extent to which attention networks, such as the dorsal and ventral attention systems, interact with auditory cortex during training, and how these interactions differ with age, remains unknown. Addressing this gap, the present thesis provides a time-resolved,

region-specific comparison of auditory learning in younger and older adults, using MEG to characterize age-related differences in neural activity during perceptual learning, across time-domain, time-frequency, and connectivity-based measures.

Table 1.1: Overview of literature on neural effects of auditory training in older adults. Comprehensive summary of studies investigating the neural effects of auditory training in older adults, detailing experimental paradigms, imaging modalities, participant cohorts, and key neurophysiological outcomes. Rows in purple highlight particularly relevant studies; the final row summarizes the present study. ABRs: auditory brainstem responses, ERPs: event-related potentials, TF: time-frequency analysis, PLV: phase-locking value, SPIN: Speech-in-Noise test, ITL: inferior temporal lobe, SPC: superior parietal cortex, AC: auditory cortex, DAN: dorsal attention network, VAN: ventral attention network, $\uparrow/\downarrow$: increase/decrease in amplitude or power, =: significant correlations between variables.

Study	Training paradigm	Participants (age)	Imaging settings	Behavioral results	Neural training effects
2008 Alain and Snyder	Rapid learning: double-vowel discrimination One session with 5 blocks: 40 mins	Younger (YA): 16 (24 $\pm$ 4.6) Older (OA): 14 (67.8 $\pm$ 5.8)	EEG: ERPs Sessions: 1 across all blocks Task: Same as training	OA : lower accuracy, but no learning rate differences with YA; higher response times than younger	Training: $\downarrow$ frontocentral N1 amplitude OA : $\downarrow$ mastoid and cerebellar N1 amplitude; $\uparrow$ P1; earlier N1; $\uparrow$ P2, later and frontal YA : 140-320 ms component related to performance
2013a Anderson et al.	Brain Fitness™ auditory cognitive training (Posit Science Corporation) 8 weeks: 40 hours	Older: 58 (64.09 $\pm$ 5.5) Hearing loss control (HLC): 15 Hearing loss training (HLT): 15 Normal hearing control (NHC): 14 Normal hearing training (NHT): 14	EEG: ABRs Sessions: 2; pre and post Task: [da] synthetic syllable in quiet and in background noise	HLT : $\uparrow$ attention, $\uparrow$ SPIN NHT : $\uparrow$ attention, $\uparrow$ memory	HLT : before training, increased envelope representation. After training, decrease in representation (similar to NHC/T)
2013b Anderson et al.	Brain Fitness™ auditory cognitive training (Posit Science Corporation) 8 weeks: 40 hours	Older: 67 (63.0 $\pm$ 3.7) Active training (AT): 35 Active control (AC): 32	EEG: ABRs Sessions: 2; pre and post Task: [da] synthetic syllable in quiet and in background noise	AT : $\uparrow$ SPIN, $\uparrow$ auditory short-memory, $\downarrow$ processing speed	AT : earlier syllable response in noise compared with quiet; $\downarrow$ latency in noise only; $\downarrow$ interpeak variability in noise
2014 Anderson et al.	Brain Fitness™ auditory cognitive training (Posit Science Corporation) 8 weeks: 40 hours	Older: 30 [6-month follow-up from Anderson et al. (2013b)]	EEG: ABRs Sessions: 3; pre, post and 6-month follow-up Task: [da] synthetic syllable in quiet and in background noise	AT : processing speed conserved	AT : decreased latency conserved
2014 Mishra et al.	Two trainings: Adaptive distractor training (ADT ; “Beep Seeker”) Adaptive target training (ATT) 4-6 weeks: 6 hours	Older: 47 (69) ADT : 17 ATT : 15 untrained (UT): 15 Younger: 15 (24) [behavior only]	EEG: ERPs, TF, PLV Sessions: 2; pre and post Task: Same as training	ADT : $\uparrow$ discrimination, $\downarrow$ false positives ATT : $\downarrow$ false positives, but due to response bias and not discrimination	ADT : $\downarrow$ 150-160 ms response that correlated with $\uparrow$ discrimination; located in STG and BA22; $\uparrow$ frontal theta (50-150ms) to targets; $\downarrow$ theta = $\downarrow$ 150-160ms response
2014 Strenziok et al.	Three trainings: Brain Fitness™ (BF) Space Fortress™ (SF) Rise of Nations™ (RON) 6 weeks: 36 hours	Older: 42 (69 $\pm$ 5)	fMRI: connectivity, axial diffusion (AD) and other tractography measures Sessions: 2; pre and post Task: Resting state (no task)	BF : $\uparrow$ performance, $\uparrow$ matrix and everyday reasoning SF : $\uparrow$ performance, $\uparrow$ working memory, $\uparrow$ matrix and everyday reasoning RON : $\uparrow$ performance, $\downarrow$ working memory, $\downarrow$ matrix reasoning	Training: $\uparrow$ AD in left lingual gyrus and right thalamus BF : $\uparrow$ AD in right temporo-occipital junction (rTOJ) = better everyday reasoning, but lower working memory accuracy; $\downarrow$ ITL-SPC connectivity = better everyday reasoning SF : $\downarrow$ AD in rTOJ; $\downarrow$ ITL-SPC connectivity RON : $\downarrow$ AD in rTOJ; $\uparrow$ ITL-SPC connectivity

Continued on next page

Table 1.1: Overview of literature on neural effects of auditory training in older adults. (Continued)

Study	Training paradigm	Participants (age)	Imaging settings	Behavioral results	Neural training effects
2017 O'Brien <i>et al.</i>	Brain Fitness™ auditory cognitive training (Posit Science Corporation) 10 weeks: 16 hours	Older: 24 Trained (OT): 9 (69.69±7.66) Control (OC): 15 (71.60±8.29)	EEG: ERPs Sessions: 2; pre and post Task: active auditory oddball	No changes in oddball identification (already at 99% accuracy)	OT: ↓ parietal and frontal P3b; no changes in P1-N1-P2 ↑ posterior P3b amplitude = ↑ self-reported auditory cognitive difficulties
2018 Yang <i>et al.</i>	Bimodal audio-visual stimulus (block based increase of difficult when accuracy exceeded 60%) 4 weeks: 4 hours	Older: 26 Training (OT): 13 (70.7) Control (OC): 13 (68.1) Younger: 26 Training (YT): 13 (20.1) Control (YC): 13 (20.5)	EEG: ERPs (P3 only) Sessions: 2; pre and post Task: Active auditory oddball-like task: count target stimuli (20%)	OT: ↑ performance, lower MMSE scores than YT YT: ↑ performance	OT: ↑ P3 amplitude YT & YC: ↓ P3 latency compared to OT
2019 Alain <i>et al.</i>	Visual art or music classes at Royal Conservatory of Music 12 weeks: 36 hours	Older: 53 Music training (MT): 17 (67.7±5.8) [15 at follow-up] Visual art training (VT): 19 (68.9±6) [14 at follow-up] Control (C): 17 (68.5±6)	EEG: ERPs, TF Sessions: 3; pre, post and 3-month follow-up Task: Two auditory oddball paradigms using pitch (piano tones) or speech (/u/ or /ou/); and one visual Go/NoGo task	MT: ↓ Stroop speed, maintained at 3-month follow-up; ↑ Digit Symbol task VT: ↑ Digit Symbol task	MT: ↑ N1 and P2 for pitch oddball, conserved after 3-month follow-up; ↓ MMN latency VT: ↑ N1 and P2 for pitch oddball More training effects observed for visual Go/NoGo task.
2022 Bugos <i>et al.</i>	Visual art or music classes at Royal Conservatory of Music 12 weeks: 36 hours	Older: 50 Music training (MT): 16 (67.75±6.02) Visual art training (VT): 17 (68.47±6.21) Control (C): 17 (57.5±5.99)	EEG: ERPs, TF Sessions: 3; pre, post and 3-month follow-up Task: Two oddball paradigms using pitch (piano tones) or speech (/u/ or /ou/)	Presented in Alain <i>et al.</i> (2019)	Training: ↑ frontal theta power to standard stimuli VT & MT: ↑ frontal and frontocentral theta power (100–175ms); ↑ mid-frontal alpha power (MT > VT); increase in theta power preserved in 3-month follow-up
2024 Ren <i>et al.</i>	Adaptive bimodal audio-visual training based on Yang <i>et al.</i> (2018) (difficulty change: 3 up, 1 down) 5 days: 5 hours	Older: 40 Training (OT): 20 (59.3±6.1) Control(OC): 20(57.5±3.7) Younger: 40 Training (YT): 20 (20.1±1.1) Control(YC): 20(19.9±1.2)	EEG: ERPs, TF, connectivity Sessions: 2; pre and post Task: similar to training. Non-adaptive audio-visual discrimination task with auditory (A), visual (V) and audiovisual (AV) stimulus	OT & YT: ↑ hit rate (AV > A or V), ↓ false alarm, ↑ perceptual sensitivity (AV > A > V) OT: ↓ response time to AV YT: ↓ response time to A and V Response bias greater and response times slower for older than younger	Significant audiovisual integration at N1, P1, and P3, but training effect only in P3. OT: ↑ P3 in left anterior, right anterior and central regions (and greater than younger); ↑ alpha power in right anterior, left posterior and right posterior; ↑ global functional connectivity (AV > A or V) YT: no clear training effects
Current work	Adaptive auditory perceptual discrimination task 12 days: 3 hours	Older (OA): 8 (61.63±13.76) Younger (YA): 8 (23.38±5.29)	MEG: ERFs, TF, connectivity Sessions: 4; day 1, 5, 9 and 12 of training Task: Same as training	OA: ↑ performance, ↑ Stroop, ↑ auditory attention (RAVLT) YA: ↑ performance, ↑ Stroop	OA: ↑ M100 response in right AC; ↑ preM100 response in right DAN; right DAN→right AC mediation effect; ↑ rightD DAN→right AC connectivity; ↓ pre-stimulus theta in DAN; ↑ preM100 response in VAN YA: ↓ baseline in left AC; ↓ preM100 DAN; ↑ post-stimulus theta; ↑ alpha in AC & DAN = ↑ performance

2

Methodology

2.1 Participants

Sixteen adults participated in the auditory training study, divided into two age groups. The younger adults group consisted of eight individuals aged 20–34 years (mean age: 23.4 years; 5 females) and the older adult group included eight individuals aged 42–77 years (mean age: 61.6 years; 4 females). In addition, data from eight younger individuals aged 20–28 years (mean age: 23.25 years; 7 females) who did not undergo the training were included for test-retest reliability in the cognitive assessments (see [Section 2.7](#) and [Section 3.1.4](#)). All participants were right-handed except for one left-handed individual in the younger trained group. They self-reported being healthy and free from cognitive impairment. Participants provided informed consent for data acquisition and use. This study was approved by the Research Ethics Board of the Montreal Neurological Institute.

Demographic information was collected through a structured questionnaire. Participants provided their date of birth, gender, handedness, and highest level

of education attained (Table 2.2). They also indicated if they were currently enrolled in an educational program or had an incomplete degree. Total years of education were calculated by summing the standard years associated with each completed education level, as outlined in Table 2.1. For instance, a participant who completed high school (12 years) and a 4-year university degree would have a total of 16 years of education. The unique Quebec education system includes CEGEP (Collège d'enseignement général et professionnel), equivalent to two years of pre-university education.

Table 2.1: Equivalence of education levels to years of education.

Education level finished	Years of education equivalence
Less than High school	< 12
High school diploma	12
CEGEP (Quebec only) ^a	14
Bachelor's degree	16
Master's degree	18
Doctoral degree (Ph.D./MD)	23

^a CEGEP: Collège d'enseignement général et professionnel (General and Vocational College in Quebec).

Language Proficiency Index (LPI)

Participants reported the languages they spoke, the percentage of daily conversations in each language, the age they began learning each language, years of practice, and the age at which they achieved fluency. For each language, they self-assessed their proficiency in reading, writing, speaking, and listening on a scale from 1 ("Very poor") to 7 ("Native-like"). The overall proficiency score for each language was obtained by summing the scores across the four categories (maximum of 28 points per language).

The language proficiency index (LPI) was then computed as the sum of these proficiency scores across all languages, divided by 28. An LPI of 1 corresponds to a monolingual individual with native-like proficiency in all four skills, while an LPI of

2 reflects a total proficiency score of 56, which can be achieved by a fully bilingual individual or someone speaking three or more languages at varying proficiency levels. No maximum value was set, as it depends on the number of languages spoken and their respective proficiency levels. The formula for the LPI is as follows:

$$\text{LPI} = \frac{\sum_{j=1}^n (R_j + W_j + S_j + L_j)}{28}$$

where R_j, W_j, S_j, L_j are the self-assessed scores for reading, writing, speaking, and listening, for language j , and n is the number of languages.

Musical education

Participants detailed their musical training, specifying:

- a) **Musical Education (ME):** Total years of formal and informal musical education.
- b) **Average Weekly Practice during Past Musical Education (AWP_{past}):** Average hours per week practiced during those years.
- c) **Current Average Weekly Practice (AWP_{current}):** Hours per week currently dedicated to musical practice.
- d) **Musicality Index (MI):** Calculated as $\text{MI} = \text{ME} \times \text{AWP}_{\text{past}}$, representing the cumulative musical practice over their lifetime.

Participants also listed instruments played and whether they were currently practicing any instrument. The final scores for each measure were pooled across all described instruments.

2.2 Audiometric evaluation

Each subject underwent a formal audiometric evaluation using a Maico MA 728 audiometer (Maico, Minneapolis, MN, USA) to confirm normal hearing thresholds. Pure-tone audiometry was conducted at frequencies of 0.5, 1, 2, 3, 4, 6, and 8 kHz for

each ear. The decibels hearing level (dBHL) per frequency (Avg_f) were calculated by averaging the measurements from both ears:

$$Avg_f = \frac{dBHL_{Left.f} + dBHL_{Right.f}}{2}$$

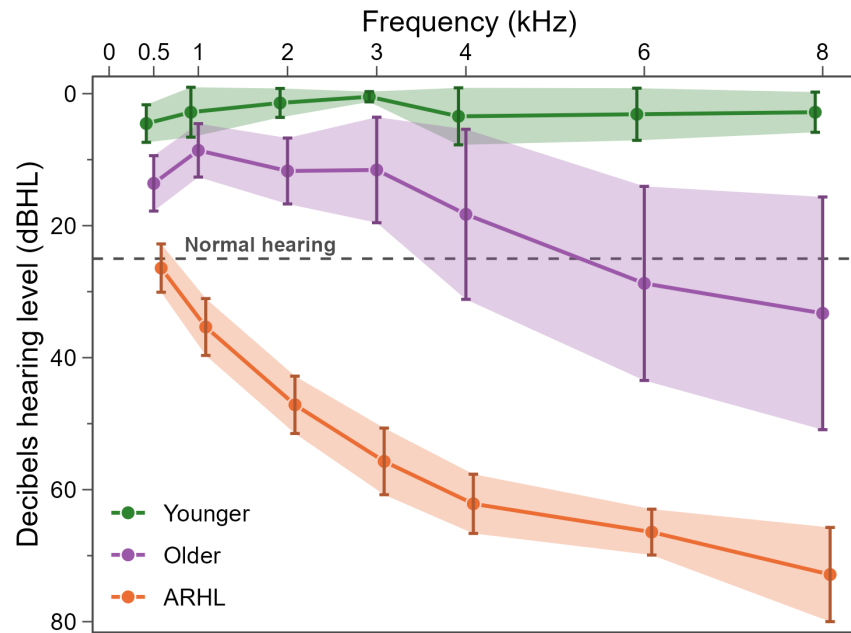


Figure 2.1: Audiometric thresholds averages across age groups with normal hearing reference. Mean audiometric thresholds of hearing level (in dBHL) across frequencies (in kHz) are shown for Younger (green) and Older (purple) participants, with a comparison group of diagnosed age-related hearing loss individuals (ARHL, orange). Shaded areas represent 95% confidence intervals around the means. The horizontal dashed line at 25 dB indicates the threshold for normal hearing.

The average hearing level at each tested frequency for each age group, along with a comparison to a separate group with diagnosed age-related hearing loss, can be found in Figure 2.1. From the average of each participant, three key values were derived:

- a) **Standard Pure Tone Average (PTA_{std}):** As reported by Gates and Hoffman (2011), this value is the four-frequency average of 0.5, 1, 2 and 4 kHz.

$$PTA_{std} = \frac{Avg_{0.5} + Avg_1 + Avg_2 + Avg_4}{4}$$

- b) **Full range PTA (PTA_{full}):** The average of all measured frequencies.

$$PTA_{full} = \frac{Avg_{0.5} + Avg_1 + Avg_2 + Avg_3 + Avg_4 + Avg_6 + Avg_8}{7}$$

- c) **Higher frequencies PTA (PTA_{high}):** The average of the highest frequencies (4, 6 and 8 kHz) which are particularly affected by aging.

$$PTA_{high} = \frac{Avg_4 + Avg_6 + Avg_8}{3}$$

A summary of the audiometric variables per age group can be found in [Table 2.2](#). Participants with PTA_{std} exceeding 25 dBHL were considered to have hearing impairment. No participants were excluded based on standard audiometric criteria.

Table 2.2: Summarized demographic and audiometric data of trained participants divided by age group. The table shows the number of participants (n), the number of females, the number of left-handed participants, and the mean (μ), median (Mdn), and range of all the other collected variables from the participants that underwent the auditory training, divided by age group.

Demographic		Younger	Older
n		8	8
Gender (n females)		5	4
Handedness (n left-handed)		1	0
Age	μ	23.4	61.6
	Mdn	21	66
	range	20–35	42–77
Education (total years)	μ	16.4	18
	Mdn	16	17
	range	14–23	14–23
Languages (n)	μ	2.3	2
	Mdn	2	2
	range	1–4	1–5
Language Proficiency Index (LPI) $LPI = \frac{\sum_{j=1}^n (R_j + W_j + S_j + L_j)}{28}$ ^a	μ	1.9	1.6
	Mdn	2	1.3
	range	1–2.5	1–3.4

Continued on next page

Table 2.2: Summarized demographic and audiometric data of trained participants divided by age group. (Continued)

Demographic		Younger	Older
Musical Education (ME) ME = years of musical education	μ	8.4	1.3
	Mdn	9.5	1.5
	range	0–14	0–3
Current Average Weekly Practice Time (AWP_{current}): current hours/week of musical practice	μ	1.1	1
	Mdn	0.3	0
	range	0–5	0–3
Musicality Index (MI) MI = ME $\times$ AWP_{past} ^b	μ	42.2	4.3
	Mdn	35	4.5
	range	0–96.5	0–11
Standard Pure Tone Average (PTA_{std}) $Avg_f = \frac{dBHL_{\text{Left}\cdot f} + dBHL_{\text{Right}\cdot f}}{2}$ ^c $PTA_{\text{std}} = \frac{Avg_{0.5} + Avg_1 + Avg_2 + Avg_{4\text{kHz}}}{4}$ ^d	μ	3	13
	Mdn	1.6	11.3
	range	0.6–11.3	3.1–21.9
Full range PTA $PTA_{\text{full}} = \frac{Avg_{0.5} + \dots + Avg_{8\text{kHz}}}{7}$ ^{d e}	μ	2.5	17.8
	Mdn	2.0	15.5
	range	0.4–6.8	2.9–31.8
Higher frequencies PTA $PTA_{\text{high}} = \frac{Avg_4 + Avg_6 + Avg_{8\text{kHz}}}{3}$ ^d	μ	2.8	26.4
	Mdn	2.1	25
	range	0–7.5	2.5–48.3

^a Calculated per subject. n : number of languages spoken by selected subject. R , W , S , and L : self-assessed scores for reading, writing, speaking, and listening, respectively, for each language j . Each score ranged from 1 ("Very poor") to 7 ("Native-like").

^b AWP_{past} : average weekly practice (AWP) during the years of musical education.

^c f : frequency in kHz. $dBHL_{\text{Left}\cdot f}$ and $dBHL_{\text{Right}\cdot f}$: decibels hearing level (dBHL) for the left and right ears, respectively, at frequency f .

^d Average hearing loss (Avg_f) at specified frequency in kHz

^e PTA_{full} : average hearing loss across all tested frequencies (0.5, 1, 2, 3, 4, 6 and 8 kHz).

2.3 Auditory perceptual training task

A training session consisted of 125 trials, of which only one-third contained the target stimulus. The structure of a single trial is illustrated in [Figure 2.2](#). Each trial of the perceptual training task required participants to determine whether they heard a target stimulus or not. The target tone changed for each training session and was presented twice at the beginning of the session for reference. Before the training, participants were instructed to press a response button only when they identified the target stimuli. Participants were instructed to keep their eyes open and fixate on a cross at the center of a blank screen throughout the training duration, to minimize eye movement artifacts. Each trial began with a random inter-trial interval (ITI) of 500–2000 ms. After this, an auditory cue (frequency: 5 kHz, duration: 25 ms) was presented to prevent a startle response, followed by 750 ms of silence. Then, either a target or a non-target stimulus was played for 250 ms, followed by 2200 ms of silence. Afterwards, a visual cue (green cross) signaled the participant to press the response button if they identified the stimulus as the target. Both, the cue and the stimuli signals had onset and offset ramps lasting 5 ms.

This response period ended as soon as the button was pressed or after 2000 ms if no response was registered. Finally, visual feedback was provided for 1000 ms, with the fixation cross changing to “o” for a correct response or to “x” for an incorrect one.

2.4 Stimuli description and staircase procedure

The difficulty of the auditory perceptual training task varied trial-by-trial as a function of the participant’s response following a standard staircase procedure. The difficulty increased by one level each time the stimulus was correctly identified as the target with a button press (hit). If the participant responded incorrectly, either by pressing the button when a non-target stimulus was presented (false positive, FP) or by abstaining from responding when the target was played (miss), the difficulty level decreased by

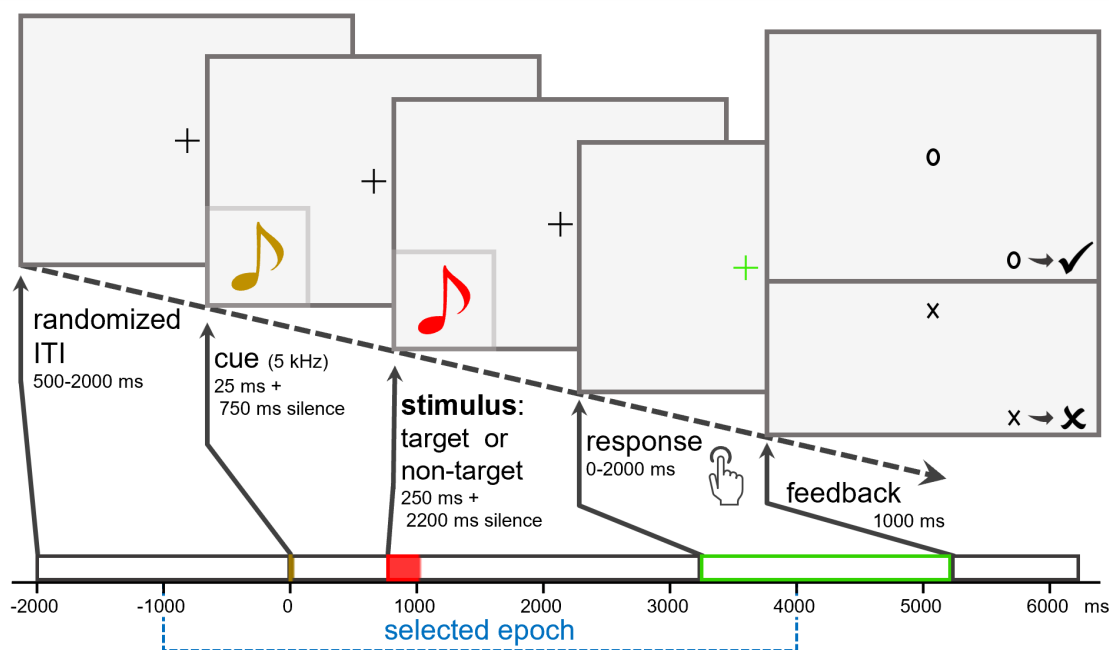


Figure 2.2: Structure of a single trial of the auditory task. The trial begins with a random inter-trial interval (ITI) followed by a brief auditory cue to prevent a startle response. After a period of silence, an auditory stimulus (either the target or a non-target) is presented. Following another silence interval, a change in the color of the fixation cross signals the subject to respond with a button press if they identify the stimulus as the target. If a button press is registered, the response period ends immediately; otherwise, it continues until 2000 ms have elapsed. Finally, visual feedback is provided via a change to the fixation cross symbol (o = correct response, x = incorrect response).

one. If the participant correctly recognized a non-target and withheld the button press (withhold, WH), the difficulty level did not change (Figure 2.3a).

All stimuli, whether target or non-target ones, were composed of five pure tones (Figure 2.3b): a base tone with a frequency of 220 Hz and four additional tones whose frequencies changed depending on the training session (target) and the difficulty level (non-targets). At the start of each training session, the four tones composing the target were randomly chosen in pairs from a frequency range of 0.6 to 4.8 kHz (equivalent to 1.6 and 4.4 octaves from the base frequency), while maintaining a fixed difference of 1.25 octaves between each pair of tones. The tones within each pair differed by 0.15 octaves.

Once the target was selected, task difficulty was manipulated in two ways: by modifying the *spectral similarity* between target and non-target stimuli (Figure 2.3c),

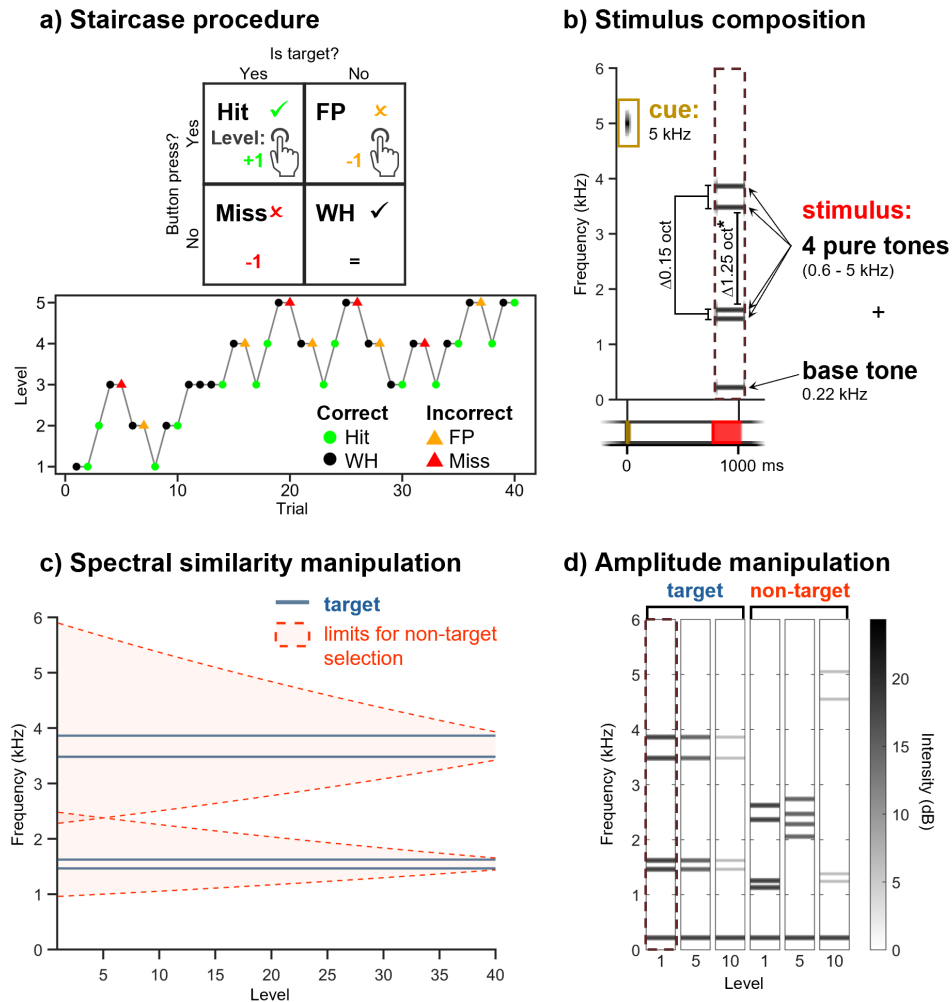


Figure 2.3: Description of the stimulus and its staircase difficulty progression. **a)** The difficulty level increased following correct target identifications (hits) and decreased after incorrect responses: false positives (FP) or missed targets. No change in difficulty occurred after correctly ignoring non-targets (withholds, WH). The lower panel illustrates difficulty progression over the first 40 trials of a training session, including response types and difficulty adjustments. **b)** Each stimulus consisted of a base tone of 220 Hz and four additional pure tones that were selected in pairs. In the target stimuli only (*), the difference between the two pairs was fixed at 1.25 octaves. Within each pair, the two tones were always 0.15 octaves apart. The task increased in difficulty through two manipulations: increasing the spectral similarity of the non-targets to the target (**c**), and reducing the amplitude of the distinguishing frequency components of the stimuli (**d**). **c)** The frequencies of the target tones (blue) were selected at the start of the training session and remained fixed throughout. Spectral similarity was manipulated by dynamically selecting the non-target tone pairs from a frequency range (dotted line) that gradually approached the target frequencies as the difficulty level increased, such that by level 40 the tones were so similar that performance would be at chance level. **d)** Amplitude was manipulated by attenuating the four modulated tones in both target and non-target stimuli as difficulty increased, while keeping the amplitude of the base tone constant, effectively reducing the perceptual salience of the spectral features. Example of intensity in decibels (dB) at each frequency component of the target and non-target tones at levels 1 (variable tones: 37 dB, base tone: 37 dB), 5 (variable tones: 30 dB, base tone: 37 dB) and 10 (variable tones: 13 dB, base tone: 37 dB) are shown.

and by adjusting the *amplitude* of the distinguishing frequency components of all stimuli (Figure 2.3d). For the *spectral similarity manipulation*, the frequencies of the two pairs of tones in non-target stimuli were dynamically selected throughout the training session, becoming increasingly similar to the target frequencies as difficulty increased (Figure 2.3c). Importantly, unlike the target stimuli, the difference in frequency between the two pairs of tones in non-targets was not fixed, allowing greater variability across trials. In parallel, the *amplitude manipulation* involved progressively attenuating the amplitude of the four variable tones in both target and non-target stimuli at higher difficulty levels, while keeping the amplitude of the base tone (220 Hz) constant (Figure 2.3d). This attenuation reduced the perceptual prominence of the spectral features that differentiated the stimuli, effectively decreasing the quality of the acoustic signal (signal-to-noise ratio, SNR) and making it more challenging to distinguish between target and non-target sounds at higher difficulties.

2.5 Evaluation of task performance

Given the adaptive nature of the task (Figure 2.3a), performance was primarily evaluated using the average level reached across all trials per training session, as it best captured task performance (Figure 2.4). To relate task performance to the physiological data acquired on Days 1, 5, 9 and 12 (Figure 2.5), we measured performance from those specific sessions.

2.6 Longitudinal training paradigm

Each participant completed twelve consecutive days of training, as depicted in Figure 2.5. The training task was performed either during MEG recordings (Days 1, 5, 9 and 12) or at home using a provided tablet and headphones on the remaining days. Some younger participants (Subjects 1 to 6) underwent a fifth recording on Day 3, as the initial paradigm included five MEG sessions. However, it was later determined that this schedule was too demanding for the older participants, so the number of sessions was

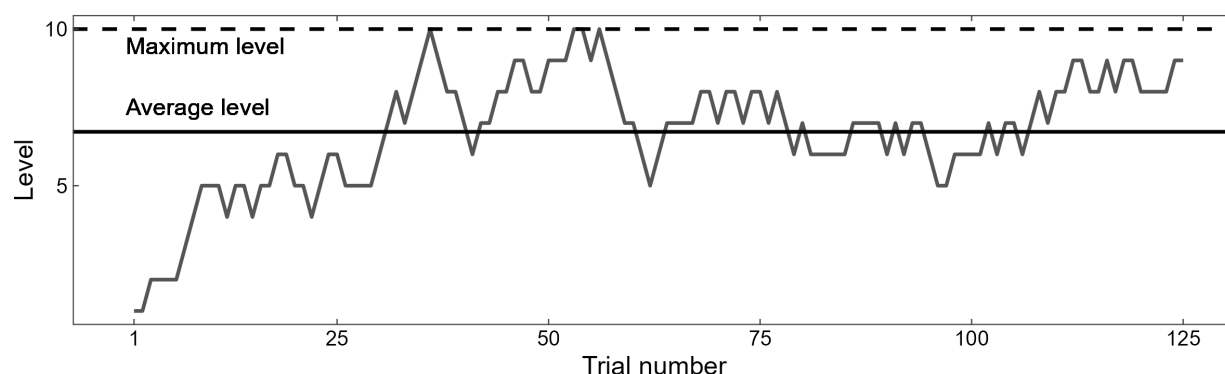


Figure 2.4: Task performance evaluation measures. Example of a training session showing level progression level across all trials. The solid line represents the average level reached during the session, while the dashed line indicates the maximum level. The average level provides a better overall descriptor of task performance.

reduced to four. To standardize the number of MEG sessions across participants, the extra session on Day 3 was excluded from the analysis. The demographic information and the audiometric evaluation, detailed in [Sections 2.1](#) and [2.2](#), and [Table 2.2](#), were collected before the first training session on Day 1.

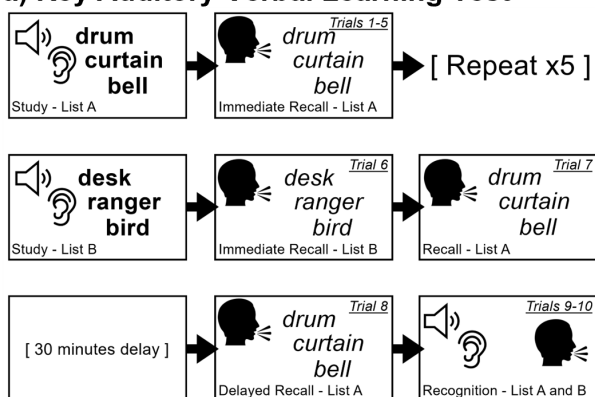
Days	1	2	3*	4	5	6
MEG recording (training is recorded)						
Cognitive tests						
Training at home						
MRI recording						

Figure 2.5: Study schedule. All participants underwent auditory perceptual training over twelve consecutive days. The training task was performed either during MEG sessions (Days 1, 5, 9, and 12) or at home using a tablet. Cognitive tests were also administered before training on Day 1 and following the MEG training session on Day 12. A structural MRI volume was acquired on Day 12 following the last MEG session. *Some participants in the younger group had an additional MEG session on day 3.

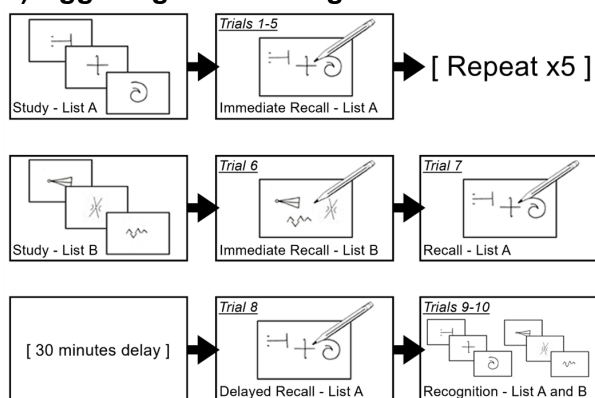
2.7 Cognitive assessments

Three different cognitive tests were administered to each participant before the first training session on Day 1 and after the last training session on day 12 (Figure 2.5): the Rey Auditory Verbal Learning Test (RAVLT), the Aggie Figures Learning Test (AFLT) and the Stroop Color and Word Test (SCWT). This section describes the tests and the scoring methods used to evaluate participant performance.

a) Rey Auditory-Verbal Learning Test



b) Aggie Figure Learning Test



c) Stroop Color Word Test

1	2	3	4	1	2	3	4
Rouge	Jaune	Vert	Bleu	☐	☐	☐	☐
Bleu	Vert	Rouge	Jaune	☐	☐	☐	☐
Jaune	Rouge	Vert	Bleu	☐	☐	☐	☐
Vert	Bleu	Jaune	Rouge	☐	☐	☐	☐
Bleu	Jaune	ouge	Vert	☐	☐	☐	☐
Rouge	Vert	Bleu	Jaune	☐	☐	☐	☐
Jaune	Bleu	Vert	Rouge	☐	☐	☐	☐
Bleu	Jaune	Rouge	Vert	☐	☐	☐	☐
Vert	Rouge	Jaune	Bleu	☐	☐	☐	☐
Bleu	Jaune	Vert	Rouge	☐	☐	☐	☐
Jaune	Bleu	Rouge	Vert	☐	☐	☐	☐
Rouge	Vert	Jaune	Bleu	☐	☐	☐	☐
Vert	Rouge	Bleu	Jaune	☐	☐	☐	☐
Rouge	Jaune	Bleu	Vert	☐	☐	☐	☐
Bleu	Vert	Rouge	Jaune	☐	☐	☐	☐
Rouge	Jaune	Bleu	Vert	☐	☐	☐	☐

Figure 2.6: Description of the cognitive tests used to evaluate generalization to untrained tasks. **a)** Description of the Rey Auditory Verbal Learning Test. **b)** Description of the Aggie Figure Learning Test modified from Robertson *et al.* (2018). **c)** Example of the written Stroop Color Word Test used.

A separate group of eight younger participants (20–28 years; mean age: 23.5 years; 6 females) who did not undergo auditory training was included to control for potential test-retest effects on the cognitive assessments (Bürki *et al.*, 2014; Fehr *et al.*, 2014). This untrained control group completed the same cognitive tests as the trained participants

during two sessions separated by twelve days (same time interval as the training period).

Rey Auditory Verbal Learning Test (RAVLT)

The RAVLT is a neuropsychological tool used to assess episodic memory by evaluating verbal learning and memory (Rey, 1964). The test involves five consecutive presentations of a 15-word list (List A). After each presentation, the participant is asked to verbally recall as many words as possible (Trials 1–5). Next, a new 15-word list (List B) is presented, followed by a recall test for List B (Trial 6). Afterwards, the participant is asked to recall the words from List A again (Trial 7). After completing other tasks for approximately 30 minutes, the participant is asked to recall the words from List A again (Trial 8). Finally, two recognition trials follow, where all the words from List A are mixed with some words from List B and with 20 distractor words absent on either list. The participant then identifies which words belong to List A (Trial 9), and the same process is repeated for List B (Trial 10) using all words from List B, some words from List A, and the distractor words (Figure 2.6a). To minimize test-retest effects, different word lists were used for each session.

To score the RAVLT, five measures were selected, as described in Table 2.3. **Total Score** reflects the retention of words across the five repetitions (Trial 1–5). **Learning Gain** measures learning progress by showing the difference in word retention between the first (Trial 1) and the last (Trial 5) trials. The **Delayed Recall Index** represents the forgetting rate of learned words, indicating how many words were forgotten during delayed recall (Trial 8), which occurs around 30 minutes after the final repetition (Trial 5). **Retroactive Interference** illustrates the difficulty of retaining List A in memory after learning List B. **Proactive Interference** captures the challenge of learning new words (List B) when a previous list (List A) already exists in memory.

Table 2.3: Score calculation and interpretation of RAVLT performance.

Name	Calculation	Interpretation	Reference
Total Score	$Trial1 + Trial2 + Trial3 + Trial4 + Trial5$	Total retention of words across repetitions	Moradi <i>et al.</i> (2017)
Learning Gain	$\frac{(Trial5 - Trial1)}{Trial1}$	Retention difference after trial repetition: higher number means more learning	Modified from "RAVLT Learning" Moradi <i>et al.</i> (2017)
Delayed Recall Index	$\frac{(Trial8 - Trial5)}{Trial5}$	Forgetting rate of learnt words: negative numbers mean words forgotten	Modified from "RAVLT forgetting" in Moradi <i>et al.</i> (2017)
Retroactive Interference	$\frac{(Trial5 - Trial7)}{Trial5}$	Interference of List B to retain List A information: higher number means more words forgotten due to interference	Modified from Ricci <i>et al.</i> (2012)
Proactive Interference	$\frac{(Trial1 - Trial6)}{Trial1}$	Interference of List A retention to learn List B information: higher number means less words learnt from List B due to interference	Modified from Ricci <i>et al.</i> (2012)

Aggie Figure Learning Test (AFLT)

The AFLT is a visual memory test designed as a non-verbal analog of the RAVLT (Majdan *et al.*, 1996; Sziklas and Jones-Gotman, 2008), and thus has a similar structure (Figure 2.6b). Participants are first presented with a set of 15 abstract symbols (List A) and asked to draw as many symbols as they can remember. This process is repeated five times (Trial 1–5). Next, a second set of 15 abstract symbols (List B) is presented, and the participant must recall and draw symbols from List B (Trial 6), followed by another recall attempt for List A (Trial 7). After a 30-minute delay, during which other tasks are completed, participants are asked to recall symbols from List A again (Trial 8). Finally, all symbols from List A are then mixed with symbols from List B and distractor symbols not found in either List, then participants must identify which symbols belonged to List A (Trial 9). The same procedure is repeated for List B (Trial 10). To compare between visual (AFLT) and auditory (RAVLT) modalities, AFLT performance was evaluated using

the same scoring measures as the RAVLT (Table 2.3). Additionally, retest effects were minimized by using different symbol lists on each testing session.

Stroop Color and Word Test (SCWT)

The SCWT is widely used to evaluate cognitive interference inhibition, with several scoring methods available (Scarpina and Tagini, 2017). For this study, we employed a simplified, time-constrained version of the Stroop test, focusing solely on the color-word condition. Each participant received a printed Stroop list (Figure 2.6c) consisting of two sections: the color-word Stroop task with 100 words and response boxes, both arranged in four columns. The layout was adapted to each participant's handedness by positioning the response boxes on the left for left-handed individuals, and to their language preference by using either French or English words. Participants were instructed to write the first letter of the ink color in which each word was printed in the corresponding box. The final score for this task, referred to as "*color-word score*", was based on the total number of correct responses recorded within the 40-second time limit.

2.8 Magnetic Resonance Imaging

For each participant, a three-dimensional T1-weighted structural MRI volume covering the entire brain was acquired on Day 12 (Figure 2.5) using a 3T Siemens Prisma scanner with an 8-channel head coil, to obtain high-resolution anatomical images for segmentation and co-registration with the functional imaging data. The scanning parameters were: repetition time = 27 ms, echo time = 9.20 ms, between 176 and 192 sagittally oriented slices with a slice thickness of 1 mm, voxel size of $1 \times 1 \times 1 \text{ mm}^3$, and field of view = $240 \times 256 \text{ mm}^2$.

2.9 Magnetoencephalography

All MEG recordings were processed following recommended good practices for group analysis (Gross *et al.*, 2013; Tadel *et al.*, 2019) using MATLAB 2021b in combination with the *Brainstorm* software (Tadel *et al.*, 2011). Each step of the analysis, from data acquisition to connectivity assessment, is described in subsequent sections.

2.9.1 MEG acquisition and stimuli presentation

First, the head of each participant was digitized with at least 100 points distributed across the scalp, eyebrows, and nose, using a *Polhemus FASTRACK* system (Polhemus Inc., Colchester, VT, USA), to co-register individual MEG data with structural MRI. To control for head movement inside the MEG helmet, three head-positioning coils were placed at fiducial anatomical locations (nasion, left and right pre-auricular points).

Blinks and eye movements were recorded using bipolar electro-oculographic (EOG) leads placed about 1 cm above and below one eye, and about 1 cm lateral of the outer canthi. Two channels, placed under the right clavicle and at the bottom left of ribcage, were used to record electrocardiographic (ECG) activity. An electrical ground was located at the left clavicle. MEG was recorded using a 275-channel (axial gradiometers) whole-head MEG system (CTF MEG International Services Ltd.) in a magnetically shielded room at a rate of 12 kHz. An empty room recording (a recording without the participant inside the shielded room) was acquired immediately before or after each MEG session.

Stimuli were generated using a *Sound Blaster X-Fi Titanium HD* audio card (Creative, Jurong East, Singapore) connected to a pair of *E-A-RTONE 3A* insert earphones (3M Company, Indianapolis, Indiana) via a plastic tube. The inducers were secured under a shielded sheath on the floor to prevent electromagnetic contamination of MEG signals. The audio output was measured against the stimulus using a sound level meter and an ear-canal adapter, revealing no significant attenuation below 7 kHz.

2.9.2 MEG pre-processing

Head tissue segmentation and cortical surface tessellation were obtained with *Freesurfer* (Dale *et al.*, 1999; Fischl *et al.*, 2002; Reuter *et al.*, 2012), which is documented and freely available online (<http://surfer.nmr.mgh.harvard.edu/>). The anatomy, head mask and surface reconstruction were reviewed and co-registered with the scalp digitization from the MEG sessions, as detailed by Tadel *et al.* (2023).

All data were resampled to 600 Hz. A band-pass filter (0.3–200 Hz) and notch filters (60, 120, and 180 Hz) were applied to remove noise from lower frequencies and power line contaminations. Using the EOG and ECG channels, vertical and horizontal eye movements and cardiac events were detected and removed using signal-space projection (SSP).

A power spectral density (PSD) of MEG sensor data was estimated using Welch's method to identify noisy channels and detect artifacts. Any repeatable artifacts not removed by previous processing were then eliminated by applying generic SSPs or rejecting bad segments.

Each trial was identified by their response type (Hit, WH, Miss and FP) and imported to *Brainstorm*. Epochs were defined as the period from -1 to 4 seconds, with 0 corresponding to the onset of the cue, as detailed in Figure 2.2. Any epochs still containing artifacts were excluded if they deviated by more than ± 3 median absolute deviations from the calculated median of either signal amplitude or gradients, using an algorithm described by Wiesman *et al.* (2022), now integrated into *Brainstorm* (Tadel *et al.*, 2024).

2.9.3 MEG Source Mapping

Cortical source models were constrained to the cortical surface of each participant. Individual head models were computed using the overlapping-spheres method implemented in *Brainstorm*, with default parameters and a resolution of 15,000 vertices.

The orientations of the MEG dipoles were constrained to be perpendicular to the cortical surface.

Dynamic statistical parametric mapping (dSPM) was used for source estimation (2018 *Brainstorm* version), incorporating noise covariance statistics derived from empty-room recordings, with regularization based on the median eigenvalue. All other parameters followed the default *Brainstorm* settings, including a regularization SNR of 3, and a depth-weighting order of 0.5.

Table 2.4: *Brainstorm* “scouts” used to create each ROI. The scout labels shown can be found as-is in the *Brainstorm* version of the 100-parcel 7-Network Schaefer surface under the label “Schaefer_100_7net”.

ROI	Hemisphere	<i>Brainstorm</i> “scout” label
Auditory cortex	Left	SomMot_1 L
	Right	SomMot_1 R
Dorsal Attention Network	Left	DorsAttn_FEF_1 L, DorsAttn_Post_1 L, DorsAttn_Post_2 L, DorsAttn_Post_3 L, DorsAttn_Post_4 L, DorsAttn_Post_5 L, DorsAttn_Post_6 L, DorsAttn_PrCv_1 L
	Right	DorsAttn_FEF_1 R, DorsAttn_Post_1 R, DorsAttn_Post_2 R, DorsAttn_Post_3 R, DorsAttn_Post_4 R, DorsAttn_Post_5 R, DorsAttn_PrCv_1 R
Ventral Attention Network	Left	SalVentAttn_FrOperIns_1 L, SalVentAttn_FrOperIns_2 L, SalVentAttn_Med_1 L, SalVentAttn_Med_2 L, SalVentAttn_Med_3 L, SalVentAttn_ParOper_1 L, SalVentAttn_PFCI_1 L
	Right	SalVentAttn_FrOperIns_1 R, SalVentAttn_Med_1 R, SalVentAttn_Med_2 R, SalVentAttn_TempOccPar_1 R, SalVentAttn_TempOccPar_2 R
Visual cortex	Left	Vis_1 L, Vis_2 L, Vis_3 L, Vis_4 L, Vis_5 L, Vis_6 L, Vis_7 L, Vis_8 L, Vis_9 L
	Right	Vis_1 R, Vis_2 R, Vis_3 R, Vis_4 R, Vis_5 R, Vis_6 R, Vis_7 R, Vis_8 R

Sources were estimated for each individual trial and subsequently projected onto the *ICBM 152 2009c Non-linear Asymmetric* brain template (Fonov *et al.*, 2009, 2011) to

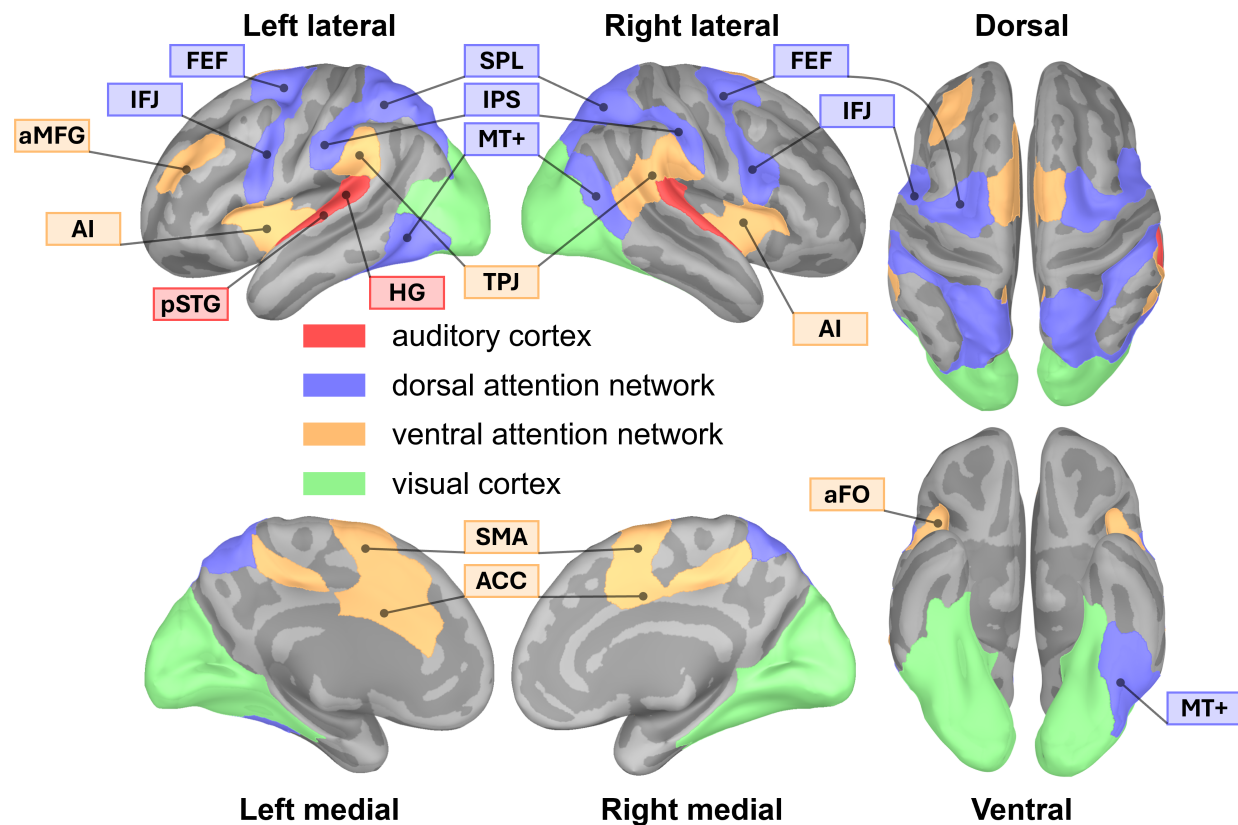


Figure 2.7: Regions of interest. The auditory cortex (AC; red), dorsal attention network (DAN; blue), ventral attention network (VAN; orange), and visual cortex (green), as defined by [Yeo et al. \(2011\)](#) and [Schaefer et al. \(2018\)](#); see [Figure 1.6](#)), are shown across lateral, medial, dorsal, and ventral views. Subregions are labeled according to common nomenclature in the literature: auditory cortex includes Heschl's gyrus (HG) and posterior superior temporal gyrus (pSTG); DAN includes frontal eye fields (FEF), intraparietal sulcus (IPS), superior parietal lobule (SPL), middle temporal area (MT+), and inferior frontal junction (IFJ); VAN includes anterior insula (AI), anterior middle frontal gyrus (aMFG), anterior cingulate cortex (ACC), supplementary motor area (SMA), anterior frontal operculum (aFO), and temporoparietal junction (TPJ).

enable group analyses.

2.9.4 ROI definition

Based on the background described in Introduction ([Section 1.3.1](#)), the following regions of interest (ROIs) were selected: auditory cortex (AC), dorsal attention network (DAN), ventral attention network (VAN), and the visual cortex as a control region. Each of these ROIs was defined using multiple parcels from the *100-parcel 7-Network Schaefer* surface atlas ([Schaefer et al., 2018](#)) adapted for *Brainstorm* (labelled as “Schaefer_100_7net”).

The specific parcels chosen for each ROI and hemisphere are indicated in [Table 2.4](#), and a visualization of the ROIs on the cortex is shown in [Figure 2.7](#).

2.9.5 Time-domain analysis

For the analysis of event-related responses, individual trials were first low-pass filtered at 20 Hz, following the recommendations of [Zhang et al. \(2024\)](#). Subsequently, all trials from each response type (Hits, Withholds, or both) were averaged, and their absolute values were calculated. A z-score baseline correction was applied using the -500 to 0 ms interval as the baseline. The average across all vertices in each defined ROI (as listed in [Table 2.4](#)) was then extracted.

We defined five time segments of the event-related MEG responses as of interest to our study, as detailed in [Table 2.5](#). The period preceding the cue, referred to as “**Baseline**”, captured baseline activity prior to the cue and was extracted from non-baselined averages of the trials. The maximum cortical response to the cue was termed “**Cue**”, while the maximum response to the training stimuli was referred to as “**M100**”, representing the primary auditory response. The preparatory activity leading up to the M100 response was measured in the ERF time segment labelled as “**preM100**”. Finally, the time segment labelled “**Later component**” was used to explore the extended activity following the M100 response.

To assess hemispheric differences, we calculated a laterality index for the selected ERF segments ([Table 2.5](#)), following the method described by [Seghier \(2008\)](#). The index was computed as the difference in activation between the left (L) and right (R) hemispheres, scaled by their sum of absolutes:

$$\text{Laterality index} = \frac{L - R}{|L| + |R|}$$

This approach provides a normalized measure of hemispheric dominance, where positive and negative values indicate left- and right-hemisphere dominance, respectively. The use of the absolute sum ensures the calculation is robust when the

measures used might include negative values such as z-scores. For bilateral ROIs such as the DAN and VAN (Figure 2.7), activation was separated into regions corresponding to the left and right hemispheres before calculating the index, as detailed in Table 2.4.

Table 2.5: Overview of selected event-related fields components and their related measures. Time periods are relative to Cue onset unless specified otherwise.

ERF segment	Descriptor	Time period	Measure
Baseline^a	Baseline activity prior to the cue	-500 to 0 ms	Average amplitude
Cue	Cortical response to the cue	50 to 150 ms	Maximum amplitude
preM100	Preparatory activity leading up to the M100	475 to 775 ms (-300 to 0 ms) ^b	Average amplitude
M100	Primary auditory response	825 to 925 ms (50 to 150 ms) ^b	Maximum amplitude
Later component	Extended response following M100, reflecting later cognitive effects	975 to 1275 ms (200 to 500 ms) ^b	Average amplitude

^a Non-baselined data was used to calculate the average amplitude.

^b Period relative to the Stimulus onset.

2.9.6 Time-frequency analysis

To transform the cortical time series into the time-frequency domain, we used the `mtmconvol` function from the FieldTrip toolbox (Oostenveld *et al.*, 2011), as implemented in *Brainstorm*. A Hann (i.e., “hanning”) taper with a fixed window length of one second and time steps of 25 ms was applied prior to a Fast Fourier Transform (FFT) across the full epoch (-1 to 4 s) for frequencies from 2 Hz to 50 Hz in steps of 1 Hz, selecting power as the output measure. Then, the average power of each cortical source time series across individual trials for each response was computed. Finally, the mean power across all cortical sources within each ROI was calculated.

Three periods within the epoch were selected based on the observed spectral activity in the grand average of all recording sessions across all participants (Figure 2.8). The “**Baseline**” period, spanning from -500 to -25 ms before cue onset, was chosen

to examine changes independent of the task. The pre-stimulus ("**preStim**") period, covering from 250 to 650 ms after cue onset, was selected to assess preparatory activity leading up to the response to the stimuli. Finally, the post-stimulus ("**postStim**") period, from 1000 to 1500 ms after cue onset (or 225 to 725 ms following stimulus presentation), was used to examine response-related activity. For pre- and post-stimulus periods, baseline normalization was applied to the average power of each ROI using the event-related perturbation method on the interval between -500 and -25 ms before the cue. No baseline correction was applied for the analysis of the Baseline period. The average power across these periods in the alpha (8–12 Hz) and theta (4–7 Hz) bands was extracted.

2.9.7 Connectivity

To assess the functional connectivity between the right dorsal attention network (right DAN) and right auditory cortex (right AC), complex coherence was computed through *Brainstorm* on *active* (**preM100**: 475 to 775 ms after the Cue or -300 to 0 ms prior stimulus onset) and *passive* (**baseline**: -300 to 0 ms) periods between the cortical time

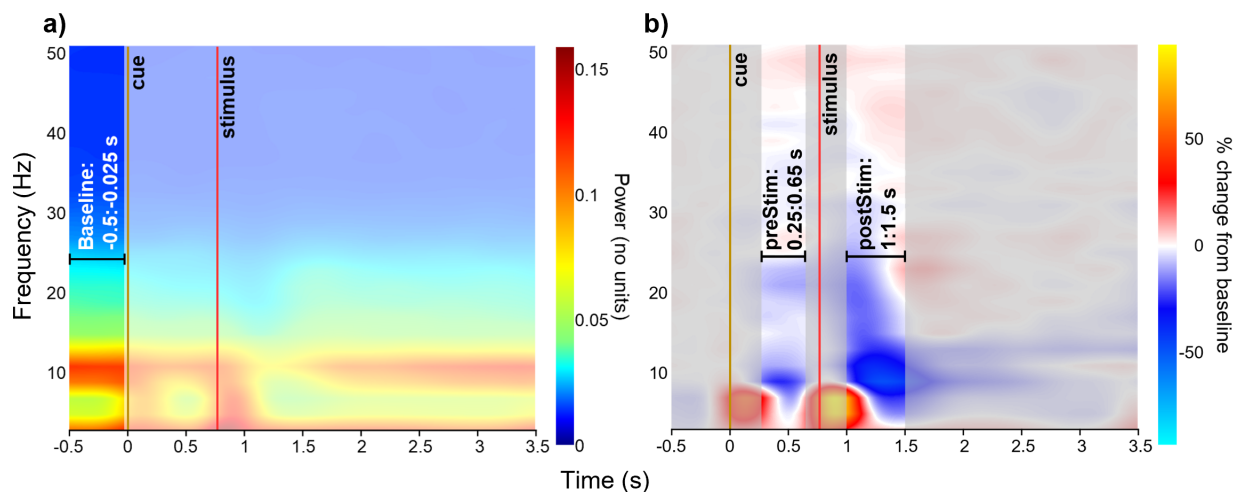


Figure 2.8: Time sections selected for the time-frequency analysis. Both panels show the average spectrograms across all recorded training sessions for all participants without baseline normalization (**a**) to extract the "**Baseline**" period, or with baseline normalization using the event-related perturbation method (**b**) to obtain the pre- and post-stimulus periods ("**preStim**" and "**postStim**", respectively).

series of the right AC and the right DAN per each individual trial.

Coherence was estimated using the magnitude-squared coherence method, which evaluates the consistency of phase and amplitude between time series. A Fourier transform with default parameters was chosen to obtain the time-frequency transformation. After obtaining the connectivity metric, the mean coherence was determined for each ROI, and coherence estimates were then averaged across all trials. Then, the average coherence across all frequencies between 1 and 20 Hz was computed, using the same frequency range as in the time-domain analysis (Section 2.9.5).

Finally, coherence estimates during the preM100 period were scaled with respect to connectivity values observed over the passive (baseline) periods:

$$\% \text{ change} = \frac{\text{active} - \text{passive}}{\text{passive}}$$

This resulted in percent-change estimates from baseline for each participant, day, and response type.

2.10 Statistical analysis

Considering the repeated measures design (*age group > subject > training day*) implemented in this project (Figure 2.5), we used general linear models and linear mixed models, as they accommodate dependent variables by including both fixed and random effects. Statistical analysis formulas are provided in the supplementary tables (Section S.1) displaying the statistical estimates (est.), with participants and training sessions treated as random effects where appropriate. All linear mixed-effects modeling was conducted using the *lme4* package (Bates *et al.*, 2015) in *R* (R Core Team, v4.3.1; 2023), with the *predictmeans* package (Luo *et al.*, v1.0.8; 2022) used for significance testing, *easystats* (Lüdtke *et al.*, v0.7.0; 2022) for model diagnostics and *dplyr* (Wickham *et al.*, v1.1.3; 2023) for data processing. When interaction terms were not significant, models were simplified to include only the main effects to provide a clearer interpretation of the primary relationships. Multiple comparisons were

corrected across related hypotheses using the [Benjamini and Hochberg \(1995\)](#) method to control the false discovery rate (FDR), with a significance threshold set at $p_{FDR} < 0.05$. Outliers were identified and excluded based on standardized residuals from each model. Data points with absolute residuals exceeding the 97.5th percentile were removed from the analysis.

2.10.1 Regressions and correlations

The association of different regressors, such as demographic or cognitive variables, with the behavioral and neurophysiological data was computed using linear models. To evaluate the contribution of individual regressors to the explained variance, the difference in marginal coefficients of determination (R^2) was calculated using the *MuMIn* package ([Barton, v1.47.5; 2023](#)) in *R*. The marginal R^2 represents the proportion of the variance explained solely by the fixed effects of a linear mixed model. First, the marginal R^2 of the full model (R^2_{full}), which included all regressors of interest, was computed. Next, a reduced model was constructed by excluding the regressor of interest (fixed effect), and its marginal R squared (R^2_{red}) was determined. Finally, the contribution of the specific regressor to the explained variance was obtained by subtracting the marginal R^2 of the reduced model (R^2_{red}) from that of the full model (R^2_{full}). This approach isolates the variance uniquely attributable to the regressor of interest while controlling for the influence of other fixed effects in the model.

2.10.2 Mediation

A causal mediation analysis was performed to examine whether the effect of the independent variable (training day) on the dependent variable (outcome) was facilitated by an intermediary variable (mediator). The model employed linear mixed-effects models to account for the hierarchical structure of the data. The mediator model was specified as:

$$[Mediator\ variable] \sim Day + (1 + Day \mid Subject)$$

while the outcome model was represented as:

$$[Outcome\ variable] \sim Day + [Mediator\ variable] + (1 + Day \mid Subject).$$

Model specifications and statistical results for each mediation analysis are provided in their respective supplementary table (Section S.1). The *mediation* package in *R* (Tingley *et al.*, 2014) was used to perform this analysis.

2.11 Visualization

All cortical maps and time-frequency visualizations were produced with *Brainstorm*. Event-related response plots and task descriptions were created with MATLAB R2021b. Additional visualizations were produced in *R* using the *ggplot* (Wickham, 2016) and *ggprism* (Dawson, v1.0.4; 2022) packages.

3

Results

In this chapter, we present the results of our study on the effects of auditory perceptual training in younger and older adults. We begin by describing participants' behavioral performance on the auditory task, including improvements over the course of training and transfer effects to untrained cognitive tasks ([Section 3.1](#)). Next, we analyze training-induced neurophysiological changes in the auditory cortex, focusing on the M100 component of auditory event-related responses and differences associated with age ([Section 3.2](#)). We then investigate the role of attention in training-induced auditory cortical plasticity, assessing pre-stimulus activity in attention networks and changes in power in the alpha and theta frequency bands ([Section 3.3](#)). Finally, we explore the relationship between behavioral performance and the observed neurophysiological changes ([Section 3.4](#)).

3.1 Age-related differences in performance and learning transfer of an auditory perceptual training task

3.1.1 Overview and rationale

We mentioned in the Introduction (Section 1.4) that studies of perceptual learning have reported beneficial behavioral effects in both younger and older adults (Bieber and Gordon-Salant, 2021; Colby *et al.*, 2018; Gilbert and Rogers, 1996; Karawani *et al.*, 2016). However, other studies show decreased performances in older adults (Alain and Snyder, 2008; Brehmer *et al.*, 2016). Following perceptual training with an auditory task, generalization of performance gains to other tasks has been observed inconsistently (Delhommeau *et al.*, 2002; Fitzgerald and Wright, 2011; Karawani *et al.*, 2016; Zaltz *et al.*, 2020), but becomes more robust when training paradigms are more challenging (Flegal *et al.*, 2019).

In the present study we aimed to:

- 1) Measure changes in performance on the auditory perceptual discrimination task throughout training in both age groups.
- 2) Assess the generalization of any gain in task performance induced by auditory training to other cognitive tasks.

We hypothesized that both older and younger participants would benefit from auditory perceptual training, showing significant improvements in task performance across training days. Additionally, given the challenging nature of the auditory task, we anticipated that training benefits would generalize to other cognitive tasks such as the Rey Auditory Verbal Learning Test (RAVLT). In particular, we expected that older adults, who generally have lower baseline cognitive performances compared to younger adults (Daigneault *et al.*, 1992; Van Der Elst *et al.*, 2005; Savage and Gouvier, 1992; Tuokko *et al.*, 2017; Wecker *et al.*, 2000), would have greater potential for improvement.

3.1.2 Perceptual task performance improves with training

We implemented linear mixed effects models (LMM) to examine the effect of training on task performance across age groups. We found a significant interaction between training day and age group on the average performance level reached per day (est.=0.29,

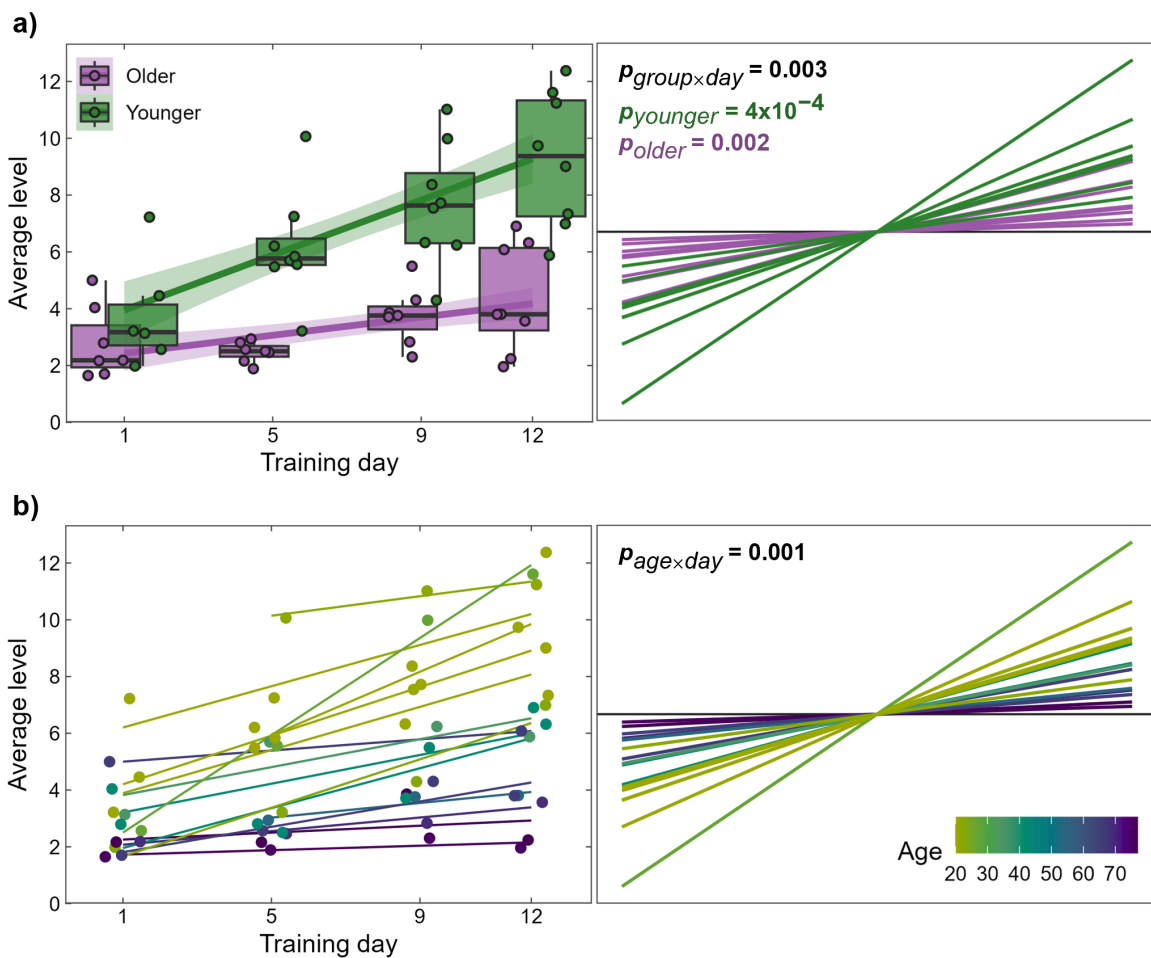


Figure 3.1: Performance improves across training days. **a)** Average level reached per day per participant (individual points), separated by age group (younger: green, older: purple). The linear mixed model fit (solid line) per age group is shown across training days, with the shaded area representing the 95% confidence interval. Slopes for each participant (right panel) are displayed, showing significant differences between age groups (interaction effect) and the improvement in task performance with training. **b)** Average level reached per day with continuous age as predictor. Each line represents the linear fit for a participant, with colors representing their age (color scale from 20 to 77 years). The right panel shows the model fit for each participant, highlighting the age effect on performance. The interaction effect between training day and group ($p_{group \times day}$) or age ($p_{age \times day}$) is shown. $p_{younger}$ and p_{older} represent the main effects of training day for the younger and older groups, respectively. Significance threshold is set as $p < 0.05$ for all comparisons.

$p=0.003$), suggesting distinct improvement patterns for each age group over time (Figure 3.1a). Additionally, to test whether this relationship was influenced by the grouping of participants by age, we used another LMM with age in years as a continuous predictor instead of age group. This model also indicated a significant interaction between age and training day (est.=-0.01, $p=0.001$) as shown in Figure 3.1b. When each age group was evaluated separately, both showed significant task improvement over time (Younger: est.=0.45, $p=4\times 10^{-4}$; Older: est.=0.16, $p=0.002$; Figure 3.1a). All sixteen participants improved in the task, with mean slopes of 0.43 (SD=0.21) in younger adults and 0.16 (SD=0.11) in older adults. Similar results were observed while evaluating performance with the maximum level reached on each day, as described in Table S.1.

3.1.3 Experimental setting influences behavioral performance

For a comprehensive assessment of task performance, we also analyzed the behavioral data collected from tablets during the home training sessions and compared behavioral performances between the at-home and MEG sessions (Table S.2). We found that average performances during MEG sessions were substantially lower than during at-home sessions (est.=-2.54, $p=4\times 10^{-14}$; Figure 3.2) with no significant interaction between group and day (est.=0.16, $p=0.145$). In both experimental settings, we observed significant improvements in performance with training for both groups, both when pooled together (est.=0.30, $p=5\times 10^{-5}$) and separately (Younger: est.=0.36, $p=1\times 10^{-6}$; Older: est.=0.23, $p=0.026$). The experimental setting did not exhibit differential effects on the performance of older and younger adults (est.=-0.81, $p=0.187$).

3.1.4 Gains in performance generalize to untrained memory and inhibition tasks

We tested whether learning transfer effects manifested on the Rey Auditory Verbal Learning Test (RAVLT) and the Stroop Color-Word Test (SCWT), as described in Methods (Section 2.7). In the RAVLT (Figure 3.3a, Table S.3), participants showed higher

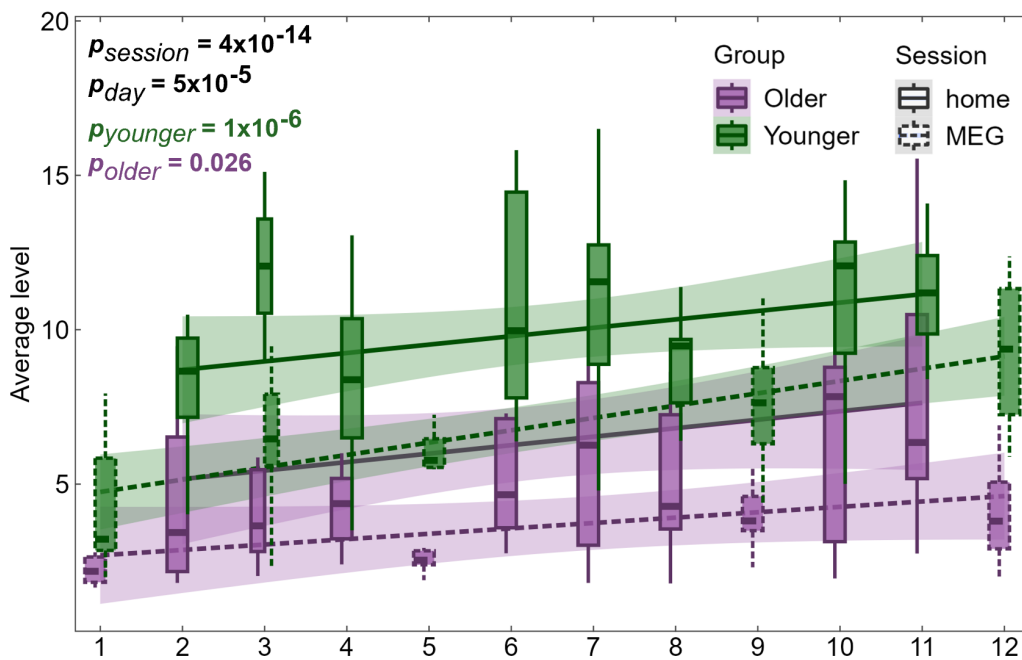


Figure 3.2: Performances are affected by experimental settings. Average task performance levels of younger (green) and older (purple) participants across MEG sessions (dashed line) and at-home sessions (solid line). Performances were significantly different between session types (p_{session}), although both groups of participants improved across training days in both settings (p_{day} , p_{younger} and p_{older}).

Learning Gain scores (est.=0.36, $p_{\text{FDR}}=0.029$) and lower Proactive Interference (est.=-0.31, $p_{\text{FDR}}=0.004$) after the training protocol. When each age group was analyzed separately, older participants exhibited significant improvements in both measures, with 87.5% of them improving in Learning Gain ($\mu=0.61 \pm 0.43$, est.=0.61, $p_{\text{FDR}}=0.016$) and 100% in Proactive Interference ($\mu=-0.41 \pm 0.18$, est.=-0.42, $p_{\text{FDR}}=0.003$). Younger adults showed mixed results, with 42.9% ($\mu=0.11 \pm 0.63$, est.=0.09, $p_{\text{FDR}}=0.663$) and 62.5% ($\mu=-0.20 \pm 0.43$, est.=-0.20, $p_{\text{FDR}}=0.476$) of the participants improving in Learning Gain and Proactive Interference, respectively. Interaction effects were not significant after correcting for multiple comparisons (Learning Gain: est.=-0.52, $p_{\text{FDR}}=0.168$; Proactive Interference: est.=0.32, $p_{\text{FDR}}=0.168$). However, without the interaction term, we found significant group differences in Total Score (est.=8.69, $p_{\text{FDR}}=0.013$) and Proactive Interference (est.=-0.22, $p_{\text{FDR}}=0.038$), with younger adults outperforming older adults.

We then performed t-tests to compare the respective performances of the two

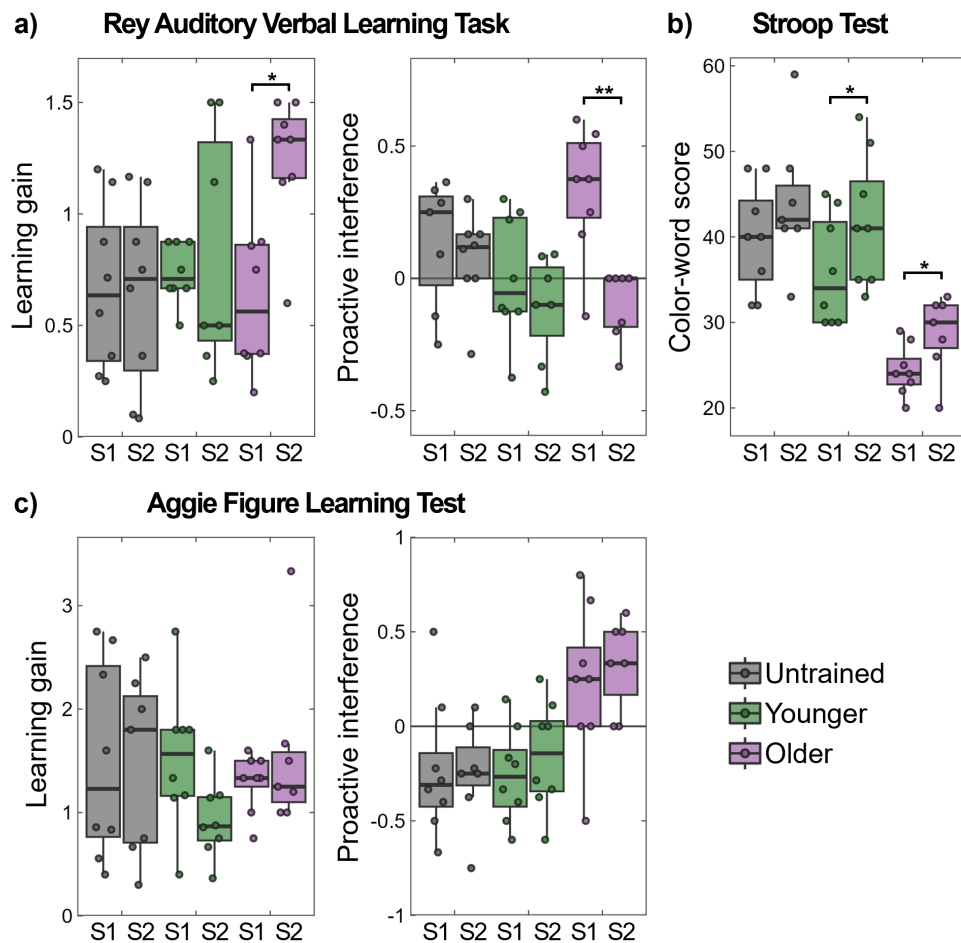


Figure 3.3: Learning transfer effects on RAVLT, SCWT and AFLT measures. We observed significant learning transfer effects in measures from the Rey Auditory Verbal Learning Test (RAVLT, panel **a**) and Stroop Color and Word Test (SCWT, panel **b**). Scores are shown per individual and group for Pre- (S1) and Post-training (S2) sessions. Participants are split by age and training status, with untrained and trained younger adults shown in gray and green, respectively, and trained older adults in purple. **a)** Learning gain (left) and Proactive Interference (right) scores exhibit significant improvements only in older adults after training. **b)** Color-word score of each participant in the SCWT, showing significant training effects on both age groups. **c)** Learning gain (left) and Proactive Interference (right) scores in the Aggie Figure Learning Test (AFLT), used to evaluate whether transfer effects were specific to the auditory modality. No significant training effects were observed. Only effects with p -values below 0.05 after multiple comparisons corrections are signaled. For statistical results on non-significant effects or additional comparisons, refer to [Tables S.3 to S.5](#). ** $p < 0.01$, * $p < 0.05$.

age groups before and after training. For Learning Gain, we observed no significant differences between the two groups in any session (all $p > 0.05$). In contrast, we observed a reduction in performance disparity in Proactive Interference, where the performance of older adults improved and became statistically equivalent to that of younger adults

after training (Pre-training: $\text{est.}=-0.33$, $p=0.015$; Post-training: $\text{est.}=-0.10$, $p=0.447$).

In the SCWT (Figure 3.3b, Table S.4), training led to higher color-word scores in 86.67% of participants ($\text{est.}=5.03$, $p_{\text{FDR}}=0.001$). Specifically, 87.50% of younger ($\mu=5.88\pm4.02$, $\text{est.}=5.88$, $p_{\text{FDR}}=0.026$) and 85.71% of older adults ($\mu=4.00\pm3.87$, $\text{est.}=4.17$, $p_{\text{FDR}}=0.035$) showed significant improvements in Stroop scores. We also observed significant differences between younger and older adults ($\text{est.}=12.47$, $p_{\text{FDR}}=0.002$) that persisted in both pre- ($\text{est.}=11.62$, $p=4\times10^{-4}$) and post-training ($\text{est.}=13.16$, $p=0.002$) sessions, with younger adults consistently outperforming older adults.

To confirm that the observed transfer effects were not driven by repeated exposure to the cognitive tasks, we included an untrained younger control group, which showed no change between sessions on any measure (all $p>0.3$; Figure 3.3). We next evaluated whether the transfer effects were specific to the auditory modality through performances on the visual-attention Aggie Figure Learning Test (AFLT, Figure 3.3c, Table S.5), which would reveal broader cognitive benefits of the auditory training beyond those that are modality specific. We observed an interaction effect for Learning Gain (Session $\times$ Group: $\text{est.}=-0.86$, $p=0.041$), indicating that the performance of all younger adults declined after training ($\mu=-0.60\pm0.68$, $p=0.043$), while 57.14% of older adults showed improvements ($\mu=0.23\pm0.84$, $p=0.651$). No other significant training effects were found (all $p>0.05$). Significant group differences emerged across multiple measures: Total Score ($\text{est.}=21.69$, $p=0.001$), Delayed Recall Index ($\text{est.}=0.13$, $p=0.003$), Retroactive ($\text{est.}=-0.17$, $p=8\times10^{-5}$) and Proactive Interference ($\text{est.}=-0.48$, $p=0.001$), with younger adults generally performing better than older adults, as expected.

Finally, we assessed potential relationships between task performance and the cognitive measures showing learning transfer. We computed correlations for each age group between the change in task performance, determined by the slope of each participant's average level across training days, and the change in cognitive scores between sessions (Table S.6). The cognitive scores were based on the difference between Post- and Pre-Session values for Learning Gain and Proactive Interference

measures in the RAVLT, as well as the SCWT scores. We found a correlation trend between task performance and Learning Gain in RAVLT in older adults ($p=0.050$).

3.1.5 Summary

We measured the performance of younger and older adults in the auditory perceptual training task, their progress across training days, and evaluated possible learning transfers to untrained cognitive tasks. Both age groups showed significant improvements in task performance across training days, with older adults exhibiting more modest performance increases. Task performances were lower during MEG sessions compared to at-home sessions, but both training settings yielded significant improvements over sessions. Training effects generalized to the RAVLT and SCWT, with significant gains for RAVLT measures only by older adults, while both age groups showed improvements in the SCWT. However, no significant relationships were found between task performance and measures of learning transfer.

Overall, these results align with our initial hypotheses, demonstrating that both younger and older participants benefited from auditory perceptual training. Both groups showed significant task improvements across training days, with evidence of learning transfer to untrained cognitive tasks, particularly in older adults. These findings establish the training paradigm's ability to elicit meaningful behavioral improvements. In the next section, we explore whether these gains correspond to measurable changes in brain activity.

3.2 Age-dependent activation of right auditory cortex during perceptual auditory training

3.2.1 Overview and rationale

To investigate the cortical mechanisms underlying improvements in task performance after auditory training, we examined related neurophysiological changes in the auditory cortex. As outlined in [Section 1.4.1](#), auditory training has been previously linked to various manifestations of neural adaptation, especially modulations of ERP components with EEG. Accordingly, we analyzed auditory responses across multiple segments of evoked brain responses, with a focus on the M100 MEG component.

Our specific aims were to:

- 1) Evaluate whether longitudinal perceptual learning differentially influences cortical auditory processes in young and older individuals, especially around the ~ 100 -ms M100 latency.
- 2) Perform an exploratory analysis of possible modulations of other event-related cortical responses with auditory training.
- 3) Examine if these changes are associated with improved task performance and/or the generalization to untrained cognitive tasks.

The auditory cortex displays functional lateralization, with the right hemisphere exhibiting superior auditory spectral resolution ([Albouy et al., 2020](#); [Zatorre and Belin, 2001](#)). Because our training task involved frequency discrimination, we expected most changes induced by learning to manifest in the right auditory cortex. Based on cognitive aging models (CRUNCH and HAROLD), we predicted that older adults would exhibit higher activity and reduced right-hemisphere lateralization in auditory cortices for similar levels of task performance compared to younger adults. We also

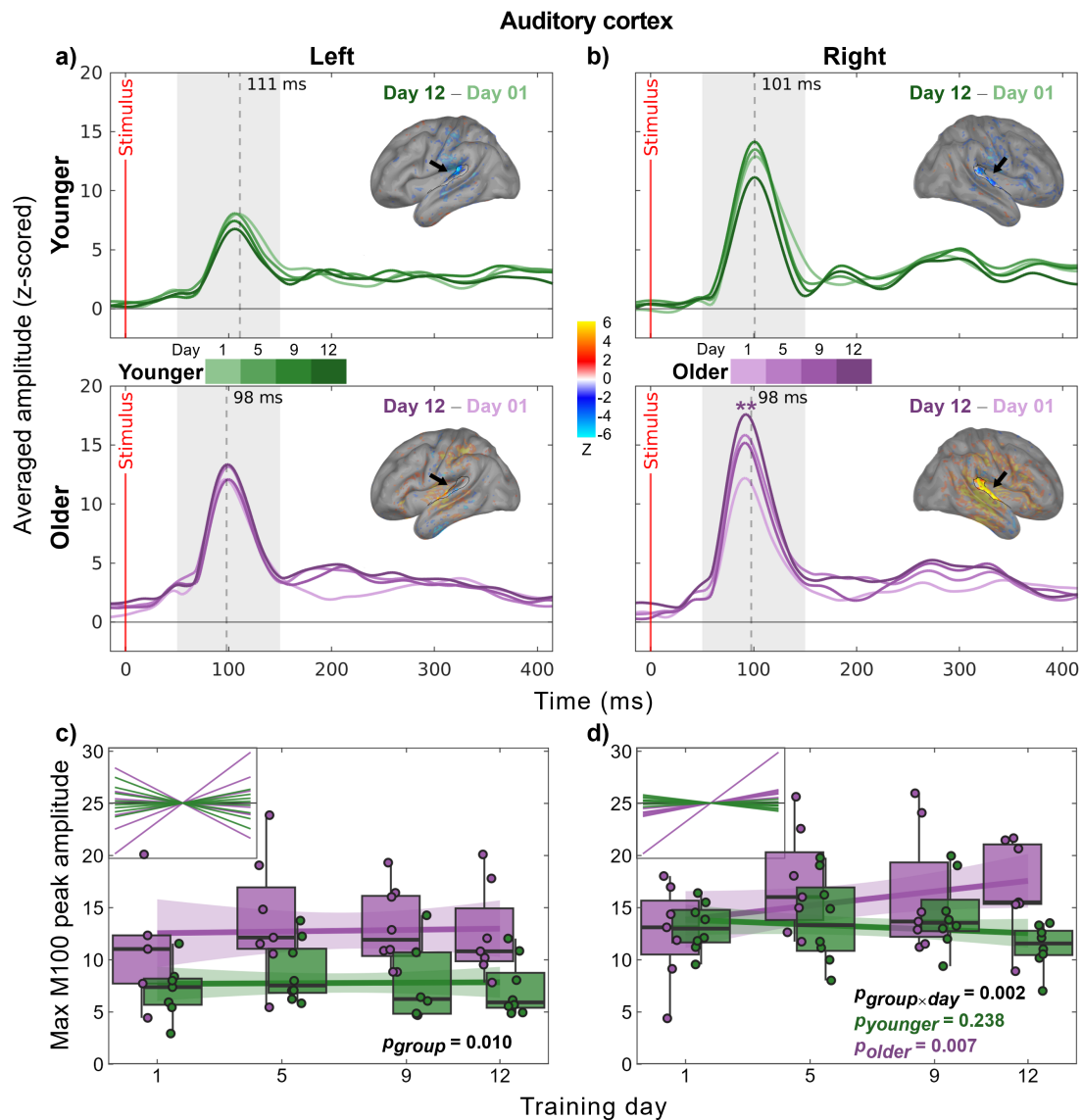
hypothesized that these age-related differences would be mitigated or even reversed after training, with responses from the auditory cortex of older adults becoming more aligned with those of younger adults.

3.2.2 Age-related amplitude differences of the M100 auditory response across training

The M100 auditory response within 50–150 ms following stimulus onset reflects the initial cortical encoding stages of the auditory stimulus (Biermann and Heil, 2000; Pratt, 2011). Therefore, we did not expect to observe amplitude or latency differences of the M100 between the Hit versus Withhold trials. For this reason, we combined both trial types into a single category labelled as “Correct Responses”. Incorrect responses, comprising Misses and False Positives, were excluded from the analysis as these response errors may have resulted from either distraction or genuine mistakes on behalf of the participants.

For each MEG training session per participant, the maximum amplitude of the M100 response (50–150 ms post-stimulus onset; 825–925 ms after Cue onset) was extracted bilaterally from the auditory cortex (see Table 2.4 and figure 2.7 for ROI definitions), using MEG cortical source maps averaged across all correct trials (Hits and Withholds). We used linear mixed models (Table S.7) to examine changes in these M100 amplitudes in each hemisphere across age groups and training sessions.

There was no significant interaction between training sessions and age groups, nor any training-related effect, in the left auditory cortex; however, a significant group difference was identified (est.=-5.63, $p=0.010$; Figure 3.4c): older adults exhibited stronger M100 responses in the left auditory cortex, compared to younger adults (Figure 3.4a). In the right auditory cortex, we found a significant interaction between training day and group (est.=-0.52, $p=0.002$; Figure 3.4b,d). Separate analyses for each age group revealed a significant increase of the M100 amplitude over the course of training in older adults (est.=0.41, $p=0.007$), with 100% of participants in this group



exhibiting a positive slope ($\mu=0.60$, $SD=0.65$). In contrast, no such change was observed in younger adults (est. $=-0.12$, $p=0.238$), with only 25% of the participants showing such increases ($\mu=-0.12$, $SD=0.17$). To explore this effect further, we used years of age as a predictor instead of age group. This approach also revealed a significant interaction of the M100 amplitude with training days and years of age, albeit only in the right auditory cortex (est. $=0.01$, $p=0.031$).

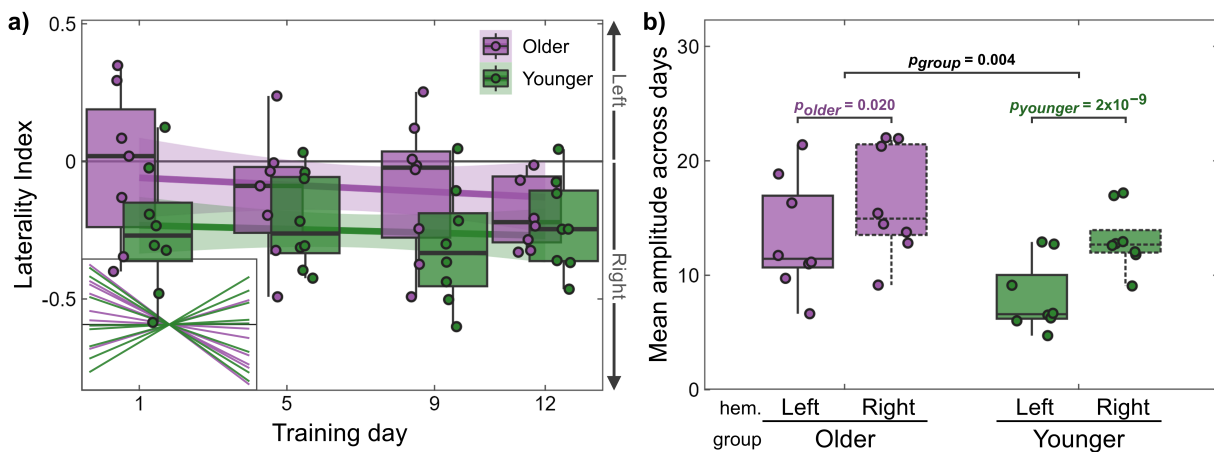


Figure 3.5: Auditory hemispheric differences in M100 amplitude during auditory training. **a)** Laterality index $[(L-R)/(|L|+|R|)]$ over training days for younger (green) and older (purple) adults. Positive and negative values indicate left- and right-hemisphere dominance, respectively. No significant interactions nor main effects were observed across training days or between age groups. Linear mixed model fits (solid lines) are shown per age group across training days, with shaded areas representing 95% confidence intervals. The inset displays the slopes fitted for each participant. **b)** Mean amplitude across days in the left (solid line) and right (dashed line) auditory cortices, by age group. Linear model revealed main effects of group and hemisphere: both younger and older adults showed greater activation in the right auditory cortex compared to the left.

Because M100 amplitude changes were observed only in the right hemisphere and older adults exhibit a loss of hemispheric asymmetry in cortical processes (Cabeza, 2002), we examined whether M100 lateralization changed as a function of training day or age group (Figure 3.5 and table S.8). We used the laterality index described in Methods (Section 2.9.5) to get a normalized measure of hemispheric dominance. There was no significant interaction nor main effects on lateralization, either across participants or within the older adult group only (all $p > 0.1$, Figure 3.5a).

We used linear models to analyze the interaction between training day, age group,

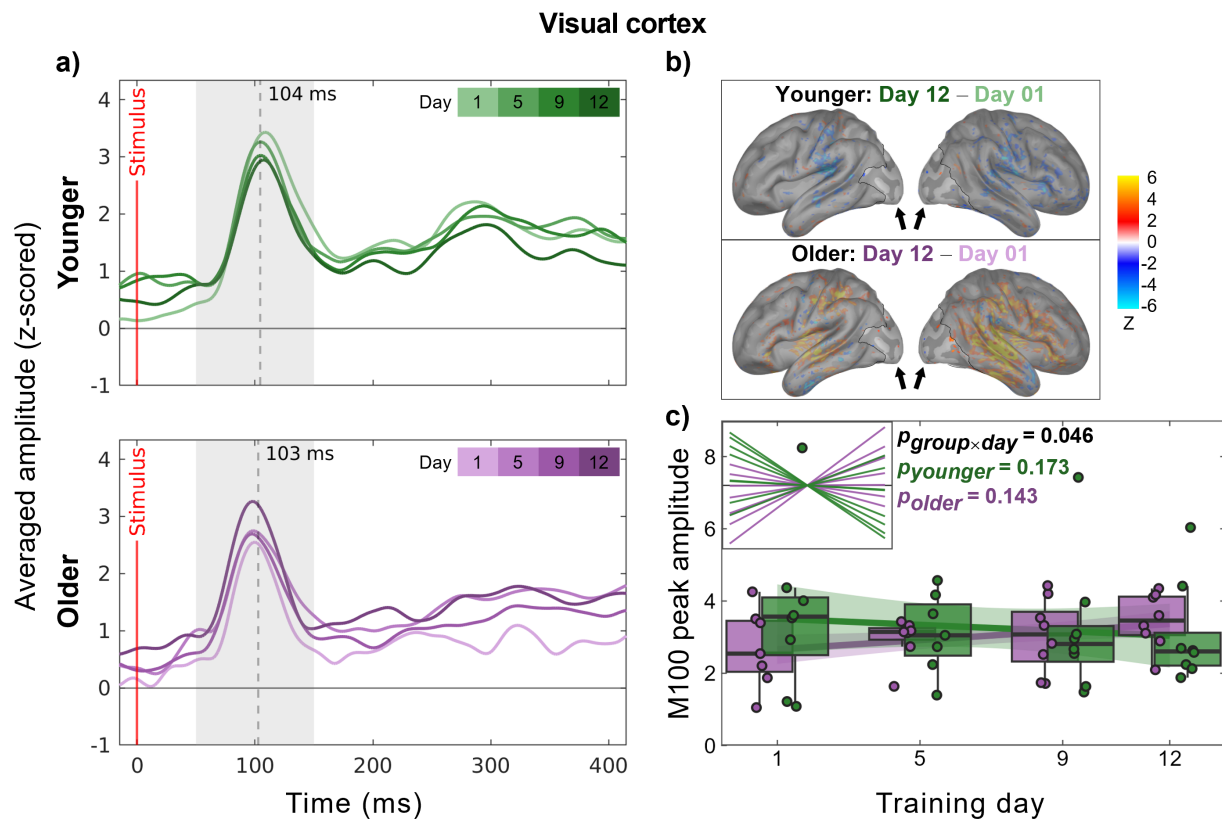


Figure 3.6: Visual cortex does not exhibit the M100 changes observed in the auditory cortex. **a)** Comparison of the averaged response per training day in the visual cortex of younger (*top*) and older (*bottom*) adults. The shaded region (50–150 ms after cue onset) highlights the time window used to extract the maximum M100 amplitude. **b)** Cortical maps, using a 40% amplitude threshold and projected onto a default brain, show the difference in baseline-corrected brain activity between Day 12 and Day 1 at the average latency of the maximum M100 amplitude (marked by a dashed grey line in panel **a**, with latency values in ms). Arrows indicate the ROI (unshaded region) used to extract the averaged response. **c)** Individual maximum M100 amplitude per day, divided by group (green: younger, purple: older). Linear mixed model fits (solid lines) are shown per age group across training days, with shaded areas representing 95% confidence intervals. The inset displays the slopes fitted for each participant. While a significant interaction was found between group and age, no main effect of training was observed in either younger or older adults.

and hemisphere. Multiple models were tested (Table S.8); the one with the lowest AIC (Akaike information criterion, indicating the best fit with lesser model complexity) did not reveal significant interaction effects (Group×Hemisphere: $\text{est.}=2.28$, $p=0.099$), but highlighted main effects of Group ($\text{est.}=-5.33$, $p=0.004$) and Hemisphere ($\text{est.}=2.77$, $p=0.006$). Subsequently, we examined each age group separately and found significantly stronger M100 responses in the right versus left hemisphere in 75% of both younger ($\text{est.}=5.05$, $p=2 \times 10^{-9}$) and older adults ($\text{est.}=2.77$, $p=0.02$; Figure 3.5b).

Finally, as a control measure, we examined possible MEG source leakage of M100 responses in the occipital visual cortex (Figure 3.6). While a significant interaction between group and training day was observed (est.=-0.11, $p=0.046$), no significant changes were found when analyzing the groups separately (Younger: est.=-0.06, $p=0.173$; Older: est.=0.06, $p=0.143$), nor when age was used as a predictor (est.= 2×10^{-3} , $p=0.155$).

3.2.3 Response to the cue is not affected by auditory training

We investigated whether the training-related modulations of the M100 response in older adults were also present in response to the Cue (Table S.9). In the left auditory cortex, no interaction between Training Day and Group, and no main effects were found (all $p>0.10$; Figure 3.7a, left). In the right auditory cortex, no interaction was observed either; however, we identified a significant Group main effect, with younger adults showing a stronger M100 response to the Cue across all days (est.=3.24, $p=0.039$; Figure 3.7a, center). No significant effect of Training Day was detected in either hemisphere.

Motivated by these Group differences in the right auditory cortex, we compared the M100 responses to the Cue between the two hemispheres in both age groups (Figure 3.7a, right) and found a significant interaction between Group and Hemisphere (est.=2.68, $p=0.003$). Among younger adults, 62.5% exhibited significantly stronger M100 responses on the right versus left auditory cortex (est.=2.13, $p=0.002$). In contrast, while 50% of older adults also showed right-hemispheric dominance, this effect was not significant (est.=-0.55, $p=0.352$).

3.2.4 Age-specific effects of auditory training on baseline activation

Since there were no training-related differences in response to the Cue, we investigated whether the increase of M100 amplitude in response to the stimuli could be attributed

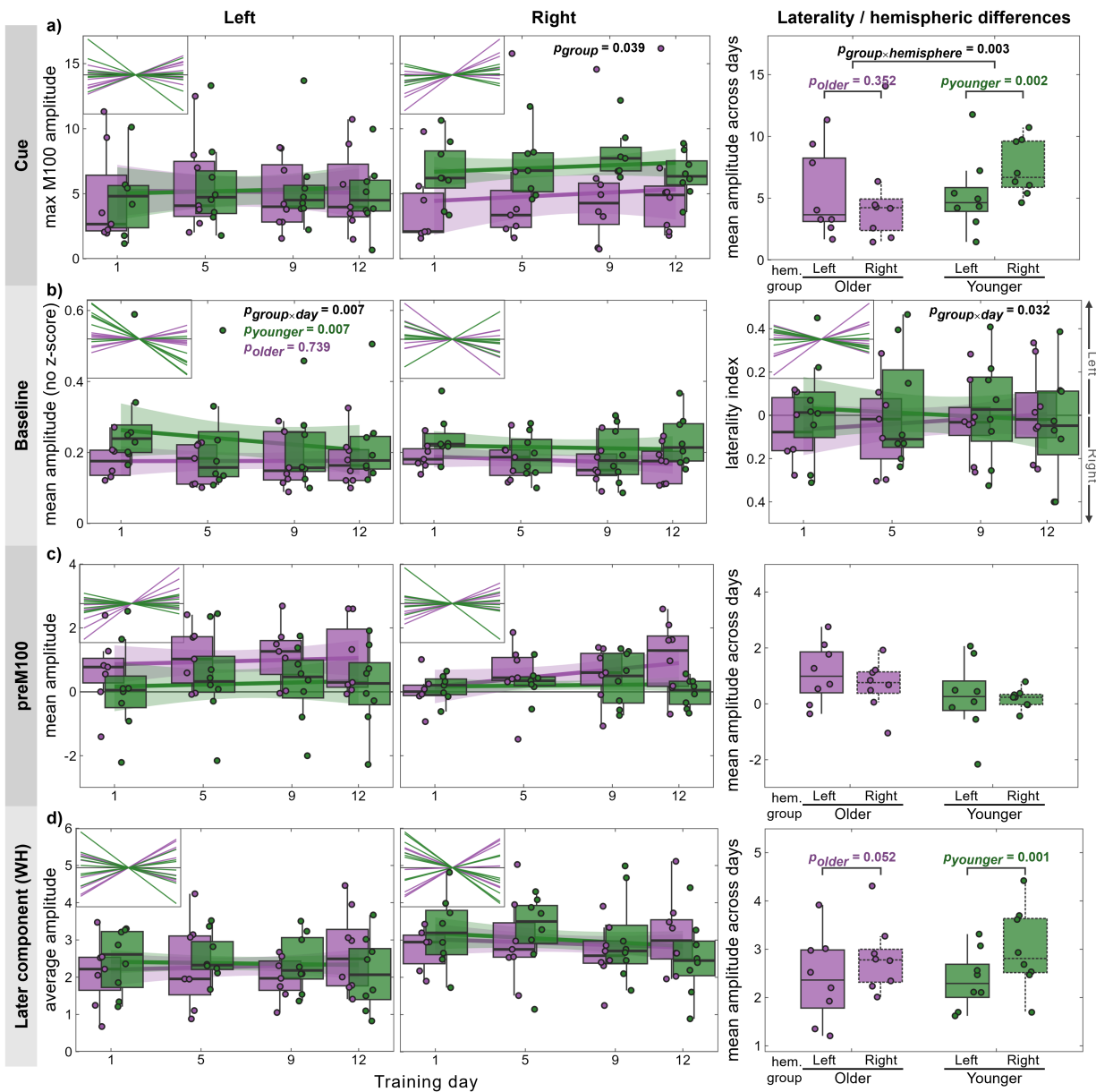


Figure 3.7: Changes in auditory activation during the Cue, Baseline, preM100 and Later Component periods. The amplitude of the auditory response is compared between younger adults (green) and older adults (purple) in multiple components of the event-related response: **a)** Cue (50–150 ms post-Cue onset), **b)** Baseline (-500–0 ms pre-Cue onset), **c)** preM100 period (-300–0 ms pre-stimulus onset), and **d)** Later Component (200–500 ms post-stimulus onset). *Left* and *center* columns show the activation in the left and right auditory cortices, respectively. *Right* column displays either a comparison of the mean amplitudes across all training days between the left (solid box) and the right (dotted box) hemispheres (**a**, **c**, **d**); or the laterality index changes over training days (**b**). Linear mixed model fits (solid lines) are presented per age group across training days, with shaded areas representing 95% confidence intervals. The inset displays the slopes fitted for each participant. Baseline amplitudes (**b**) were extracted from non-baselined trial averages. Averages from Correct Responses were used for panels **a**, **b** and **c**, while only withholds (WH) are shown in panel **d**. *p*-values are displayed for comparisons where significant differences were detected. Detailed statistics can be found in [Tables S.9 to S.12](#).

to an overall increase in baseline activity. We first extracted the average baseline activity of the auditory cortex from trial-averaged responses with no baseline correction (-500 to 0 ms prior to Cue onset; [Figure 3.7b](#)) and used linear mixed models to examine its relationship with training day and age group. In the left auditory cortex, we observed a significant interaction between Group and Training Day (est.=-0.01, $p=0.007$; [Figure 3.7b, left](#)). Among younger adults, 75% showed a training-related decrease in average baseline activity ($\mu=-5\times 10^{-3}$, $SD=4\times 10^{-3}$; est.=-0.01, $p=0.007$). Older adults did not exhibit such decrease (est. $=5\times 10^{-4}$, $p=0.739$). This relationship was further supported by a significant interaction between Day and Age (est. $=1\times 10^{-4}$, $p=0.008$; [Table S.10](#)). In the right auditory cortex, no significant interaction or main effects were observed (all $p>0.15$; [Figure 3.7b, center](#)).

In light of the relationship between Training Day and left hemisphere baseline activity, we searched for changes in baseline lateralization ([Figure 3.7b, right](#)). We found a significant interaction between Age group and Training Day (est.=-0.01, $p=0.032$); however, no significant differences were observed when each group was analyzed independently (Younger: est.=-0.01, $p=0.141$; Older: est.=0.01, $p=0.189$). No other hemispheric differences were identified ([Table S.10](#)).

We then examined the period directly preceding stimulus onset (-300 to 0 ms) to detect whether the observed training-related M100 changes could be related to pre-stimulus activity ([Table S.11](#)). There were no significant interactions nor main effects of such preM100 activity in either auditory cortex (all $p>0.05$; [Figure 3.7c, left and center](#)). Additionally, we found no differences in preM100 activity between the two hemispheres (all $p>0.05$; [Figure 3.7c, right](#)).

3.2.5 Later auditory responses exhibit hemispheric lateralization but no training effects

Later ERP components such as the P2 (~200 ms post stimulus) and P3 (~300 ms post stimulus) are influenced by auditory training ([Tong et al., 2009](#); [Tremblay et al.,](#)

2014) and are also affected by top-down processes in response to auditory stimuli (Joos *et al.*, 2014; Pratt, 2011). For this reason, we conducted an exploratory analysis of auditory responses beyond the M100 period, analyzing Hits and Withholds (WH) separately. We measured the mean cortical activity 200–500 ms post-stimulus for each response type and used linear mixed models to assess relationships with age group and training (Table S.12). We found no significant association between training day and later brain responses of the left nor right auditory cortex, for either response types (all $p > 0.05$; Figure 3.7d, *left and center*). However, our analysis revealed that the right hemisphere exhibited significantly higher later activity during Withholds (est.=0.54, $p = 4 \times 10^{-4}$; Figure 3.7d, *right*). Furthermore, we found this effect was significant in younger participants (est.=0.64, $p = 0.001$), with 62.5% of them exhibiting higher activity on the right auditory cortex. Similarly, 87.5% of the older participants also showed this pattern with a statistical trend (est.=0.44, $p = 0.052$).

3.2.6 Relationships between training-related auditory and behavioral measures

To explore the association between cortical responses and behavioral changes induced by training, we compared the training-related neural correlates identified above with the behavioral variables reported in Section 3.1. Specifically, we examined the M100 amplitude in the right auditory cortex and the baseline amplitude in the left auditory cortex in relation to the average performance level achieved during training, the RAVLT Learning Gain and Proactive Interference measures, and SCWT scores (Table S.13).

There was no association between the amplitude of the right M100 response and training task performance across age groups (est.=−0.05, $p = 0.340$). Since differences in M100 amplitude were observed exclusively in older adults, we conducted a separate analysis focusing on this group, which did not reveal any significant association (est.=0.04, $p = 0.503$). Similarly, baseline activity of the left auditory cortex was not associated with the average training task level reached per day across both age groups

(est.=4.38, $p=0.154$). A follow-up analysis of younger adults, where training-related effects were observed, suggested a statistical trend (est.=8.11, $p=0.063$).

We then derived the slope of M100 and baseline changes across training days in each individual, and assessed their correlation with changes in cognitive test scores between Post and Pre-training sessions. We found a weak association in older adults between improvements in RAVLT Learning Gain and M100 amplitude increases in the right auditory cortex (est.=1.43, $p=0.075$). All other comparisons, detailed in [Table S.13](#), were not statistically significant (all $p>0.2$).

3.2.7 Summary

In this section, we examined changes in auditory cortical responses associated with perceptual training, focusing on the M100 component as a key indicator of auditory perception. Only older adults exhibited significant training-related increases of the M100 amplitude in the right auditory cortex. Left auditory cortex M100 responses were higher in older adults compared to younger adults, but no significant training-related differences were observed. Despite these hemispheric differences, no changes in lateralization were identified across training sessions. Cortical responses to the auditory cue remained unaffected by training.

Younger adults exhibited a training-related decrease in baseline activity in the left auditory cortex, while older adults maintained stable baseline activity. Analysis of later components of the cortical event-related auditory responses revealed no significant training effects. However, right hemisphere activity was higher than the left during withholds, primarily in younger adults. Finally, the M100 amplitude and baseline activation changes showed limited associations with task performance improvements or cognitive gains.

These results partially align with our initial predictions. As hypothesized, significant training-related changes were observed in the right auditory cortex, consistent with its prominent role in frequency discrimination. However, contrary to expectations,

older adults showed increased auditory cortex activation with training, rather than the anticipated reduction or normalization toward the activation patterns of younger adults. Additionally, while lower hemispheric asymmetry was observed in older adults, training did not alter lateralization.

These findings suggest that auditory learning in older adults may be related to compensatory mechanisms, such as increased brain activation and stronger involvement of the left auditory cortex, resulting in reduced lateralization of auditory responses during pitch discrimination. While aligning with the CRUNCH and HAROLD models, these observations also diverge from the prediction that training counteracts age-related neural adaptations. To better understand these cortical changes, it is essential to consider the influence of higher cognitive processes, such as attention. To this end, the next section studies how attention mechanisms regulate the observed changes in auditory cortex activity.

3.3 Dorsal attention network age-dependent modulation of auditory perceptual response

3.3.1 Overview and rationale

As reported in Introduction (Section 1.3.1), attention is essential for the prioritization and selection of relevant sensory inputs, bridging bottom-up sensory input with higher-order perception (Price and Moncrieff, 2021; Vossel *et al.*, 2014). The dorsal attention network (DAN), in particular, exerts top-down control over perceptual resources (Katsuki and Constantinidis, 2014). The ventral attention network (VAN) is involved in the processing of salient stimuli (Rossi *et al.*, 2014) and is activated during top-down attention shifts in auditory paradigms (Alho *et al.*, 2015; Salmi *et al.*, 2009). Considering the role of attention in auditory regulation and the modulation of auditory cortex following training, we investigated whether attentional networks were associated with the increase in auditory M100 amplitude in older adults and the behavioral improvements observed after training.

Beyond canonical event-related responses like the M100, we also investigated whether effects would manifest in the alpha (8–12 Hz) and theta (4–7 Hz) bands, known to be involved in attentional regulation and sensory processing (Harris *et al.*, 2017; Keller *et al.*, 2017; Strauß *et al.*, 2014; Wiesman and Wilson, 2020), prominently in regions related to the dorsal and ventral attention networks (Kasten *et al.*, 2024). Specifically, alpha modulation is associated with selective attention, the inhibition of irrelevant stimuli, and the protection of memory against distractors (Bonnetfond and Jensen, 2012; Deng *et al.*, 2020; Kasten *et al.*, 2024; Weisz *et al.*, 2014; Wöstmann *et al.*, 2019; Zhou *et al.*, 2023). Likewise, theta oscillations are implicated in top-down cognitive control, stimulus recognition, and memory maintenance (Harris *et al.*, 2017; Keller *et al.*, 2017; Ostrowski and Rose, 2024; Wiesman and Wilson, 2020). They have also shown sensitivity to both aging and auditory training (McNair *et al.*, 2019; Mishra *et al.*, 2014; Strzelczyk and Langer, 2024). Building on this previous evidence, we explored

whether frequency-specific activity within attention networks was associated with the observed training effects on auditory processing and behavior.

Accordingly, we pursued the following specific objectives:

- 1) Characterize pre-stimulus activity in dorsal and ventral attention networks and evaluate age-related differences.
- 2) Determine whether these changes are related to the increased activation of the auditory cortex and to behavioral changes.
- 3) Investigate whether alpha or theta activity is modulated by training and whether such modulation varies across age.

We hypothesized that attention networks, particularly the DAN, would exhibit changes induced by training, especially in older adults. Given our main hypothesis that these networks modulate auditory cortex activation in response to stimuli, we also expected that changes in attentional activity would be associated with the observed increases of M100 amplitude in older adults following perceptual training. Additionally, we anticipated that these attentional changes would also correlate with the behavioral improvements in the training task and in untrained cognitive measures. Finally, we tested whether alpha and theta activity was modulated by age and related to the training-induced changes observed in the auditory cortex and, putatively, the dorsal attention network.

3.3.2 Training and aging shape pre-stimulus right dorsal attention network activity

As described in Introduction (Section 1.3.1), the DAN is organized bilaterally, with each hemisphere primarily allocating perceptual and attentional resources to the contralateral hemifield. However, there is evidence of asymmetric or bilateral functions, such as with right DAN regions being involved in the control of both hemifields, unlike the left (Bartolomeo and Seidel Malkinson, 2019; Mengotti *et al.*, 2020). In addition, the HAROLD and CRUNCH models (see Section 1.2.2) describe an age-related loss of lateralization, which is compensated by the recruitment of more brain regions. Therefore, to account for potential hemispheric differences, we measured the activation of DAN regions for each hemisphere separately.

This hemispheric distinction is particularly relevant to the training-related increase of M100 amplitude observed exclusively in right auditory cortex of older adults (Section 3.2). We anticipated that this auditory cortex modulation may be driven by increased involvement of the dorsal attention network prior to the emergence of M100 (50 to 150 ms after stimulus onset). We therefore analyzed early DAN activation averaged across the network's regions over the preM100 period (-300 to 0 ms before stimulus onset; see Table 2.4 and figure 2.7 for ROI definitions). We then used linear mixed models to evaluate whether this pre-stimulus DAN activation was associated with age group and training day (Table S.14).

We did not observe an interaction between training day and age group across left hemisphere DAN regions. However, we measured a significant increase of DAN activity during the preM100 period, with a prevalence of 75% across participants (est.=0.02, $p=0.019$; Figure 3.8a,c). This effect remained significant when using age as a continuous predictor (est.=0.02, $p=0.018$). When analyzed separately, neither age group showed a significant training day effect, despite 87.50% of younger (est.=0.02, $p=0.120$) and 62.50% of older participants (est.=0.02, $p=0.163$) exhibiting higher pre-stimulus left

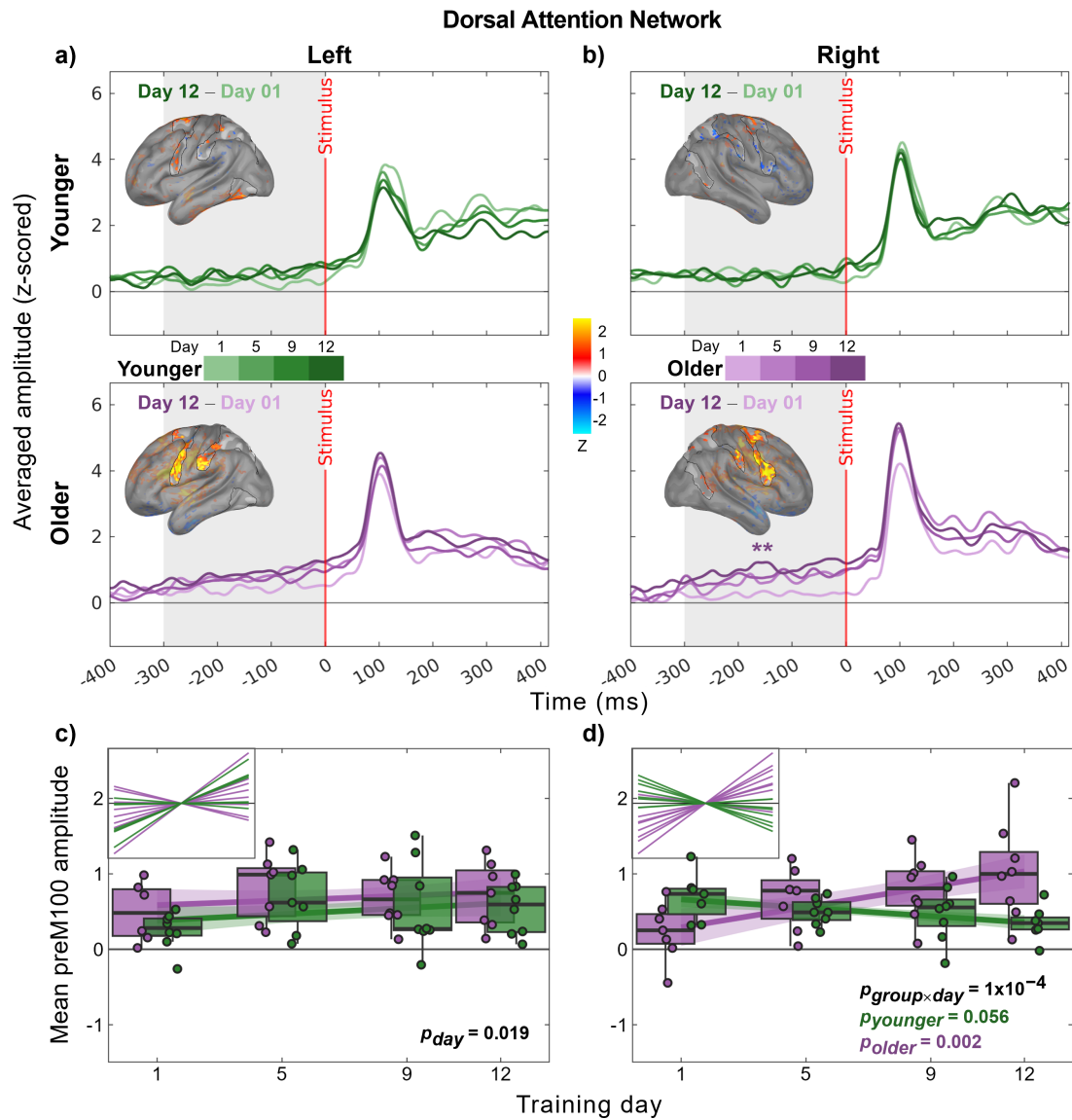


Figure 3.8: Age-related differences in right dorsal attention network activity during preM100 period. Top panels (a and b): Comparison of the averaged response per training in the left (a) and right (b) dorsal attention network (DAN) for each group (top row: younger adults, bottom row: older adults). The shaded region (-300 to 0 ms before stimulus onset) highlights the time window used to extract the mean preM100 amplitude. Inlaid cortical maps, using a 40% amplitude threshold and projected onto a default brain, show the difference in average preM100 activity between Day 12 and Day 1. **Bottom panels (c and d):** Individual mean preM100 activity per day, divided by group (green: younger, purple: older) and hemisphere (left: c, right: d). Linear mixed model fits (solid lines) are shown per age group across training days, with shaded areas representing 95% confidence intervals. The inset displays the slopes fitted for each participant. A training day effect was observed in the left DAN (c), but no interaction or group effect. In the right DAN, an interaction between group and training day was observed (d): older adults showed a significant increase in preM100 activity, while younger adults showed a non-significant decrease (d). ** $p < 0.01$.

DAN activation.

In contrast, we found a significant interaction between training day and age group in the right DAN (est. $=-0.10$, $p=1 \times 10^{-4}$; [Figure 3.8b,d](#)). Specifically, older adults displayed a significant effect of training (est. $=0.07$, $p=0.002$), with 87.50% of participants showing increased activity in the preM100 period across days ($\mu=0.06$, $SD=0.05$). Younger adults, however, exhibited a non-significant trend toward reduced right DAN activity (est. $=-0.03$, $p=0.058$), observed in 75% of participants ($\mu=-0.03$, $SD=0.03$). This interaction effect was replicated using years of age as a continuous predictor (est. $=2 \times 10^{-3}$, $p=4 \times 10^{-4}$).

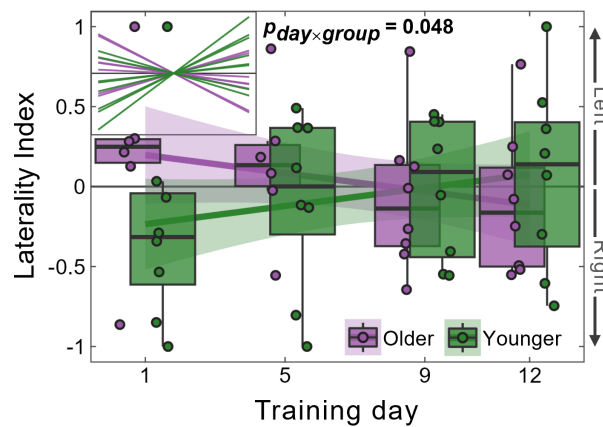


Figure 3.9: Training-related changes in preM100 laterality in dorsal attention network depend on age. Laterality index $[(L-R)/(|L| + |R|)]$ over training days for younger (green) and older (purple) adults. Positive and negative values indicate left- and right-hemisphere dominance, respectively. Linear mixed model fits (solid lines) are shown per age group across training days, with shaded areas representing 95% confidence intervals. The inset displays the slopes fitted for each participant. A significant interaction between training day and age group was found, but no significant effects were observed when analyzing each group separately.

Since preM100 activity was different between hemispheres, we investigated whether preM100 lateralization changed over the course of training or between groups. We identified a significant interaction between training day and group (est. $=0.05$, $p=0.048$; [Figure 3.9](#)). However, no significant effects were observed when each group was analyzed separately, even though 75% of older adults showed increased right lateralization (est. $=-0.02$, $p=0.243$) and 75% of younger participants displayed higher left lateralization (est. $=0.03$, $p=0.140$). Notably, the interaction effect persisted with age as predictor (est. $=-1 \times 10^{-3}$, $p=0.024$). While these findings highlight training-related

changes in preM100 DAN activity and lateralization, we found no significant correlation between the average task level reached per day and the preM100 DAN activity nor its lateralization (all $p > 0.05$).

3.3.3 Dorsal attention network fully mediates training-related changes in the auditory response of older adults

Thus far, our findings have indicated that auditory perceptual training leads to increased neural responses in older adults both before and after stimulus onset: enhanced pre-stimulus activity in the right DAN (-300–0 ms; [Section 3.3.2](#) and [figure 3.8](#)) and increased M100 responses in the right auditory cortex (50–150 ms; [Section 3.2.2](#) and [figure 3.4](#)). Given these observations, we performed a regression analysis to determine if preM100 DAN activity predicted auditory M100 amplitudes beyond the effects of training day ([Table S.15](#) and [figure 3.10](#)). We found that preM100 right DAN activity significantly predicted M100 amplitude in the right auditory cortex, only in older adults (est.=5.27, $p=0.014$; Younger: est.=-0.69, $p=0.603$). Notably, adding preM100 right DAN activity as a predictor removed the previously observed training day effect on right AC M100 amplitude (before: est.=0.41, $p=0.007$; [Table S.7](#); after: est.=0.07, $p=0.746$; [Table S.15](#)), suggesting that the right DAN may play a role in mediating training-related changes in the auditory cortex of older adults.

We then conducted a causal mediation analysis to determine whether the effect of training day on the right auditory cortex in older adults operated through right DAN activation ([Table S.16](#)). We found that right DAN exhibited a full mediation effect on right auditory cortex ([Figure 3.11](#)), as indicated by a significant average causal mediation effect (ACME = 0.38, $p=0.010$) and a non-significant average direct effect (ADE = 0.04, $p=0.834$). Mediation accounted for 91% of the total effect of training day on the right AC M100 amplitude (Total Effect = 0.42, $p=0.002$), supporting the role of DAN in facilitating training-induced neuroplasticity in the auditory cortex of older adults.

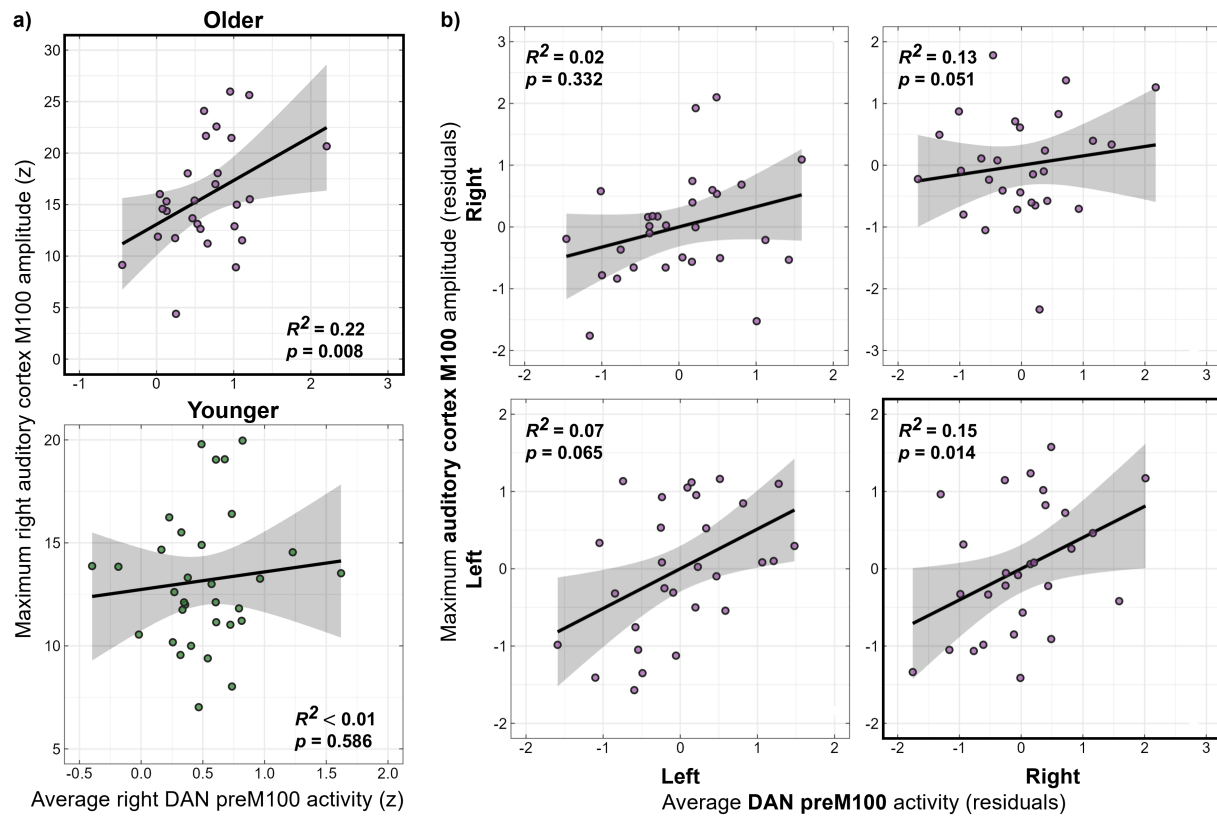


Figure 3.10: Right preM100 dorsal attention network activity predicts right auditory M100 amplitude in older adults. **a)** Simple regression analysis comparing younger (*bottom*) and older (*top*) adults on the linear relationship between right preM100 dorsal attention network (DAN) and right auditory M100 amplitude. Each data point represents individual activity measured across different days and ROIs. **b)** Relationships between left and right DAN preM100 activity and right (*top*) and left (*bottom*) auditory M100 amplitude. Data points correspond to residuals from linear mixed models that included day as a factor (see [Table S.15](#) for statistical details). Solid lines indicate linear model fits, with shaded areas representing 95% confidence intervals. Highlighted plots illustrate the same relationship before (**a**) and after (**b**) accounting for training day effects.

To determine whether preM100 DAN activation and mediation in older adults were distinct effects rather than a consequence of an increased preM100 auditory activity, we conducted a regression and a mediation analysis between preM100 and M100 right auditory activity. No significant relationship (est.=-0.54, $p=0.534$; [Table S.15](#)) nor mediation (ACME=-0.02, $p=0.812$; [Table S.16](#)) were found. Instead, we observed that the training-related increase in M100 amplitude was primarily explained by a direct effect (ADE=0.44, $p=0.004$). These findings suggest that changes in DAN activity preceded and contributed to M100 modulation, rather than being a consequence of

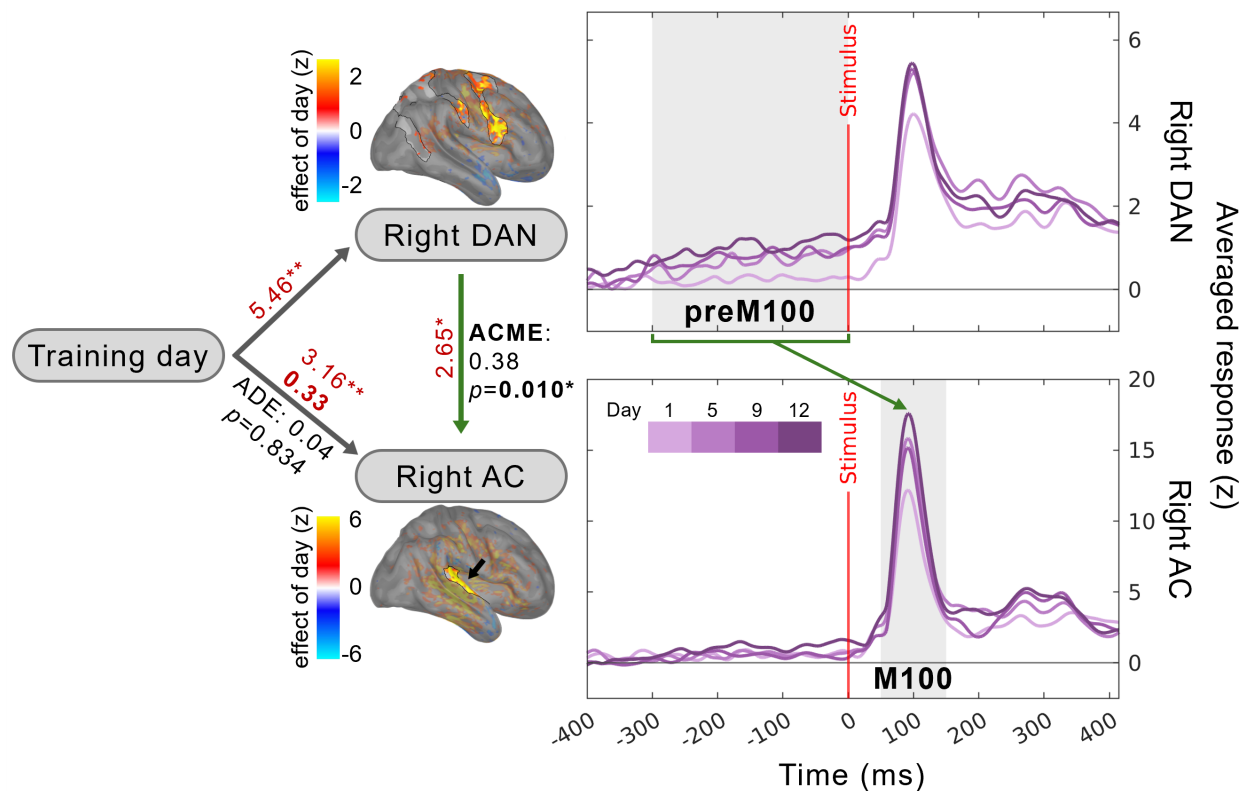


Figure 3.11: Right DAN fully mediates training-related changes in right auditory cortex M100 response in older adults. Averaged responses across training days (**right**) for the right DAN (*top*) and the right auditory cortex (*bottom*). The shaded regions highlight the time windows used to extract average preM100 (-300 to 0 ms) and maximum M100 (50 to 150 ms) amplitudes. The path diagram (**left**) illustrates the relationship between training day, right DAN preM100 activity and right auditory M100 response. Linear mixed effects model statistics (*t*-values) are shown in red, with asterisks indicating statistical significance. The bold *t*-value in the bottom path represents the relationship between training day and right auditory M100 response when right DAN preM100 activity is included in the model. The average causal mediation effect (ACME) and the average direct effect (ADE) estimates and *p*-values are shown, confirming a full mediation effect. Cortical maps depict the difference in averaged brain activity between Day 12 and Day 1 during the preM100 period (*top*) and the M100 peak (*bottom*). For additional mediation models, refer to [Table S.16](#). ** $p < 0.01$, * $p < 0.05$.

pre-stimulus auditory activation.

To further investigate the functional asymmetry of DAN, we examined whether left and right DAN activation predicted auditory activity in either hemisphere beyond training-related effects ([Figure 3.10b](#)). No significant relationships were found between preM100 DAN and M100 auditory activity in either age group (all $p > 0.05$); however, trending effects emerged ([Table S.15](#)). In older adults, specifically, we found a weak association between right DAN and left AC activity (est.=3.59, $p = 0.051$), but further

mediation analysis revealed no significant training-related effect (est.=0.13, $p=0.296$; Table S.16). Additionally, a marginal relationship was observed between left DAN and right AC activity (est.=3.23, $p=0.065$). Subsequent analysis showed a significant direct effect of training day on right AC activity (ADE=0.46, $p=0.040$) but no significant mediation via left DAN (ACME=0.14, $p=0.106$). These results suggest that training-related changes in right AC activation are primarily mediated by right preM100 DAN activity, with no evidence of left DAN involvement in this process.

3.3.4 Widespread training-related increase of alpha power in younger adults, but not older adults

In the previous section, we found that early (preM100) DAN activity mediated the training-related increase of auditory M100 amplitude in older adults. To further explore the role of the dorsal attention network in shaping auditory processing, we analyzed frequency-specific activity in the auditory cortex and DAN around stimulus presentation. Specifically, we focused on alpha-band activity (8–12 Hz) because of its involvement in sensory processing and attention suppression (Deng *et al.*, 2020; Kasten *et al.*, 2024; Weisz *et al.*, 2014). We first examined baseline alpha power (-500 to -25 ms before Cue) to assess training-related changes in spontaneous alpha activity (Iemi *et al.*, 2017). We found no significant training-related effects in either younger or older participants across all ROIs (all $p>0.05$; Table S.17).

Alpha desynchronization (power reduction) following sensory cues marks selective attention and regulates cortical excitability in sensory regions (Weisz *et al.*, 2014). Therefore, we analyzed the pre-stimulus period (-525 to -125 ms before the stimulus) to determine whether the observed DAN mediation of the auditory M100 was associated to a reduction in alpha power. We evaluated withholds (WH) trials because their greater number improved signal-to-noise ratio and because no differences were expected between Hit and Withhold trials before stimulus presentation. Across both age groups, we found a significant training-related increase in alpha power in left auditory cortex

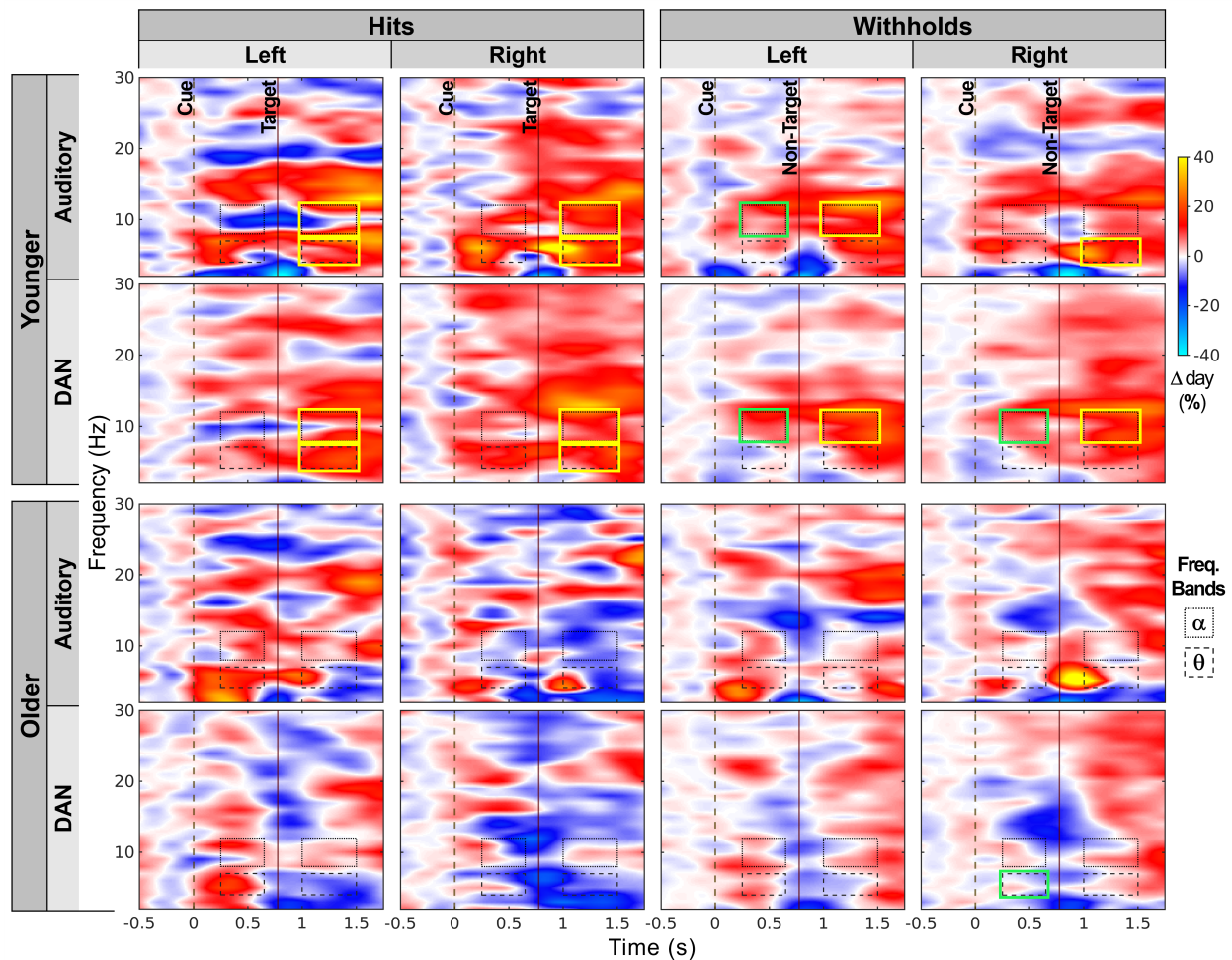


Figure 3.12: Training-related changes in spectral power in the auditory cortex and dorsal attention network by response type and age group. Grand-averaged spectrograms of the auditory cortex and DAN, separated by hemisphere, showing the difference in percent change from baseline (%) between Day 12 and Day 1 of training. Power changes are plotted across frequencies (Hz, y-axis) and time (s, x-axis). Vertical lines represent the onset of the Cue (black, dashed) and the stimulus (red, solid), which was either a target (hits) or a non-target sound (withholds). Each spectrogram corresponds to a specific combination of age group, ROI, hemisphere, and response type. Black rectangles outlined the analyzed frequency bands (alpha: α , dotted, 8–12 Hz; theta: θ , dashed, 4–7 Hz) and time periods (pre-stimulus and post-stimulus). Colored boxes highlight time-frequency regions where significant effects were found (green: pre-stimulus, Figure 3.13 and table S.18; yellow: post-stimulus, Figure 3.14 and table S.19).

(est.=0.64, $p=0.001$; time-frequency representations in Figure 3.12, individual data in Figure 3.13 and statistical results in Table S.18). In younger adults, 87.50% ($\mu=0.81$, $SD=0.52$) exhibited such increase over training days (est.=0.80, $p_{FDR}=0.001$), which also predicted changes in task performance (est.=0.10, $p=0.021$, $p_{FDR}=0.064$). No significant changes were observed in older participants, nor in right auditory cortex of either

group ($p > 0.05$; Table S.18).

In left DAN, alpha power showed a significant overall increase with training across all participants (est.=0.60, $p=0.009$). However, separate analyses by age group revealed that this effect was primarily driven by younger adults, with 87.50% showing increases ($p=0.026$, $p_{\text{FDR}}=0.103$, $\mu=0.65 \pm 0.42$), while no significant changes were observed in older adults ($p > 0.05$). In right DAN, there was a significant interaction between training day and age group ($p=0.017$), suggesting that training influenced alpha power differently in younger versus older participants. However, training-related effects within each group were not statistically significant. Specifically, 87.50% of older adults exhibited a decrease in alpha power ($\mu=-0.23 \pm 1.26$, $p=0.127$, $p_{\text{FDR}}=0.323$), while 87.50% of younger adults showed increased alpha power ($\mu=0.55 \pm 0.83$, $p=0.070$, $p_{\text{FDR}}=0.140$).

Alpha-band activity is also involved in stimulus-driven (exogenous) attentional modulation via top-down processes, contributing to the suppression of irrelevant stimulus features (Harris *et al.*, 2017; Wiesman and Wilson, 2020). Additionally, post-stimulus alpha activity marks the reactive suppression of distractors and shifts toward endogenous attention to prioritize and protect relevant information from interference (Bonnefond and Jensen, 2012; Kasten *et al.*, 2024; Weisz *et al.*, 2020; Zhou *et al.*, 2023). Therefore, we examined post-stimulus (225 to 725 ms after stimulus onset) changes of alpha activity, reflecting how training would facilitate the reallocation of attentional resources in response to the stimulus. Given the expected differences in the processing of targets (Hits) and distractors (Withholds), we analyzed them separately.

We found training-related changes in alpha power across all examined conditions, either as a main effect of training day or as an interaction with age group (Table S.19). Specifically, Group×Day interactions emerged in right auditory cortex ($p=0.006$) and right DAN ($p=0.077$) in Hits. During Withholds, significant interactions were found in left auditory cortex ($p=0.010$) and bilateral DAN regions (left: $p=0.026$; right: $p=0.036$). Additionally, significant main effects of day indicated training-related increases in alpha power in the left auditory cortex ($p=0.028$) and left DAN ($p=0.028$) for Hits, and in the

right auditory cortex ($p=0.019$) for Withholds.

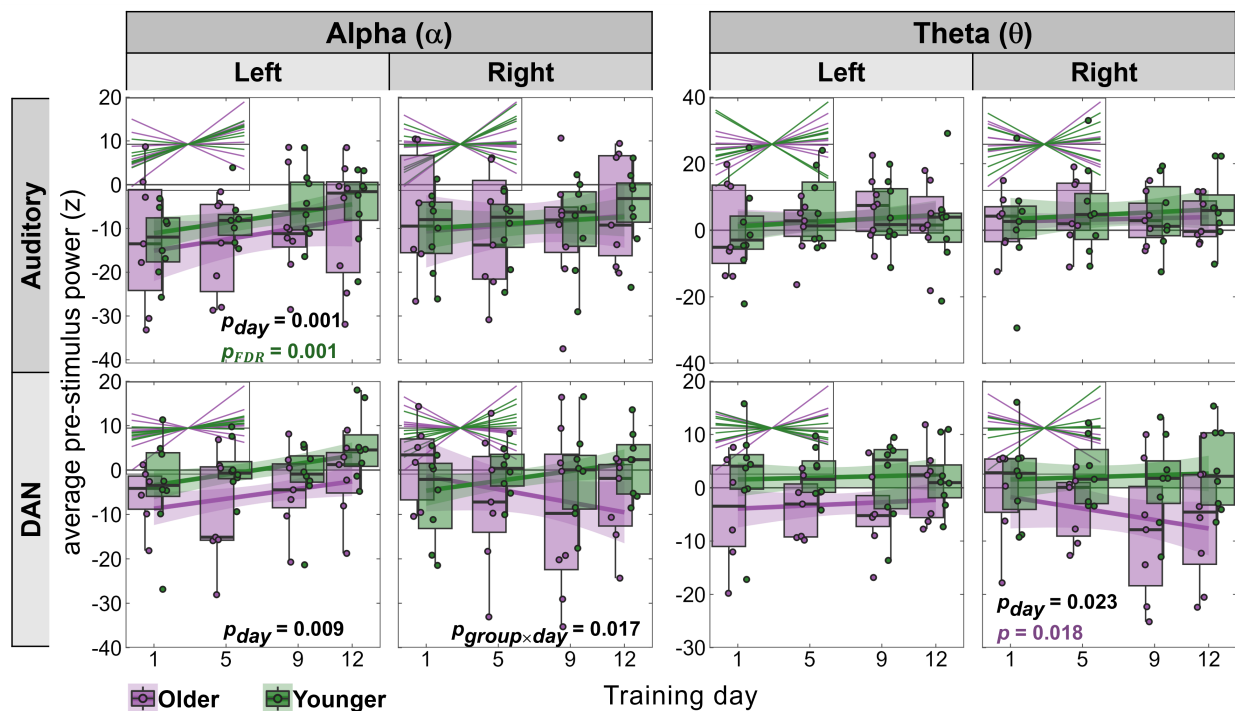


Figure 3.13: Training-related changes in pre-stimulus alpha and theta power in the auditory cortex and DAN. The power of alpha- (α , 8–12 Hz, *left*) and theta-band (θ , 4–7 Hz, *right*) activity during the pre-stimulus period (-525 to -125 ms before stimulus onset) is shown for withholds in each hemisphere of the auditory cortex and dorsal attention network (DAN). Each plot presents individual data points for younger (green) and older (purple) participants. Linear mixed model fits (solid lines) are provided per age group across training days, with shaded areas representing 95% confidence intervals. The inset in each panel displays individual participant slopes. p -values for significant effects ($p < 0.05$) are reported, with FDR corrections applied when necessary. Non-significant effects and statistical results for hits can be found in [Table S.18](#).

Group-specific analyses revealed that these effects were primarily driven by younger participants, who exhibited a significant increase in post-stimulus alpha across both response types and ROIs (all $p_{FDR} < 0.05$), with the exception of right auditory cortex in Withholds (see [Figure 3.12](#) for time-frequency representations, [Figure 3.14](#) for individual data and [Table S.19](#) for statistical results). Specifically, younger adults displayed higher alpha power across days in left (Hits: Prev.=62.50%, $\mu=0.70 \pm 0.79$, $p_{FDR}=0.046$; WH: Prev.=87.50%, $\mu=2.31 \pm 1.63$, $p_{FDR}=4 \times 10^{-4}$) and right auditory cortex (Hits: Prev.=75%, $\mu=1.07 \pm 1.30$, $p_{FDR}=0.012$), in addition to left (Hits: Prev.=87.50%, $\mu=0.82 \pm 1.01$, $p_{FDR}=0.029$; WH: Prev.=100%, $\mu=1.54 \pm 0.95$, $p_{FDR}=0.008$) and right (Hits:

Prev.=75%, $\mu=1.04\pm1.38$, $p_{\text{FDR}}=0.029$; WH: Prev.=87.50%, $\mu=1.32\pm1.48$, $p_{\text{FDR}}=0.011$) dorsal attention network. No significant training-related effects were found in older adults (all $p>0.05$).

These findings indicate training-related modulations of pre- and post-stimulus alpha power in both the auditory cortex and DAN of younger adults; however, only the increase in pre-stimulus alpha power in the left auditory cortex was associated with task performance (est.=0.10, $p=0.021$, $p_{\text{FDR}}=0.064$). No other significant relationships were found between any alpha power changes and the daily average level reached in the training task (all $p>0.05$, [Tables S.18](#) and [S.19](#)).

3.3.5 Training-related modulation of theta power differs across time windows and age groups

Because we did not find significant training-related changes in alpha power in older adults, we investigated potential sensory and cognitive processing effects reflected in the theta band. Pre-stimulus theta activity has been associated with the integration of acoustic information ([Kubetschek and Kayser, 2021](#)), as well as successful memory encoding ([Ostrowski and Rose, 2024](#)) and retrieval ([Addante et al., 2011](#)). Notably, age-related differences in pre-stimulus theta activity have also been reported during learning ([Strzelczyk and Langer, 2024](#)). Moreover, post-stimulus theta activity has similarly been linked to perceptual processing and discrimination ([Brilliant et al., 2024](#); [Harris et al., 2017](#); [Mishra et al., 2014](#); [Wiesman and Wilson, 2020](#)). Based on this evidence, we focused on both pre- and post-stimulus theta activity as potential neurophysiological markers of training-related behavioral changes in older adults.

We examined pre-stimulus theta activity (4–7 Hz; -525 to -125 ms before stimulus onset) to explore age-related changes in preparatory activity following training. To optimize signal quality, and because no pre-stimulus differences were expected between conditions, we focused our analysis on the more frequent WH trials. We found a significant interaction between age-group and training day in right DAN ($p=0.023$; see

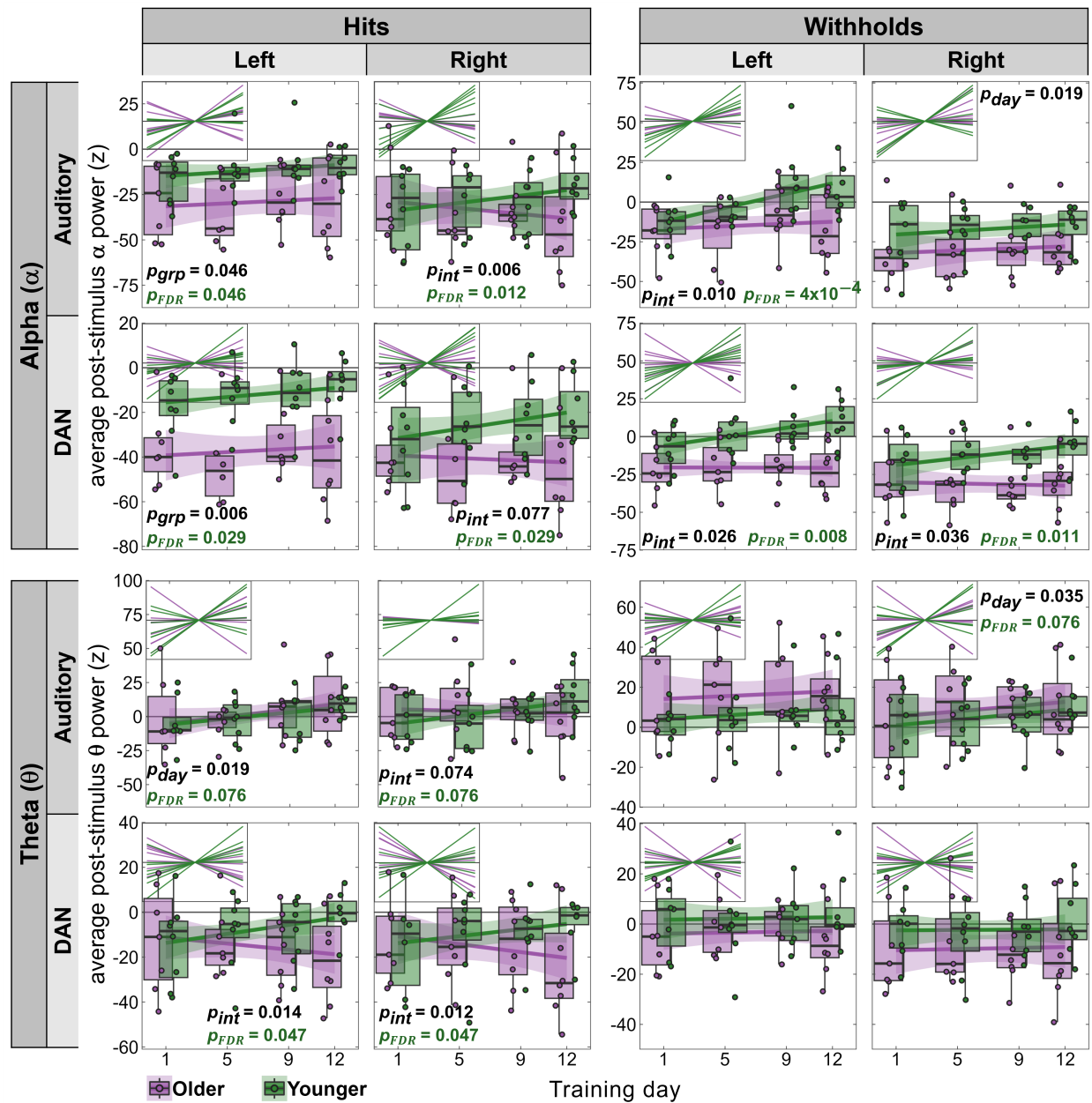


Figure 3.14: Age- and training-related changes in alpha and theta during the post-stimulus period in auditory cortex and dorsal attention network. The power of alpha- (α , 8–12 Hz, **top**) and theta-band (θ , 4–7 Hz, **bottom**) activity during the post-stimulus period (225 to 725 ms after stimulus onset) is shown for hits (*left*) and withholds (*right*) in each hemisphere of the auditory cortex and dorsal attention network (DAN). Each plot presents individual data points for younger (green) and older (purple) participants. Linear mixed model fits (solid lines) are provided per age group across training days, with shaded areas representing 95% confidence intervals. The inset in each panel displays individual participant slopes. p -values for significant effects ($p < 0.05$) are reported (p_{int} : age $\times$ group interaction effect, p_{grp} : group main effect), with FDR corrections applied when necessary. Non-significant effects and more statistical details can be found in [Table S.19](#).

Figure 3.12 for time-frequency representations, Figure 3.13 for individual data, and Table S.18 for statistical results). Follow-up analyses within each group revealed a significant decrease in theta power in right DAN in 87.50% of older adults following training ($p=0.018$, $\mu=-0.43\pm0.83$). No significant changes were found in younger adults or in other brain regions (all $p>0.05$). Informed by the mediation effect of the right M100 auditory response by right DAN preM100 activity in older adults reported in Section 3.3.3, we tested whether the pre-stimulus decrease in theta power was related to training-related increases in auditory or DAN activity. However, we found no such associations, nor any relationship with task performance (all $p>0.05$; Table S.18).

We then analyzed whether post-stimulus theta activity changed in response to the stimuli. Based on prior evidence that theta responses differ depending on whether the stimulus is a target or a distractor (Mishra *et al.*, 2014), we analyzed Hits and Withholds separately. In contrast with the pre-stimulus period, we observed significant interactions or main effects in response to targets (see Figure 3.12 for time-frequency representations, Figure 3.14 for individual data, and Table S.19 for statistical results). Specifically, during Hits, there was a trend in right auditory cortex ($p_{\text{Day}\times\text{Group}}=0.074$), as well as significant interactions in left ($p=0.014$) and right DAN ($p=0.012$). Additionally, we observed a main effect of day in left auditory cortex ($p=0.019$). For Withhold trials, only a main effect of day was found in right auditory cortex ($p=0.035$). Only younger adults showed training-related changes. During Hits, they exhibited non-significant increases in theta power in left (Prev.=75%, $\mu=1.17\pm1.80$, $p_{\text{FDR}}=0.076$) and right auditory cortex (Prev.=75%, $\mu=2.71\pm4.70$, $p_{\text{FDR}}=0.076$), and significantly higher theta activity in left (Prev.=87.50%, $\mu=0.95\pm1.57$, $p_{\text{FDR}}=0.047$) and right DAN (Prev.=75%, $\mu=0.34\pm1.84$, $p_{\text{FDR}}=0.047$). In response to non-target stimuli (WH), younger adults showed a trend toward higher theta power in right auditory cortex (Prev.=62.50%, $\mu=0.98\pm1.47$, $p_{\text{FDR}}=0.076$). No other effects were observed during withholds or in older adults. The observed changes in theta power in younger adults were not related to task performance (all $p>0.05$; Table S.19).

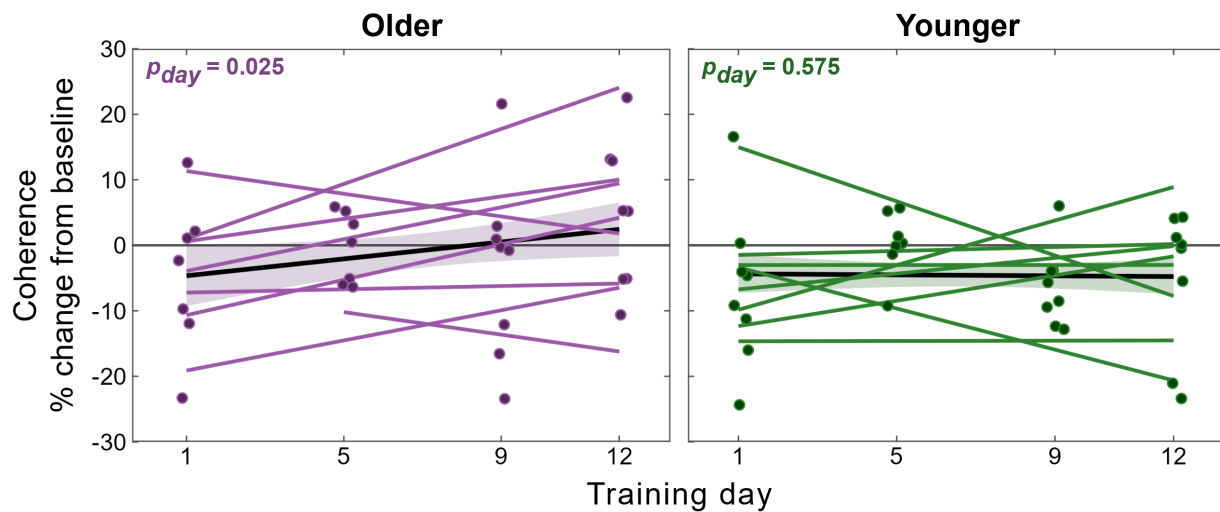


Figure 3.15: Training-related increase in DAN-auditory coherence in older adults. Changes in coherence (percent change from baseline) between DAN and auditory cortex during the preM100 period (-300 to 0 ms before stimulus onset). Each panel shows individual data points and linear mixed model fits (solid black line) with 95% confidence intervals (shaded area). Individual slopes for each participant are displayed as colored lines. p -values for the effect of training day are shown.

3.3.6 Training-related increase of pre-stimulus connectivity in older adults

In older adults, we previously reported an M100 amplitude increase in right auditory cortex following training (Section 3.2.2) and higher pre-stimulus activity of the right dorsal attention network, which mediated the training-related change in auditory cortex activity (Sections 3.3.2 and 3.3.3). Therefore, we examined whether training also modulated pre-stimulus functional connectivity between auditory cortex and DAN. As we did not find training modulations of auditory or DAN alpha and theta-band activity in older adults, we measured coherence between these two sets of regions across a broad frequency range (1–20 Hz; see Section 2.9.7), consistent with the bandwidth used in time-domain analysis (Section 2.9.5). We found coherence between right DAN and right auditory cortex significantly increased with training in 75% of older adults ($\mu=0.63\pm1.07$, $p=0.025$; Figure 3.15 and table S.20). This effect was absent in younger adults ($\mu=0.04\pm1.14$, $p=0.575$). However, this increase in coherence did not predict the M100 amplitude changes in right auditory cortex and showed a trend with right DAN

over the preM100 period ($p=0.064$). No significant association was found between coherence and task performance.

3.3.7 Increased activation of bilateral ventral attention network with training in older adults not predictive of auditory response

The ventral attention network (VAN) has been associated with top-down modulation of auditory attention (Alho *et al.*, 2015; Salmi *et al.*, 2009). Given our above findings that the dorsal attention network mediated auditory cortex responses, we examined whether VAN also contributed to the regulation of auditory processing. We computed the average VAN activity across the preM100 period (-300 to 0 ms prior to stimulus onset), and assessed the effects of age and training using linear mixed models (Table S.21).

In left VAN, we observed a trending interaction between training day and age group ($p=0.056$). Additionally, training day had a significant main effect across all participants (Prev.=68.75%, est.=0.05, $p=0.008$), and older adults showed significantly higher activation on left VAN across all days (est.=0.38, $p=0.038$; Figure 3.16c). This significant training-related effect across all participants remained when age was used as a continuous predictor (est.=0.05, $p=0.007$). When examined separately, training-related increases in VAN activation were only observed in older participants (Prev.=87.50%, $\mu=0.08\pm0.06$, $p=0.019$; Figure 3.16a), with no significant effects in younger adults ($p=0.245$).

A similar pattern manifested in right VAN, where training effects differed significantly both between age groups ($p_{\text{Day}\times\text{Group}}=0.035$; Figure 3.16d) and when age was used as predictor ($p_{\text{Day}\times\text{Age}}=0.001$). Among older adults, 87.50% exhibited a training-related increase in average preM100 activity of right VAN ($\mu=0.07\pm0.06$, $p=0.010$). In contrast, no significant changes were found in younger participants (Prev.=75%, $\mu=0.01\pm0.04$, $p=0.528$).

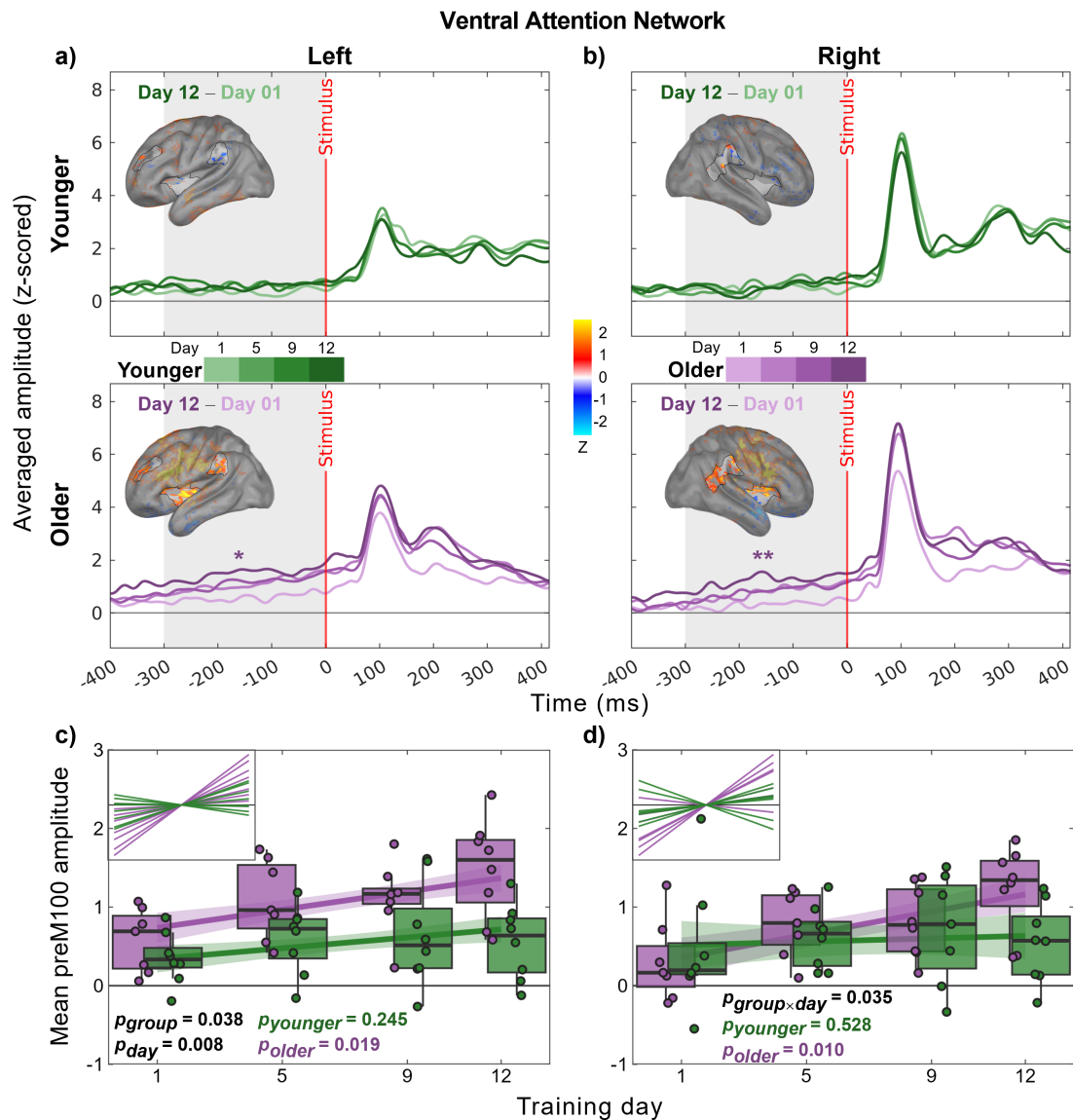


Figure 3.16: Age-related differences in ventral attention network activity during preM100 period. **Top panels (a and b):** Comparison of the averaged response per training in the left (a) and right (b) ventral attention network (VAN) for each group (top row: younger adults, bottom row: older adults). The shaded region (-300 to 0 ms before stimulus onset) highlights the time window used to extract the mean preM100 amplitude. Inlaid cortical maps, using a 40% amplitude threshold and projected onto a default brain, show the difference in average preM100 activity between Day 12 and Day 1. **Bottom panels (c and d):** Individual mean preM100 activity per day, divided by group (green: younger, purple: older) and hemisphere (left: c, right: d). Linear mixed model fits (solid lines) are shown per age group across training days, with shaded areas representing 95% confidence intervals. Insets display the slopes fitted for each participant. A significant training day effect was observed in the left VAN (c) and an interaction between group and training day was found in the right VAN (d); in both, only older adults showed a significant increase in preM100 activity across training sessions. $**p < 0.01$, $*p < 0.05$.

We performed linear mixed-effects analyses (Table S.21) to determine whether increased bilateral VAN activation in older adults was related to modulations of the right M100 auditory response (Section 3.2.2). We found that preM100 VAN activation in either hemisphere did not significantly predict right auditory M100 amplitude beyond the effects of training day (all $p > 0.05$). Interestingly, the previously observed training-related effect on right auditory M100 amplitude in older adults (est.=0.41, $p=0.007$; Figure 3.4d and Table S.7) was no longer significant when either the left (est.=0.33, $p=0.091$) or right (est.=0.23, $p=0.285$) VAN preM100 activity was added to the model.

We then modified the model to account for our previously observed mediation by dorsal attention network (Section 3.3.3), in order to assess the independent contribution of VAN activity to auditory cortical responses. In the adjusted model, DAN activity remained the only significant predictor of right auditory M100 amplitude when the left (right DAN: est.=5.10, $p=0.034$) and right VAN (right DAN: est.=6.14, $p=0.026$) were added to the model, consistent with DAN's role as a mediator of the auditory response. In contrast, VAN activation remained non-significant in both hemispheres (left VAN: $p=0.867$; right VAN: $p=0.586$). We did not find a significant association between changes in left and right VAN with the daily average task performance level in older adults (all $p > 0.05$; Table S.21).

3.3.8 Summary

In this section, we examined the contribution of training-related changes in dorsal attention network (DAN) activity to auditory plasticity in older adults, band-specific neurophysiological activity related to attention mechanisms (alpha and theta bands), functional connectivity between DAN and auditory cortex, and the potential regulatory role of the ventral attention network (VAN).

Our results revealed that while left DAN activity increased across all participants, only right DAN exhibited an age-dependent training effect, with increased activation

in older adults and a slight reduction in younger adults. Notably, this preparatory activity in the right DAN of older adults predicted the auditory plasticity reported in [Section 3.2.2](#), with a mediation analysis confirming that training-related changes in auditory responses in older adults were fully driven by right DAN activation. No evidence of predictive or mediating effects were found for pre-stimulus auditory activation or for left DAN in older adults. Furthermore, none of these effects were observed in younger adults, who showed no significant association between DAN activity and auditory cortex responses.

We next examined whether alpha and theta band activity contributed to the observed training-related effects in auditory cortex and dorsal attention network. Younger adults exhibited broad increases of alpha activity during both pre- and post-stimulus periods in bilateral auditory cortices and DAN. Importantly, increased pre-stimulus alpha power in younger adults predicted task performance. Theta power also increased in younger adults during the post-stimulus period, particularly in response to targets (Hits), not to withholds. In contrast, older adults showed no training-related changes in alpha activity but exhibited a reduction in pre-stimulus theta power in right DAN. This decrease was not associated with auditory or DAN event-related responses, nor with behavioral performance. We then measured pre-stimulus coherence between DAN and auditory cortex, and found a significant training-related increase in functional connectivity in older adults only.

Finally, we assessed the influence of the ventral attention network in the regulation of auditory perception. We found a training-related increase in pre-stimulus activity in both the left and right hemispheric regions of this network; however, unlike the dorsal attention network, these changes did not predict the amplitude of M100 auditory responses.

These findings support our main hypothesis that attentional mechanisms contribute to auditory plasticity in aging. As predicted, the dorsal attention network, particularly in its right hemisphere portion, showed training-related changes in older adults and

modulated auditory cortex activation. However, in contradiction with our hypotheses, alpha-band activity did not show training-related changes in older adults. Furthermore, while pre-stimulus theta power decreased in right DAN with training, this effect was not associated with auditory nor DAN event-related responses, nor to behavioral performance. The ventral attention network also exhibited increased preparatory activity in older adults; however, this effect was not related to the amplitude of M100 auditory cortex activation.

In contrast, younger adults did not exhibit training-related activation increases in either the dorsal or ventral attention networks; instead, they showed a trend of decreased pre-stimulus DAN activity, supporting our hypothesis that learning mechanisms differ with age. Younger participants also displayed increased alpha and theta activity, with pre-stimulus alpha modulations associated with task performance. These observations are consistent with our prediction of age-dependent modulations of band-specific activity, although the patterns observed in both age groups differed from our expectations.

Collectively, our results highlight distinct neural mechanisms supporting auditory learning in aging, with older adults relying more on top-down attentional modulation, and younger adults engaging neurophysiological dynamics linked to attentional engagement and task performance.

3.4 Influence of individual differences on behavioral and neural plasticity

3.4.1 Overview and rationale

Individual differences influence how auditory and cognitive processes are affected in aging and by training. For instance, hearing acuity (Campbell and Sharma, 2013; Karawani *et al.*, 2016; Lentz *et al.*, 2022), musical experience (Alain *et al.*, 2014; Dittinger *et al.*, 2019; Grassi *et al.*, 2017) and language background (Gresele *et al.*, 2013; Motlagh Zadeh *et al.*, 2018; Ressel *et al.*, 2012) are inter-individual factors influencing auditory plasticity and perception, and potentially affecting both baseline neurophysiological activity and changes induced by auditory training. Understanding the contribution of these personal characteristics is essential for interpreting inter-individual variability, and for assessing whether observed group-level effects are driven by training or underlying demographic differences, especially in smaller cohorts as in the studies reported herein.

The primary objective of this section was to examine whether the behavioral and neural changes reported in Sections 3.1 to 3.3 were related to individual demographic variables. We focused on factors most likely to affect auditory processing and training outcomes, including hearing thresholds and musical experience. We hypothesized that while some demographic variables, particularly those related to the auditory system, would be associated with specific neural or behavioral outcomes, they would not fully account for the training-related effects reported earlier.

3.4.2 Hearing ability predicts individual variability in older adults but does not account for training-related effects

We first identified all the outcome measures that showed significant training-related effects in either younger or older adults (see Table 3.1 for the selected demographic

Table 3.1: Demographic predictors and selected outcome measures with significant training-related effects. This table lists all behavioral and neural measures that showed significant training-related changes, along with the demographic variables used to assess potential associations. The section number indicates where each training-related effect was originally reported. For demographic predictors definition or computation, refer to [Methodology \(Sections 2.1 to 2.2\)](#).

Demographic predictors	Training-sensitive measure	Section
Education (total years)	Average level reached per day	3.1.2
Language Proficiency Index (LPI)	RAVLT Proactive Interference	3.1.4
Musical Education (ME)	RAVLT Learning Gain	3.1.4
Current Average Weekly Practice Time (AWP _{current})	Stroop Color-Word Score	3.1.4
Musicality Index (MI)	Right auditory M100 amplitude	3.2.2
Standard Pure Tone Average (PTA _{std} ; binaural or contralateral)	Left auditory baseline amplitude	3.2.4
Full Range PTA (PTA _{full} ; binaural or contralateral)	Right DAN preM100 amplitude	3.3.2
Higher Frequencies PTA (PTA _{high} ; binaural or contralateral)	Pre-stimulus alpha power (left AC and bilateral DAN)	3.3.4
	Post-stimulus alpha power (bilateral AC and DAN)	3.3.4
	Pre-stimulus theta power (right DAN)	3.3.5
	Post-stimulus theta power (bilateral AC and DAN)	3.3.5
	Pre-stimulus coherence (right DAN - right AC)	3.3.6
	Left VAN preM100 amplitude	3.3.7
	Right VAN preM100 amplitude	3.3.7

and outcome variables). We then used linear models to examine which demographic factors predicted the observed changes, represented by each participant's slope across training days. Across all the computed models, we found 18 cases in which demographic variables significantly predicted the rate of change across training days in behavioral or neural outcomes ([Table 3.2](#)). For these relationships, we included the relevant demographic variable as a covariate in the original models in which training

effects were observed, to assess whether the training-related changes persisted after covariate adjustment or were attributable to individual differences.

Table 3.2: Significant associations between demographic variables and training-related outcome changes. All combinations in which a demographic variable significantly predicted the rate of change across training days in behavioral or neural outcomes are listed. These relationships were identified using linear models (slope $\sim$ demographic + group) and are shown either across both age groups or within the age group that exhibited training-related effects in the corresponding outcome (see Table 3.1). For each case, the outcome measure, relevant demographic predictor, and corresponding statistics are reported. Rows shown in bold and shaded in purple indicate relationships where the demographic variable remained significant after including it as a covariate in the updated model (refer to Figures 3.17 and 3.18 for visualizations). No corrections for multiple comparisons were applied to capture all potentially relevant covariates. Additional model details and statistics are provided in Tables S.22 to S.28.

Group	Outcome measure	Demographic variable	<i>t</i>	<i>p</i>
Older	Average level	Standard PTA (PTA_{std})	-4.27	0.005
Older	RAVLT Learning gain	Standard PTA (PTA _{std})	-2.70	0.036
Older	Stroop score	Weekly music practice (AWP _{current})	3.61	0.022
Older	M100 right AC amplitude	Standard PTA (PTA _{std})	-2.84	0.029
Both	preM100 right DAN amplitude	Education years	2.79	0.015
Older	preM100 right DAN amplitude	Musical education	-3.63	0.022
Older	preM100 right DAN amplitude	Musicality index	-4.02	0.016
Both	Left AC pre-stim. α power	Language proficiency index	-2.52	0.026
Both	Right DAN pre-stim. θ power	Musical education	2.42	0.034
Both	Right DAN pre-stim. θ power	Musicality index	3.04	0.011
Younger	Right AC post-stim. α power (Hit)	Language proficiency index	4.07	0.007
Younger	Left AC post-stim. α power (WH)	Musical education	3.01	0.030
Both	Left AC post-stim. α power (WH)	Standard PTA (PTA _{std})	2.49	0.028
Both	Right AC post-stim. α power (WH)	Education years	-2.32	0.039
Both	Right AC post-stim. α power (WH)	Weekly music practice (AWP _{current})	3.09	0.011
Both	Left DAN post-stim. α power (WH)	Standard PTA (PTA_{std})	3.21	0.008
Younger	Right DAN post-stim. α power (WH)	Weekly music practice (AWP _{current})	4.01	0.007
Both	preM100 right VAN amplitude	Language proficiency index	-2.56	0.024

Hearing ability showed the most associations with training-related outcomes. Hearing thresholds, measured through different variants of pure tone averages (standard PTA, range PTA, and high-frequency PTA; see Section 2.2 for details), were associated with several behavioral and neural outcomes in older adults. Specifically,

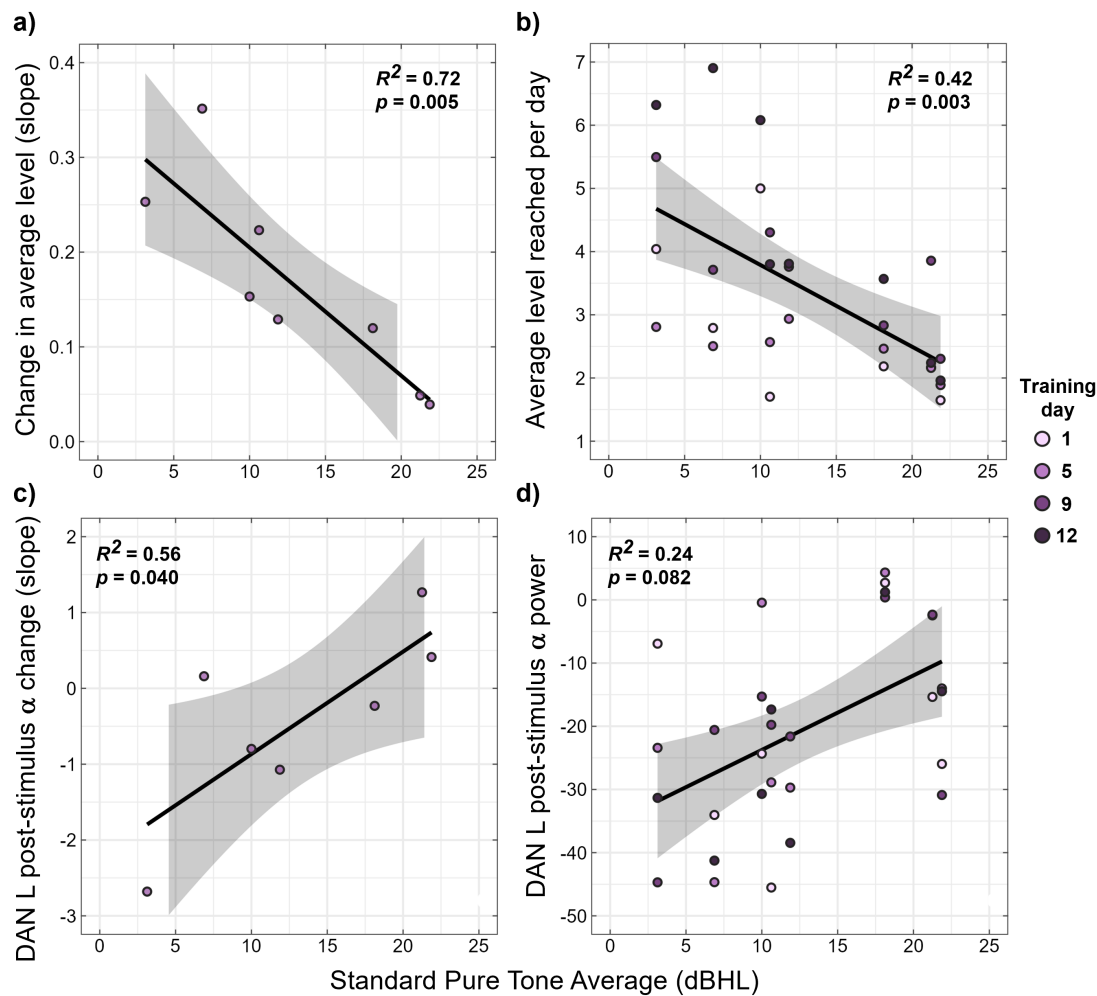


Figure 3.17: Effect of hearing thresholds on task performance and post-stimulus alpha power in older adults. Panels a and c: Simple regression models in which hearing thresholds, measured by the standard pure tone average in decibels hearing level (dBHL), significantly predicted the training-related change (slope) for average level reached in the task (**a**) and left DAN post-stimulus alpha power (**c**). **Panels b and d:** Relationship between PTA and each outcome measure using individual observations across days: task performance in **b** and left DAN post-stimulus alpha in **d**. Marker colors reflect training day, with darker shades corresponding to later sessions. Solid lines indicate linear model fits, with shaded areas representing 95% confidence intervals.

greater hearing loss was linked to lower average task performance (est.=-0.01, $p=0.005$; Figure 3.17a, Table S.22), reduced RAVLT learning gain (est.=-0.05, $p=0.036$; Table S.23), smaller M100 amplitudes in right auditory cortex (est.=-0.02, $p=0.029$; Table S.24), and higher post-stimulus alpha power in left auditory cortex (est.=0.15, $p=0.030$) and left DAN (est.=0.14, $p=0.040$; Figure 3.17c, Table S.27). Within these associations, hearing thresholds significantly predicted average task performance and post-stimulus alpha

power in left DAN when included as covariate in the full models, whereas all other relationships were not significant anymore (all $p > 0.2$). Notably, both hearing acuity (est. = -0.17, $p = 0.003$) and training day (est. = 0.16, $p = 0.007$) significantly predicted average level reached per day (Figure 3.17b), indicating that task performance improved across training sessions, and that individuals with better hearing (lower hearing thresholds) consistently reached higher performance in the training task (Table S.22). In earlier analyses (Section 3.3.4), we did not observe training-related changes in post-stimulus alpha power in older adults; yet, greater hearing loss predicted increased alpha activity in the left DAN in the covariate models (PTA_{std}: est. = 1.20, $p = 0.082$; Figure 3.17d), with the association reaching significance specifically for high-frequency hearing loss (PTA_{high}: est. = 0.54, $p = 0.023$; Table S.27).

Musical experience, assessed through years of musical education (ME), musicality index (MI), and average weekly music practice duration (AWP_{current}; see Section 2.1 for details), was also associated with training-related changes in both older and younger adults. Among older participants, musicality was related to better Stroop performance (AWP_{current}: est. = 3.61, $p = 0.022$; Table S.23), and lower right DAN preM100 activation (ME: est. = -0.04, $p = 0.022$; MI: est. = -0.01, $p = 0.016$; Table S.25). For the younger group, musical training was associated with increased pre-stimulus right DAN theta power (ME: est. = 0.10, $p = 0.089$; MI: est. = 0.02, $p = 0.039$; Table S.26), as well as higher post-stimulus alpha power in bilateral auditory cortices (Left-ME: est. = 0.17, $p = 0.030$; Right-AWP_{current}: est. = 0.60, $p = 0.055$) and right DAN (AWP_{current}: est. = 0.78, $p = 0.007$; Table S.27). However, none of these musicality-related variables remained significant predictors when included as covariates in the full models (all $p > 0.3$; Tables S.23 and S.25 to S.27), suggesting that while musical experience may be linked to individual variability in these behavioral and neural traits, it does not account for their observed training-related outcomes.

In older adults, education, quantified with total years of schooling (see Section 2.1 and Table 2.1 for details), was associated with increased right DAN preM100 amplitude

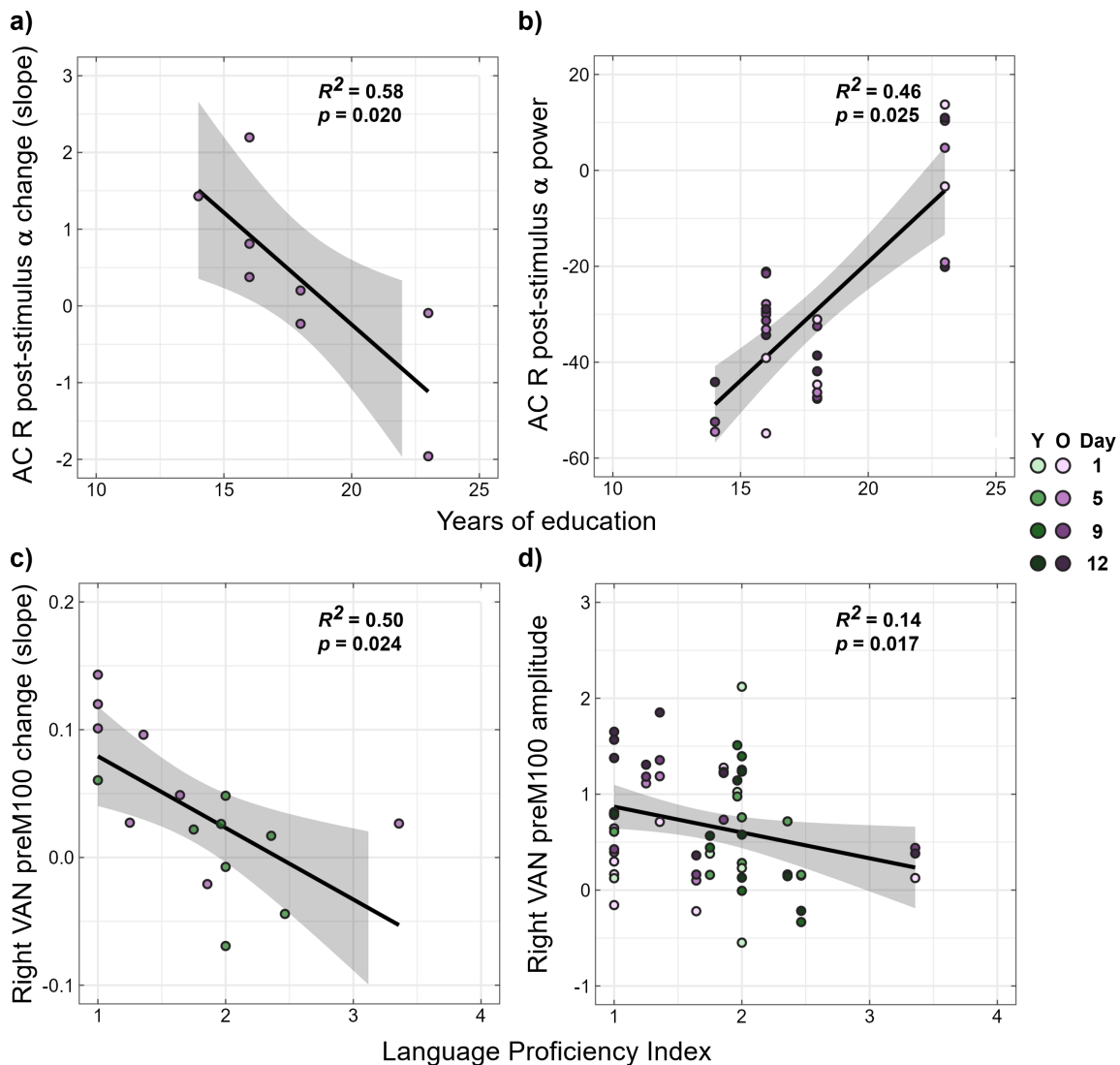


Figure 3.18: Effects of education and language proficiency in neural training-related changes. **Panels a and c:** Simple regression models showing significant associations between years of education and training-related change (slope) in right auditory post-stimulus alpha power (**a**), or language proficiency index and training-related change in right ventral attention network (VAN) pre-stimulus amplitude (**c**) in older (O, purple) and/or younger (Y, green) adults. **Panels b and d:** Corresponding relationships using individual observations across training days for each outcome measure: post-stimulus alpha power in right auditory cortex (AC, **b**) and pre-stimulus amplitude in right VAN (**d**). Marker colors reflect training day, with darker shades corresponding to later sessions. Solid lines indicate linear model fits, with shaded areas representing 95% confidence intervals.

(est.=0.01, $p=0.057$; [Table S.25](#)) and decreased post-stimulus alpha power in right auditory cortex (est.=-0.29, $p=0.020$; [Figure 3.18a](#), [Table S.27](#)). After including education as a covariate in the model, only the association with post-stimulus alpha power

remained significant, although the direction of the effect changed (est.=4.41, $p=0.025$; [Figure 3.18b](#)), suggesting that individuals with higher formal education exhibited greater right auditory alpha activity but showed smaller training-related changes in this region.

Finally, we observed a relationship between Language Proficiency Index (LPI), a normalized measure of self-assessed language proficiency ([Section 2.1](#)) and several neural measures in both groups. In older adults, LPI was negatively associated with pre-stimulus alpha power in left auditory cortex (est.=-1.04, $p=0.069$; [Table S.26](#)), while in younger adults, it showed a positive relationship with right auditory post-stimulus alpha activity (est.=2.70, $p=0.007$; [Table S.27](#)). Across both groups, higher LPI was linked to lower right VAN preM100 amplitude (est.=-0.05, $p=0.024$; [Figure 3.18c](#), [Table S.28](#)). When included as a covariate in the full models, LPI remained a significant predictor only of right VAN preM100 amplitude across both groups (est.=-0.49, $p=0.017$), and showed non-significant trends in older (est.=-0.38, $p=0.080$; [Figure 3.18d](#)) and younger participants (est.=-0.80, $p=0.097$), indicating that higher language proficiency predicted lower pre-stimulus activation in right VAN. However, LPI did not account for the training-related increase in preM100 amplitude observed in older participants, as this effect remained significant after controlling for LPI both across groups (Day×Group: $p=0.029$) and within older adults (est.=0.07, $p=0.010$).

3.4.3 Summary

In this section, we examined whether individual demographic variables, such as hearing thresholds, musical experience, education, and language proficiency, were associated with the behavioral and neural changes observed throughout training. Most associations emerged in older adults, with hearing ability being the strongest and most consistent relationship, predicting task performance and post-stimulus alpha power even when included as a covariate. Educational attainment and language proficiency were also related to several training-related outcomes. However, no single

demographic variable entirely accounted for the observed training-related effects, indicating that while these characteristics contribute to inter-individual variability, the observed neuroplastic changes were primarily induced by training.

Overall, these results are consistent with our original hypothesis, showing that individual characteristics closely related to the auditory system, such as hearing thresholds and language proficiency, only partially account for the inter-individual variability of our study outcomes, particularly in older adults. However, none of these factors accounted for the reported training-related effects, supporting the idea that the observed neural and behavioral changes effectively reflect plasticity driven by the auditory training task.

4

Discussion

In this study, we investigated the effects of auditory perceptual training on behavioral performance, cognitive function, and neural dynamics in younger and older adults. Our results revealed distinct age-related patterns of training-induced neuroplasticity within auditory and attentional brain networks. In older adults, training enhanced anticipatory activity within the right dorsal attention network, which fully mediated the observed increase in right auditory cortical responses. In contrast, younger adults did not exhibit this pattern. Instead, training modulated both pre- and post-stimulus oscillatory activity, particularly within the alpha frequency band, with pre-stimulus alpha power predicting individual differences in task performance. Overall, these findings suggest that, while both younger and older adults demonstrated behavioral improvement and learning transfer, they relied on differentiated neural processes during auditory learning, providing a foundation for the discussion that follows.

4.1 Overview of the results and key findings

Our investigation began by assessing participants' behavioral performance on the auditory task. Over twelve days of training, both age groups improved significantly in the perceptual discrimination task, with younger adults demonstrating greater gains in performance. Regardless of age, performance was lower during MEG sessions compared to at-home training. Beyond the training task, learning effects generalized to other cognitive functions, as both groups showed better inhibitory control after training, while older adults also exhibited enhancements in verbal learning and reduced auditory memory interference. These behavioral changes prompted us to examine whether such improvements were reflected in training-induced changes in brain activity.

We focused first on auditory cortical responses, where training elicited age-dependent patterns of neural modulation. Older participants exhibited increased M100 amplitude in the right auditory cortex after training, while responses in younger adults remained stable. In contrast, younger adults showed a reduction in baseline activity within the left auditory cortex. Across all auditory measures, responses were generally stronger in the right hemisphere; however, this lateralization was reduced in older adults. This modulation of perceptual responses in older adults pointed to a potential role of attentional mechanisms in shaping auditory processing.

To test whether attentional engagement accounted for the observed auditory changes, we examined pre-stimulus activity in dorsal and ventral attention networks. In the right dorsal attention network (DAN), older adults showed increased pre-stimulus activity across training, which fully accounted for the training-related increase in M100 amplitude in the right auditory cortex. This attentional modulation was further supported by increased pre-stimulus functional connectivity between the right DAN and right auditory cortex in older adults. This pattern was not observed in younger adults, who instead exhibited a slight reduction in right DAN activity and no significant changes in connectivity. For younger participants, training was associated with widespread increases in alpha activity, both before and after stimulus presentation, which also

predicted better task performance. Older adults did not exhibit changes in alpha power but showed a training-related decrease in right DAN pre-stimulus theta activity. In contrast, post-stimulus theta power increased with training exclusively in younger adults. Additionally, pre-stimulus activity in bilateral ventral attention network regions increased across training in older participants; however, this effect did not predict training-related auditory cortical modulations and was not observed in younger adults. Taken together, these findings indicate that although both age groups benefited behaviorally from training, the neural substrates underlying these improvements were markedly distinct. Older adults relied on attentional network engagements to enhance and reorient perceptual resources, whereas younger adults drew on spectral dynamics, particularly in the alpha and theta bands, to support improved performance.

In addition to training-related brain activity, we explored whether individual differences in demographic factors would account for some of the variability in learning outcomes. Hearing thresholds emerged as the most robust and consistent predictor, particularly in older adults, where greater hearing loss was linked to lower task performance and elevated post-stimulus alpha power. While education and language proficiency were linked to some neural outcomes, none of the demographic variables fully accounted for the training-induced changes, suggesting that the observed plasticity was primarily driven by the training paradigm itself.

4.2 Learning gains and generalization of training across age groups

Both younger and older adults showed improvements in performance on the auditory discrimination task across training sessions (Figure 3.1), demonstrating that the training paradigm was effective in eliciting learning throughout the adult lifespan. The improvement observed in older adults supports the notion that perceptual training remains beneficial even later in life, consistent with evidence of sustained neuroplasticity across the lifespan in both animal models (Cheng *et al.*, 2017; Cisneros-Franco *et al.*, 2018; de Villers-Sidani *et al.*, 2010; Voss *et al.*, 2016) and human studies (Mishra and Gazzaley, 2013; Mishra *et al.*, 2014).

Despite evidence of learning in older adults, the magnitude of improvement was not equivalent across age groups, with younger adults showing greater overall gains. Several factors may account for these differences in performance, many of which are likely rooted in the specific cognitive and perceptual demands of the task design (Figures 2.2 and 2.3; Sections 2.3 and 2.4). As part of the adaptive perceptual discrimination paradigm, participants were required to retain in memory a target tone that was presented only twice at the beginning of the session. As the task progressed, they needed to detect increasingly subtle frequency changes while ignoring non-target stimuli that could interfere with their representation of the memorized target. This combination of abilities, including frequency discrimination, working memory and selective attention, is particularly susceptible to age-related decline. Indeed, prior research has shown that older adults often experience deficits in discriminating between frequencies, even when hearing thresholds are accounted for (Freigang *et al.*, 2011; Moore *et al.*, 2019; Moore and Peters, 1992). Moreover, aging has been linked to a reduced capacity to suppress irrelevant auditory information (Espinoza-Varas and Jang, 2006; Kang *et al.*, 2022; Mishra *et al.*, 2014; Stothart and Kazanina, 2016), likely reflecting broader declines in selective attention (Kramer and Madden, 2008; Zanto and Gazzaley, 2016) and memory (Brehmer *et al.*, 2012; Cappell *et al.*, 2010; Choi *et al.*,

2014; Fernández-Rubio *et al.*, 2024), all of which can impair performance in frequency discrimination tasks. Additionally, age-related differences in learning rates have been documented across several training paradigms, including those targeting processing speed and working memory (Brehmer *et al.*, 2012; Bürki *et al.*, 2014). Even within the older adult cohort, younger individuals tend to benefit more from training compared to their older counterparts (Verhaeghen *et al.*, 1992). These age-related performance differences underscore the need to examine the neural mechanisms that may account for these differences. This question is addressed in the present study, and the relevant findings will be discussed in subsequent sections.

In addition to age-related differences in learning, we also observed setting-dependent performance differences. In particular, participants exhibited lower performance during MEG-based training sessions compared to at-home sessions (Figures 2.5 and 3.2). This difference likely reflects environmental and contextual factors associated with the MEG setting. Prior research has shown that cognitive performance can be negatively impacted in imaging environments due to increased anxiety, physical constraints, diminished attentional focus, or the presence of observers (van Maanen *et al.*, 2016; Paulus, 1983; Schult *et al.*, 2017). Although some studies report reduced cognitive performance outside the lab due to external distraction (Varao-Sousa *et al.*, 2018), others have highlighted that lab-based restrictions, such as the requirement to remain still, may interfere with task engagement (Ladouce *et al.*, 2017). As a result, there is growing interest in developing wearable neuroimaging technologies, including portable MEG systems (Boto *et al.*, 2018; Mellor *et al.*, 2023; Tierney *et al.*, 2020) and mobile MRI solutions (Deoni *et al.*, 2023, 2022), as well as in designing ecologically valid testing environments (Ladouce *et al.*, 2017; Parker *et al.*, 2020). While current MEG systems cannot yet be used in truly naturalistic settings, some neural measures, such as auditory brainstem responses, have shown consistency across lab and home-like environments (Parker *et al.*, 2020). The observed differences in performance between MEG and at-home sessions in this study highlight the importance to consider experimental context

when interpreting task outcomes. However, our longitudinal design demonstrated consistent training-related improvements across both environments, reinforcing the robustness of the behavioral findings and the validity of the training paradigm.

Beyond task-specific improvements, we also observed generalization of training effects to untrained cognitive domains. Both groups showed improved cognitive inhibition, while older adults additionally demonstrated gains in verbal learning and reduced memory interference. While such generalization effects have been reported in previous studies using auditory training programs, with benefits observed in verbal learning, global cognition, problem-solving, and working memory (Adcock *et al.*, 2009; Fisher *et al.*, 2009, 2015; Mishra *et al.*, 2014; Strenziok *et al.*, 2014), the literature on far-transfer effects, especially in older adults, remains inconsistent (Bürki *et al.*, 2014; Dahlin *et al.*, 2008; Fitzgerald and Wright, 2011; Karawani *et al.*, 2016). Generalization has been suggested to depend strongly on task characteristics, with greater learning transfer observed for adaptive paradigms involving well-defined cognitive skills practiced at sufficient difficulty, intensity, and duration (Brehmer *et al.*, 2012; Ferguson *et al.*, 2019; Flegal *et al.*, 2019; Green and Bavelier, 2008; Lustig *et al.*, 2009; Vinogradov *et al.*, 2012). In line with these recommendations, our auditory task was designed to engage perceptual processing, working memory, and selective attention, and was adaptively tailored to each individual's performance, requiring sustained effort across multiple sessions, which likely contributed to the observed transfer effects.

However, this generalization was not uniform across all examined cognitive domains or age groups. Transfer to the RAVLT was observed only in older adults (Figure 3.3a), which may reflect training-related remediation of age-specific cognitive deficits (Braver and West, 2008; Vinogradov *et al.*, 2012). The overlap in cognitive systems involved in auditory discrimination and verbal learning, such as selective attention and auditory memory (White *et al.*, 2013), may explain why older adults benefited in verbal learning measures. In contrast, the absence of transfer in younger adults could be due to ceiling effects, as their high baseline RAVLT scores left little room for improvement,

as reported in previous studies (Bürki *et al.*, 2014). In the Stroop task, we found training-related improvements in both age groups (Figure 3.3b), suggesting that cognitive inhibition was positively influenced by the auditory training. This is consistent with prior research showing that auditory training can enhance attentional control and reduce distractibility, particularly in older adults (Ferguson and Henshaw, 2015; Mishra *et al.*, 2014). Furthermore, no training effects were observed in AFLT, a visual learning task, indicating that training enhanced auditory functions and attentional processes that benefit tasks such as the RAVLT and SCWT, but not the AFLT, which relies on visual processing. The neural changes observed in DAN activity among older adults and alpha power modulation in younger adults support this interpretation, as discussed in the following sections.

4.3 Auditory gains and attention engagement as neural signatures of learning in older adults

Auditory training in older adults induced neurophysiological changes in both attentional and auditory regions. Specifically, we observed an increase in pre-stimulus activity within right-hemispheric regions of the dorsal attention network (Figure 3.8), which mediated the training-related increase of M100 amplitude in the right auditory cortex (Figures 3.4 and 3.11). All training effects in older adults were localized to right-lateralized cortical regions, consistent with the specialization of the right auditory cortex for fine spectral resolution (Albouy *et al.*, 2020; Zatorre and Belin, 2001) and the dominance of the right hemisphere in attentional control (Bartolomeo and Seidel Malkinson, 2019; Mengotti *et al.*, 2020; Weisz *et al.*, 2014). Importantly, no changes were observed in auditory responses to the cue, indicating that training selectively modulated the processing of the training stimulus, rather than inducing a general increase in auditory responsiveness.

However, the observed increases in auditory and attentional activity contrasted with our initial hypothesis, which predicted elevated baseline responses in older adults, followed by a decline across training sessions. Previous studies have reported reductions in neural activity following training (Alain and Snyder, 2008; Mishra *et al.*, 2014; O'Brien *et al.*, 2017), often interpreted as evidence of increased efficiency and decreased cognitive effort (Lustig *et al.*, 2009). These studies documented EEG-based, sensor-level reductions in later components (N1–P3: 150–400 ms), used non-equivalent tasks (O'Brien *et al.*, 2017), brief or non-adaptive training paradigms (Alain and Snyder, 2008), or examined changes specific to distractor processing (Mishra *et al.*, 2014). Methodological differences likely account for the discrepancies between those previous studies and our results (see Section 1.3.2 and Table 1.1), as our study employed MEG with anatomical source localization to isolate activity in specific cortical regions and a challenging task with two sources of difficulty (spectral proximity and amplitude loss; see Section 2.4 and Figure 2.3). In contrast to previous studies focusing on later

processing, our findings revealed training-related modulation of early sensory encoding (50–150 ms) and increased pre-stimulus activity, suggesting that training in older adults enhanced early encoding via preparatory attentional engagement, rather than reducing neural demands.

This pattern of increased engagement aligns with compensatory frameworks of aging. According to the CRUNCH model (Reuter-Lorenz and Cappell, 2008), the Scaffolding Theory of Aging and Cognition (STAC; Park and Reuter-Lorenz, 2009) and its revised version (STAC-r; Reuter-Lorenz and Park, 2014), older adults recruit additional neural resources to counteract structural and functional declines, particularly in response to cognitive challenge. In line with this view, and as discussed by Lustig *et al.* (2009), the progressive increases in right DAN and auditory cortical activation, along with changes in functional connectivity, suggest sustained compensatory recruitment that strengthens task-relevant networks. Thus, our results show that auditory training promotes adaptive reorganization, where older adults engage top-down attentional mechanisms to support stimulus encoding. Such findings highlight that neuroplasticity in aging can involve the reinforcement of alternative neural pathways, not just increased efficiency.

Similar increases in neural activity have been observed in other perceptual learning studies. Increased post-training activity has been reported in audiovisual (Ren *et al.*, 2024) and visual discrimination tasks (Mishra *et al.*, 2015), though often at later stages, such as the P3 component (~300 ms). The increase in early evoked activity observed in our study is particularly consistent with the work of McNair *et al.* (2019), who reported stronger P1 and N1 responses in older adults during a frequency discrimination task, as well as an influence of pre-stimulus spectral power, primarily via theta-band activity, on sensory encoding in aging. Our findings build on this by showing that pre-stimulus activity in attention networks is not static in aging, but can be dynamically modulated by training, enhancing auditory cortical responses through increased engagement and functional connectivity between the DAN and auditory cortex.

Interestingly, we also observed a reduction in pre-stimulus theta-band power across training sessions that occurred alongside the increased pre-stimulus engagement in right DAN (Figure 3.13). This theta reduction diverges from prior work associating higher pre-stimulus theta power with successful stimulus identification and memory-related processes (Addante *et al.*, 2011; Ostrowski and Rose, 2024; Strzelczyk and Langer, 2024). However, in our study, this reduction occurred alongside increased regional activity (Figure 3.8), mediation of M100 enhancement (Figure 3.11), and elevated connectivity between DAN and auditory cortex (Figure 3.15). Together, these findings suggest that training promoted a functional reorganization in the right DAN—shifting from memory-related preparatory theta activity to direct attentional engagement with auditory input. This may reflect a reduced reliance on auditory memory processes, consistent with well-established age-related memory decline (Brehmer *et al.*, 2012; Choi *et al.*, 2014; Fernández-Rubio *et al.*, 2024).

Two theoretical frameworks from distinct areas of neuroscience research may explain this functional reorganization. First, the Reverse Hierarchy Theory (Ahissar *et al.*, 2009) posits that perceptual learning begins with high-level cognitive processes and progressively recruits lower-level sensory representations via top-down mechanisms. For older adults with compromised memory, this top-down shift may be essential for improving perceptual encoding in demanding tasks (Bieber and Gordon-Salant, 2021). Second, predictive coding models by Rao and Ballard (1999) propose that during perception, the brain generates predictions about incoming sensory input and updates these predictions based on the difference between expected and actual input. In the context of aging, predictive coding models suggest that age-related declines in sensory processing and working memory drive the brain to prioritize more stable internal models over degraded external input when interpreting sensory information (Chan *et al.*, 2021; Hsu *et al.*, 2021). Our results suggest that training can counteract this trend by strengthening top-down sensory processing, providing an active alternative to passive prediction, a notion supported by animal studies showing that aging auditory systems increasingly recruit attentional mechanisms to process expected input (Cai

et al., 2016).

While training modulated theta-band activity and enhanced pre-stimulus engagement within the dorsal attention network, we found no significant training-related changes in alpha-band power. We observed the expected alpha desynchronization (i.e., decrease relative to baseline) following the Cue, as reflected by consistently negative post-Cue (pre-stimulus) alpha power across all training days (Figure 3.13). This pattern aligns with prior findings linking alpha desynchronization to attentional orienting and sensory preparation (van Ede *et al.*, 2014; Foxe and Snyder, 2011; Müller and Weisz, 2012; Weisz *et al.*, 2014). However, the lack of training-related modulations in alpha activity may be explained by age-related changes such as spectral flattening (McNair *et al.*, 2019; Voytek *et al.*, 2015), reduced spontaneous alpha power (Clements *et al.*, 2021), and deficits in attentional reorientation (Arif *et al.*, 2020). These factors may diminish the functional specificity of alpha responses and limit their trainability in older populations. Additionally, recent evidence shows that alpha activity during attentive listening arises from different cortical regions across the lifespan. In younger adults, alpha is most prominent in the superior parietal cortex, a key node of DAN, whereas older adults show reduced parietal involvement and greater activity in posterior temporal regions, potentially limiting our ability to capture alpha modulations in older adults (Herrmann *et al.*, 2023).

Beyond the DAN, training was also associated with increased pre-stimulus activity in bilateral regions of the ventral attention network (Figure 3.16). While VAN activation did not independently predict changes in auditory cortex responses, its inclusion in the model attenuated the effect of training day, suggesting shared variance between VAN engagement and training-induced plasticity. Such reduction in the training effect may reflect a functional interaction between the VAN and other networks in support of perceptual learning in aging, aligning with evidence linking VAN to top-down auditory attention (Alho *et al.*, 2015; Salmi *et al.*, 2009). The recruitment of both dorsal and ventral attention networks during training may also reflect compensatory mechanisms

supporting perceptual performance in aging, consistent with the CRUNCH model (Reuter-Lorenz and Cappell, 2008). These networks share structural and functional connections that may facilitate efficient attentional control (Mengotti *et al.*, 2020). Additional evidence reinforces the functional relevance of VAN recruitment in aging: white matter integrity in VAN regions has been linked to cognitive improvements following auditory training (Strenziok *et al.*, 2014), and functional DAN-VAN interactions predict behavioral outcomes in visual tasks (Wen *et al.*, 2012). Collectively, these findings indicate that coordinated recruitment of dorsal and ventral attention networks may support auditory plasticity in aging, though future studies are needed to clarify the nature and functional impact of these interactions.

4.4 Increased alpha power and reduced neural responses: a signature of efficiency in younger adults?

In contrast to older adults, younger participants showed no training-related changes in the amplitude or lateralization of M100 auditory responses (Figure 3.4). However, we observed a reduction in spontaneous activity in the left auditory cortex across training sessions (Figure 3.7b). Interestingly, lower baseline activity in this region was linked to lower average performance levels, independent of training day, suggesting that reduced activation may hinder performance when considered in isolation. Yet, because behavioral performance improved over time despite this reduction, this change may reflect a broader reorganization of auditory processing rather than a detrimental effect. Specifically, this activity reduction may represent the functional inhibition of task-irrelevant regions, consistent with right-hemisphere specialization for pitch-based stimuli (Albouy *et al.*, 2020; Zatorre and Belin, 2001). This interpretation is supported by evidence that disruption of the right auditory cortex during pitch-based tasks impairs discrimination learning, whereas disruption of the left auditory cortex does not (Matsushita *et al.*, 2021). Moreover, interference in the right auditory cortex can lead to compensatory increases in left auditory activity, especially in individuals with strong interhemispheric connectivity (Andoh and Zatorre, 2011, 2013). Thus, the training-related reduction in left auditory activity observed in our study may reflect adaptive downregulation of irrelevant processing streams, facilitating more efficient right-lateralized encoding.

Beyond reduced spontaneous activity in auditory cortex, a slight decrease in pre-stimulus activity in the right DAN (Figure 3.8d) also pointed toward greater processing efficiency reached with training in younger adults. This reduction may reflect that anticipatory attentional engagement becomes less necessary as the task becomes more familiar. While younger adults are generally more reliant on bottom-up sensory input than on internal predictions (Chan *et al.*, 2021), predictive coding frameworks suggest that repeated exposure to predictable stimuli should progressively reduce

prediction error, leading to attenuated neural responses with learning (Friston, 2005). Benedek *et al.* (2014) further proposed that suppressed or attenuated activity in attention-related regions may reflect top-down modulation to prevent the reorienting of attention toward task-irrelevant stimuli, thereby supporting goal-directed behavior. This interpretation also aligns with the training-related reduction in baseline activity observed in the left auditory cortex, likely to suppress distracting input from that region. Collectively, these decreases in neural activity suggest that training promoted more efficient neural processing by minimizing reliance on anticipatory engagement and inhibiting irrelevant perceptual channels.

Auditory training also led to widespread increases in alpha power, both pre- and post-stimulus, across auditory and attention-related regions (Figures 3.12 to 3.14). In particular, pre-stimulus alpha power increased across training days (i.e. decreased desynchronization) in left auditory cortex and marginally in bilateral DAN regions (Figure 3.13). The increase in alpha power in the left auditory cortex predicted task performance, with higher alpha associated with higher average performance levels. Given that alpha power has been repeatedly linked to attentional regulation and perceptual resource allocation (Deng *et al.*, 2020; Harris *et al.*, 2017; Kasten *et al.*, 2024; Keller *et al.*, 2017; Strauß *et al.*, 2014; Weisz *et al.*, 2014), these results suggest that younger participants required fewer perceptual resources to perform the task as learning progressed, providing additional evidence of improved neural efficiency. This behavioral association reinforces the role of pre-stimulus alpha activity as a learning mechanism in younger adults, consistent with findings that increased ipsilateral alpha supports attentional focus on contralateral auditory input (Weisz *et al.*, 2014). Interestingly, no pre-stimulus alpha modulation was observed in right auditory cortex—the most critical region for our spectral discrimination task—which supports the idea that increased alpha reflects top-down suppression of irrelevant regions rather than direct engagement of sensory processing.

Alpha power is also known to increase in response to degraded signal quality, such

as when auditory input is diminished (Obleser *et al.*, 2012; Weisz *et al.*, 2011; Wöstmann *et al.*, 2015). It is therefore possible that the training-related increase in alpha reflects the gradual reduction in stimulus quality embedded in our adaptive paradigm (see Figure 2.3d). As participants advanced to higher difficulty levels, they encountered stimuli with increasingly attenuated spectral cues, which may have triggered stronger alpha responses. Beyond attention and perception, alpha dynamics may also contribute to memory encoding. Recent studies have shown that increased pre-stimulus alpha power supports stimulus association and recognition (Ostrowski and Rose, 2024), and that training can amplify preparatory alpha activity in visual memory tasks (Strzelczyk and Langer, 2024), suggesting that alpha activity may contribute to target encoding and recognition in the auditory task. However, most evidence linking alpha to memory processes has focused on post-stimulus activity, which also showed training-related modulations in younger adults.

Indeed, post-stimulus alpha power increased exclusively in younger adults with training, potentially reflecting stimulus-driven attentional modulation (Harris *et al.*, 2017; Wiesman and Wilson, 2020), or a shift toward internal attention to protect task-relevant information from interference (Bonnefond and Jensen, 2012; Kasten *et al.*, 2024; Zhou *et al.*, 2023). In support of the latter, Bonnefond and Jensen (2012) demonstrated that alpha synchronization during the encoding phase predicted better memory performance, consistent with an inhibitory role for alpha when distractors are expected. In contrast, other studies have reported that decreased post-stimulus alpha power (i.e., increased desynchronization) is associated with stronger memory representations in both auditory and visual tasks (Strunk and Duarte, 2019; Weisz *et al.*, 2020). While these studies examined distractor interference during memory encoding, our task differs in that any given stimulus could function either as a distractor (i.e., non-target) that must be ignored to prevent interference, or as the target that must be encoded to strengthen the internal representation. Therefore, the post-stimulus alpha increase in our study may reflect a blend of reduced attentional demand and heightened memory prioritization: early in training, alpha desynchronization may

aid encoding, whereas with learning, alpha synchronization may indicate increased efficiency and reduced cognitive load.

Another consideration is that the observed post-stimulus alpha increases may not solely reflect independent stimulus-evoked activity. Findings from [Strzelczyk and Langer \(2024\)](#) highlight the importance of interpreting post-stimulus alpha desynchronization in the context of pre-stimulus dynamics. In their visual memory task, training was initially associated with increased post-stimulus alpha desynchronization; however, this effect reversed when pre-stimulus alpha power was included in the model, revealing a training-related increase in post-stimulus alpha activity ([Strzelczyk and Langer, 2024](#)). In our study, we did not isolate post-stimulus alpha power from the influence of pre-stimulus dynamics due to the constraints of the trial structure ([Figure 2.2](#)). Time-frequency data were baseline-corrected across both pre- and post-stimulus windows using the same reference interval (-500 to -25 ms relative to the Cue; [Section 2.9.6](#)). As a result, the post-stimulus alpha modulations we observed may partially reflect effects originating from preparatory activity.

Additionally, we observed training-related increases in post-stimulus theta power across auditory and attention regions, particularly in response to targets. This increase may reflect enhanced target recognition ([Harris et al., 2017](#); [Mishra et al., 2014](#); [Ostrowski and Rose, 2024](#); [Wiesman and Wilson, 2020](#)), though it may also be shaped by pre-stimulus theta dynamics ([Strzelczyk and Langer, 2024](#)). However, results from Hit trials should be interpreted with caution, as the number of Hits was lower than withholds, which limits the reliability of post-stimulus estimates for this condition. Finally, to clarify the distinct contributions of pre- and post-stimulus alpha and theta activity in auditory training, future studies should incorporate trial-by-trial analyses, apply methods that separate oscillatory from evoked components, and consider approaches such as neural decoding or brain stimulation to probe the functional relevance of these dynamics for task performance and working memory.

4.5 Divergent neural pathways support learning across age

The main finding of this study is that auditory learning induced different neural changes in younger and older participants, emphasizing age-related differences in how the brain adapts to the same learning experience. Younger adults showed training-related modulations in spectral dynamics, particularly alpha power, both before and after stimulus presentation. In contrast, older adults displayed increased engagement of attention-related networks, especially the right DAN, where pre-stimulus activity and functional connectivity with auditory cortex increased across training sessions. Building on prior evidence of age-related differences in neural recruitment (Braver *et al.*, 2009; Nguyen *et al.*, 2020; Reuter-Lorenz, 2002; Strzelczyk and Langer, 2024; Voytek *et al.*, 2015), the present work demonstrates these differences also emerge during learning-related neural plasticity.

These distinct neural adaptations likely reflect differences in cognitive strategies, the use of neural resources, and compensatory mechanisms associated with aging. Prior work has proposed the existence of two distinct cognitive control modes (Braver *et al.*, 2007), later shown to be differentially engaged with age depending on task demands and goals (Braver *et al.*, 2009). Younger adults typically rely on a proactive control strategy, where task-relevant information is maintained and sustained by preventing interference. In contrast, older adults engage a reactive control mode, modulating attention only after interference occurs to then manage competing information. In addition, predictive coding frameworks (Chan *et al.*, 2021; Hsu *et al.*, 2021; Rao and Ballard, 1999) suggest that younger adults rely more on perceptual feedback to minimize prediction error, whereas older adults depend on predictions, particularly when sensory input is compromised. These two complementary accounts can be integrated to interpret our results: in younger adults, increased alpha power and reduced DAN engagement may reflect efficient sensory encoding and proactive interference prevention; while in older adults, degraded input biases the system toward internal models, with training prompting a shift toward greater perceptual engaging through

attentional recruitment, consistent with the Reverse Hierarchy Theory of learning (Ahissar *et al.*, 2009; Bieber and Gordon-Salant, 2021).

In addition to age-specific mechanisms supporting auditory learning, we observed intrinsic differences in auditory processing between younger and older adults. Across both age groups, auditory processing was characterized by right-hemispheric dominance. However, older adults exhibited greater recruitment of left auditory cortex (Figure 3.4) and reduced amplitude and hemispheric asymmetry in the auditory response to the Cue (Figure 3.7). These patterns are consistent with the HAROLD model (Cabeza, 2002; Section 1.2.2) and align with our hypotheses on higher neural recruitment in older adults. In particular, the reduced response to the Cue in older adults is likely related to well-documented age-related declines in high-frequency hearing sensitivity (Keay and Murray, 1988; Wang and Puel, 2020; Wiley *et al.*, 1998), since the Cue tone was set at 5 kHz, a frequency in which older adults typically show elevated thresholds even though none of the participants met clinical criteria for age-related hearing loss (Figure 2.1). Nonetheless, these age-related patterns did not change with training, likely because they were not directly engaged by task demands. Rather than altering perceptual responses to the Cue or activity in the left auditory cortex that is not critically involved in spectral discrimination (Matsushita *et al.*, 2021), auditory training primarily enhanced perceptual processing in right auditory cortex and higher-order functions such as selective attention and memory.

While both younger and older participants benefited behaviorally from auditory training, our findings reveal fundamental differences in the neural changes elicited by the same training protocol. These results highlight the dynamic nature of neuroplasticity across the adult lifespan and emphasize the importance of tailoring training interventions to age-specific cognitive and neurophysiological profiles.

4.6 The role of hearing and other demographic factors in learning variability

To better understand the sources of individual variability in training outcomes, we examined different demographic factors that could contribute to the observed behavioral and neural changes (Table 3.1). We found that inter-individual variability in learning outcomes was shaped not only by age, but by demographic factors such as hearing ability, education and language background (Table 3.2). Differences in hearing ability emerged as key predictors of both behavioral performance and neural activity, particularly in older adults. Participants with greater hearing loss showed lower task performance and higher post-stimulus alpha power (Figure 3.17). Previous reports have shown that differences in hearing thresholds account for age-related variability in behavioral and neural responses (Alain and Snyder, 2008; Lentz *et al.*, 2022), and that alpha activity increases under challenging listening conditions (Obleser *et al.*, 2012; Petersen *et al.*, 2015; Wöstmann *et al.*, 2015). Furthermore, the central auditory system undergoes neural changes with aging that often occur independently of peripheral hearing loss and can impair the ability to process and interpret auditory input (Ouda *et al.*, 2015; Profant *et al.*, 2014). These age-related neural changes may help explain the observed relationships between hearing ability, behavioral performance and alpha activity; and they underscore the importance of accounting for hearing variability when interpreting neural data, particularly in aging and auditory paradigms. However, training-related improvements in performance remained significant even after controlling for hearing thresholds, indicating that auditory perceptual learning is preserved despite age-related perceptual decline.

Beyond hearing, we explored the influence of education, musical training, and language proficiency. Although musicality has been proposed as a protective factor in auditory aging (Fernández-Rubio *et al.*, 2024; Grassi *et al.*, 2017), we did not observe consistent associations with behavioral or neural plasticity, likely due to limited variability in musical experience within our sample. Similarly, education is a

well-established contributor to cognitive reserve (Christensen *et al.*, 2008; Reuter-Lorenz and Park, 2014; Stern, 2009) and has been shown to influence attention and working memory (Choi *et al.*, 2014). While our findings in older adults revealed that higher educational attainment was associated with changes in neural activity in right auditory and attentional regions, the direction and significance of these effects varied across analyses (Figure 3.18a,b). Specifically, individuals with more years of formal education exhibited greater right auditory alpha power but showed smaller training-related changes, pointing to a potential role of cognitive reserve in reducing the need for additional neuroplastic adaptation during training.

We also found that higher language proficiency predicted lower pre-stimulus activity in the right VAN across both age groups (Figure 3.18c,d). Indeed, multilingualism has been linked to enhanced executive control and increased cognitive reserve, with evidence of delayed cognitive decline as well as structural and functional changes across the lifespan (Antolovic *et al.*, 2023; Baum and Titone, 2014; Chung-Fat-Yim *et al.*, 2023; Reuter-Lorenz and Park, 2014). Most neural effects have been reported in left-hemisphere language regions such as the inferior frontal gyrus (Fedorenko *et al.*, 2024; Klein *et al.*, 2014, 2001; Thieba *et al.*, 2019); but more recent work has also identified associations with ventral attention network activity and global efficiency, particularly in early multilinguals (Arredondo *et al.*, 2017; Balboni *et al.*, 2025; Berken *et al.*, 2016; Gracia-Tabuenca *et al.*, 2024; Yee *et al.*, 2023). Therefore, the observed reduction in pre-stimulus VAN activity may reflect greater efficiency in attentional preparation among individuals with higher language proficiency, consistent with evidence that multilingualism refines control network function. However, our conclusions are constrained by the limited sample size and by the scope of our language measures, which did not include age of acquisition or degree of language use (see Section 2.1), both commonly used in multilingualism research (Chung-Fat-Yim *et al.*, 2023; Gracia-Tabuenca *et al.*, 2024).

Although our findings indicate that individual characteristics such as hearing ability,

education, and language proficiency are associated with differences in behavioral and neural outcomes, none fully accounted for the training-related changes reported in earlier sections, suggesting that these effects primarily reflect learning-driven plasticity and not variability inherent to individual backgrounds. The small sample size and high variability between individuals, especially among older adults, limit how these associations can be generalized; however, the consistency of certain effects, particularly the relationship between hearing ability, performance and neural activity, aligns with previous research and strengthens their interpretive value. Together, these preliminary findings provide a foundation for future studies with larger and more diverse cohorts to better understand how demographic factors shape neuroplasticity in response to auditory training across the lifespan.

4.7 Limitations

Despite the strengths of this study, notably its longitudinal design with four imaging sessions per participant, several limitations must be acknowledged. First, the relatively small sample size limited the statistical power to detect subtle effects, such as associations between neural changes and behavioral outcomes, and reduced the generalizability of the findings. This limitation was further amplified by the broad age range in the older group (42–77 years), which likely introduced additional variability in cognitive and auditory function. On the other hand, the younger group (20–35 years) consisted largely of university students, who may have shared more homogeneous characteristics in terms of education, lifestyle and cognitive reserve. This variability is supported by the STAC-r framework (Reuter-Lorenz and Park, 2014), which emphasizes that lifelong experiences contributing to neural resource enrichment (e.g. education, physical activity, multilingualism) or depletion (e.g. chronic stress, depression) shape individual trajectories of neural maintenance and compensation. As a result, increased neural recruitment in older adults does not necessarily correspond to better performance, as individuals with greater neural compromise may exhibit more activation yet perform worse than those requiring less compensation (Zahodne and Reuter-Lorenz, 2019).

Methodologically, we opted to examine large-scale regions of interest (Figure 2.7) to compensate for the small sample size and reduce the likelihood of false positives from multiple comparisons. While this approach provided us with network-level interpretations, it may have obscured localized differences, as region-specific changes in activation (Schönwiesner *et al.*, 2007) and spectral power (Arif *et al.*, 2020; López-Madróna *et al.*, 2024; Mishra *et al.*, 2014; Müller and Weisz, 2012) have been reported in auditory and learning paradigms. Future studies with larger sample sizes may benefit from the use of finer anatomical subdivisions, to distinguish between primary and secondary auditory cortices, as well as between parietal and frontal components of attentional networks.

In addition, the time-frequency windows used in this study were defined based on visual inspection of grand-averaged data (see [Figure 2.8](#)) to avoid overlapping with signal from the evoked responses. However, more rigorous approaches such as cluster-based permutation testing could improve objectivity and sensitivity to subtle training effects ([Meyer et al., 2021](#)). Furthermore, restricting the time-frequency analysis to non-phase-locked activity by removing the event-related response prior to spectral decomposition ([Harris et al., 2017](#)), as well as separating oscillatory components from the aperiodic (1/f) signal ([Voytek et al., 2015](#); [López-Madrona et al., 2024](#)) could help isolate functionally meaningful neural oscillations and reduce contamination from broadband changes. Finally, our investigation focused on alpha and theta activity; however, evidence linking beta (15–30 Hz) and gamma (30–90 Hz) frequency bands to attention reallocation, memory and cognitive processes ([Ahveninen et al., 2013](#); [Arif et al., 2020](#); [Doesburg et al., 2012](#); [Ostrowski and Rose, 2024](#); [Polomac et al., 2015](#); [Weisz et al., 2020](#)) suggests that additional frequencies may also contribute to training-related plasticity and warrant further examination.

While this study provides new insights into the neural dynamics of auditory learning across the adult lifespan, it remains constrained by the challenges of integrating multiple sources of individual variability within a relatively small sample. Nonetheless, training-related effects emerged across both behavioral and neural domains, and clear differences were observed between younger and older adults. Therefore, these findings establish a path to be followed by future research, which should aim to replicate and expand upon them in larger, more diverse populations, by incorporating time-resolved imaging, more anatomically specific ROI analyses, and longitudinal follow-ups to evaluate the durability and generalizability of training-induced changes. Such efforts will be essential for refining age-sensitive interventions and advancing our understanding of the neural mechanisms that support perceptual and cognitive learning in aging.

4.8 Implications and future directions

The present findings offer new insights into the neural mechanisms that support auditory learning across aging. While both younger and older adults demonstrated behavioral improvements following training, the underlying neural adaptations diverged: younger adults showed spectral changes in alpha power, whereas older adults exhibited increased recruitment of attentional networks. These age-related differences suggest that auditory learning does not rely on a single set of neural processes. Instead, the aging brain may shift from a proactive to a reactive attentional control strategy, recruiting different systems depending on available cognitive resources. Future studies with larger and a more continuous age distribution are needed to characterize the specific mechanisms underlying this transition and to determine whether it emerges gradually with age, and to what extent it is driven by accumulated neural changes or sensory decline.

These findings also contribute to growing evidence that cognitive benefits are more likely to emerge when training tasks are both adaptive and sufficiently challenging (Ferguson *et al.*, 2019; Flegal *et al.*, 2019; Lustig *et al.*, 2009; Vinogradov *et al.*, 2012). However, longitudinal studies are needed to determine whether the neurophysiological changes observed here persist after training ends, and whether the behavioral improvements generalize to real-world cognitive functioning in older adults. While prior work has shown that auditory training benefits can be retained for at least six months in clinical populations such as individuals with schizophrenia (Fisher *et al.*, 2010), it remains unknown whether similar long-term retention occurs in healthy aging or whether associated neural changes are maintained. Encouragingly, a recent study found that older adults who completed a three-month music training program exhibited increased theta power that persisted three months after the intervention (Bugos *et al.*, 2022). Although the training involved complex cognitive, emotional and social factors, such as social engagement, that may have contributed to the observed outcomes, the results suggest that structured auditory experiences can

induce long-lasting neuroplastic changes. This highlights the need for follow-up studies using simpler yet scalable auditory training paradigms like the one presented here.

Finally, the training paradigm used in this study could be adapted for application in clinical populations, where perceptual and cognitive decline is more pronounced. Conditions such as age-related hearing loss or mild cognitive impairment may benefit from targeted auditory training interventions, particularly given their potential for neural compensation and plasticity. Comparing learning-related changes in healthy versus clinical aging could help clarify how disease burden interacts with neuroplastic potential. Future research should explore how adaptive auditory training can be optimized to support cognitive function and perceptual abilities in these populations.

5

Conclusion

The central aim of this dissertation was to determine whether auditory learning benefits older adults and how their neural adaptations compare to those of younger adults. By combining behavioral measures, cognitive assessments, and magnetoencephalography, our findings demonstrate that both age groups improved behaviorally and generalized learning to untrained tasks, albeit through distinct neurophysiological mechanisms.

Younger adults showed modulations in spectral dynamics, particularly in alpha-band activity, and reductions in auditory and dorsal attention activity, consistent with more efficient sensory and attentional processing. In contrast, older adults exhibited increased engagement of attention-related networks, especially the dorsal attention network, which mediated training-related changes in right auditory cortex responses. These findings suggest that older adults may rely on compensatory recruitment of attentional systems to maintain auditory performance.

Although the relatively small sample size and the broad age range within the older group may have limited our ability to detect finer-grained relationships between neural and behavioral outcomes, consistent patterns emerged. Specifically, the engagement

of attention networks in older adults and alpha modulation in younger adults align with prior research on age-related changes in cognitive control and sensory processing. These results underscore the need for future studies with larger samples and extended follow-up periods to better understand individual differences in training outcomes and the persistence of neurophysiological changes. Such work will be essential for translating these findings into targeted interventions for clinical populations with sensory or cognitive decline.

A key contribution of this study is the longitudinal characterization of training-related neurophysiological changes in both younger and older adults using a unified auditory learning paradigm. Overall, our results provide compelling evidence that aging does not diminish the brain's capacity for learning-driven adaptation. Rather, it prompts a shift in the neural strategies and resources recruited to support this adaptation. This work lays the foundation for the development of age-sensitive auditory training programs aimed at enhancing perceptual and cognitive function in older populations.

*Courage doesn't always roar.
Sometimes courage is the quiet voice
at the end of the day saying,
"I will try again tomorrow".*

— Mary Anne Rademacher in
Rawson and Miner (2008)

Supplementary Materials

S.1 Statistical Tables

Table S.1: Statistical models of training task performance. Results of statistical models used to assess the average and maximum levels reached in the training task. Post-hoc analyses were conducted to evaluate each group separately. Prevalence (Prev.) represents the percentage of subjects (either across or within groups) that showed a performance improvement, as defined by a positive slope. The mean and standard deviation (SD) of the slopes are also provided. Significant results ($p < 0.05$) are highlighted in bold and results referenced in Results (Section 3.1.2) are shaded in purple.

Group	Effect	Estimate	t value	p value	Prev.	Mean ($\pm$ SD)
<i>Model: AvgLevel $\sim$ Day * Group + (1 + Day Subject)</i>						
Both	Day	0.16	2.85	0.013	100%	0.29 ($\pm$ 0.21)
Both	Group	1.40	1.69	0.121		
Both	Day:Group	0.29	3.60	0.003		
<i>Model: AvgLevel $\sim$ Day + (1 + Day Subject)</i>						
Younger	Day	0.45	6.20	4×10^{-4}	100%	0.43 ($\pm$ 0.21)
Older	Day	0.16	3.92	0.002	100%	0.16 ($\pm$ 0.11)
<i>Model: AvgLevel $\sim$ Day * Age + (1 + Day Subject)</i>						
-	Day	0.62	7.37	3×10^{-6}		
-	Age	-0.03	-1.69	0.121		
-	Day:Age	-0.01	-4.23	0.001		
<i>Model: MaxLevel $\sim$ Day * Group + (1 + Day Subject)</i>						
Both	Day	0.25	2.70	0.015	93.75%	0.36 ($\pm$ 0.29)
Both	Group	1.01	1.03	0.313		
Both	Day:Group	0.33	2.47	0.024		
<i>Model: MaxLevel $\sim$ Day + (1 + Day Subject)</i>						
Younger	Day	0.58	5.52	0.001	100%	0.48 ($\pm$ 0.33)
Older	Day	0.25	2.70	0.025	87.50%	0.24 ($\pm$ 0.21)

Table S.2: Statistical models of the effect of environmental setting on task performance. Results of statistical models used to assess the impact of the session location (Setting) on task performance. Post-hoc analyses were performed to evaluate each group separately in the simplified model (without interaction terms). Significant results ($p < 0.05$) are highlighted in bold and results referenced in Results (Section 3.1.3) are shaded in purple.

Group	Effect	Estimate	t value	p value
<i>Model: AvgLevel ~ Day + Group + Setting + (1 + Day Subject)</i>				
Both	Day	0.30	5.66	5×10^{-5}
Both	Group	3.38	2.10	0.054
Both	SettingMEG	-2.54	-8.37	4×10^{-14}
<i>Model: AvgLevel ~ Day + Setting + (1 + Day Subject)</i>				
Younger	Day	0.36	5.33	1×10^{-6}
Younger	SettingMEG	-2.87	-6.16	3×10^{-8}
Older	Day	0.23	2.82	0.026
Older	SettingMEG	-2.14	-5.61	3×10^{-7}
<i>Model: AvgLevel ~ Day * Group + Setting + (1 + Day Subject)</i>				
Both	Day	0.23	3.12	0.008
Both	Group	2.19	1.26	0.231
Both	SettingMEG	-2.56	-8.35	5×10^{-14}
Both	Day:Group	0.16	1.55	0.145
<i>Model: AvgLevel ~ Day + Group * Setting + (1 + Day Subject)</i>				
Both	Day	0.29	5.55	6×10^{-5}
Both	Group	3.76	2.30	0.037
Both	SettingMEG	-2.17	-4.91	2×10^{-6}
Both	Group:SettingMEG	-0.81	-1.32	0.187

Table S.3: Statistical models of RAVLT performance. Results of statistical models used to assess each RAVLT performance measure. Post-hoc analyses were performed to evaluate each group separately and to compare against an untrained group of younger adults. Correction for multiple comparisons was done across related hypotheses (same effect and group in RAVLT and SCWT) using the Benjamini-Hochberg method. Prevalence (Prev.) represents the percentage of subjects (either across or within groups) who showed an improvement in the RAVLT measure, based on the direction of their slopes. For most measures, improvement corresponds to positive slopes; however, for interference measures, negative slopes indicate better performance. The mean and standard deviation (SD) of the slopes are also provided. Significant results ($p_{FDR} < 0.05$) are highlighted in bold and results referenced in the Results (Section 3.1.4) are shaded in purple.

Group	Effect	Est.	t value	p value	p_{FDR}	Prev.	Mean ($\pm$ SD)
<i>Model: RAVLT_LearningGain ~ Session * Group + (1 Subject)</i>							
Both	Session	0.61	3.36	0.002			
Both	Group	0.09	0.52	0.609			
Both	Session:Group	-0.52	-2.00	0.056	0.168		
<i>Model: RAVLT_Proactive_Interference ~ Session * Group + (1 Subject)</i>							
Both	Session	-0.43	-3.99	5×10^{-4}			
Both	Group	-0.33	-3.14	0.004			
Both	Session:Group	0.32	2.06	0.049	0.168		
<i>Model: RAVLT_TotalScore ~ Session + Group + (1 Subject)</i>							
Both	Session	-2.69	-1.44	0.172	0.207	40%	-2.87 (± 7.38)
Both	Group	8.69	3.40	0.004	0.013		
<i>Model: RAVLT_TotalScore ~ Session + (1 Subject)</i>							
Older	Session	-3.76	-1.22	0.263	0.315	28.57%	-4.14 (± 8.43)
Younger	Session	-1.75	-0.72	0.479	0.600	50%	-1.75 (± 6.69)
Untrained	Session	-1.12	-0.75	0.476		37.50%	-1.12 (± 4.22)
<i>Model: RAVLT_LearningGain ~ Session + Group + (1 Subject)</i>							
Both	Session	0.36	2.61	0.014	0.029	66.67%	0.37 (± 0.57)
Both	Group	-0.16	-1.15	0.260	0.260		
<i>Model: RAVLT_LearningGain ~ Session + (1 Subject)</i>							
Older	Session	0.61	4.00	0.005	0.016	87.50%	0.61 (± 0.43)
Younger	Session	0.09	0.45	0.663	0.663	42.86%	0.11 (± 0.63)
Untrained	Session	-0.03	-0.14	0.890		50%	-0.03 (± 0.59)

Continued on next page

Table S.3: Statistical models of RAVLT performance. (Continued)

Group	Effect	Est.	t value	p value	p_{FDR}	Prev.	Mean ($\pm$ SD)
<i>Model: RAVLT_DelayedRecallIndex $\sim$ Session + Group + (1 Subject)</i>							
Both	Session	-0.05	-2.10	0.053	0.080	18.75%	-0.05 ($\pm$ 0.09)
Both	Group	0.11	1.27	0.226	0.260		
<i>Model: RAVLT_DelayedRecallIndex $\sim$ Session + (1 Subject)</i>							
Older	Session	-0.06	-3.05	0.019	0.035	12.50%	-0.06 ($\pm$ 0.06)
Younger	Session	-0.03	-0.81	0.446	0.600	25%	-0.03 ($\pm$ 0.12)
Untrained	Session	-0.13	-2.27	0.058		12.50%	-0.13 ($\pm$ 0.16)
<i>Model: RAVLT_Retroactive_Interference $\sim$ Session + Group + (1 Subject)</i>							
Both	Session	-0.003	-0.05	0.958	0.958	33.33%	0.03 ($\pm$ 0.17)
Both	Group	-0.07	-1.32	0.198	0.260		
<i>Model: RAVLT_Retroactive_Interference $\sim$ Session + (1 Subject)</i>							
Older	Session	-0.03	-0.32	0.773	0.773	42.86%	0.02 ($\pm$ 0.19)
Younger	Session	0.03	0.69	0.500	0.600	25%	0.03 ($\pm$ 0.17)
Untrained	Session	0.08	1.51	0.174		25%	0.08 ($\pm$ 0.15)
<i>Model: RAVLT_Proactive_Interference $\sim$ Session + Group + (1 Subject)</i>							
Both	Session	-0.31	-3.59	0.001	0.004	80%	-0.30 ($\pm$ 0.34)
Both	Group	-0.22	-2.49	0.019	0.038		
<i>Model: RAVLT_Proactive_Interference $\sim$ Session + (1 Subject)</i>							
Older	Session	-0.42	-6.33	0.001	0.003	100%	-0.41 ($\pm$ 0.18)
Younger	Session	-0.20	-1.49	0.159	0.476	62.50%	-0.20 ($\pm$ 0.43)
Untrained	Session	0.01	0.05	0.957		50%	0.007 ($\pm$ 0.41)
<i>Model: RAVLT_LearningGain $\sim$ Group</i>							
Both	Pre	0.09	0.66	0.523			
Both	Post	-0.42	-1.92	0.077			
<i>Model: RAVLT_Proactive_Interference $\sim$ Group</i>							
Both	Pre	-0.33	-2.76	0.015			
Both	Post	-0.10	-0.78	0.447			

Table S.4: Statistical models of Stroop task performance. Results of statistical models used to assess Stroop color-word scores between younger and older participants. Post-hoc analyses were performed to evaluate each group separately and to compare against an untrained group of younger adults. Correction for multiple comparisons was done across related hypotheses (same effect and group in RAVLT and SCWT) using the Benjamini-Hochberg method. Prevalence (Prev.) represents the percentage of subjects (either across or within groups) that improved their SCWT score, as defined by a positive slope. The mean and standard deviation (SD) of the slopes are also provided. Significant results ($p_{FDR} < 0.05$) are highlighted in bold and results referenced in the Results (Section 3.1.4) are shaded in purple.

Group	Effect	Estimate	t value	p value	p_{FDR}	Prev.	Mean ($\pm$ SD)
<i>Model: Stroop_CWScore ~ Session + Group + (1 Subject)</i>							
Both	Session	5.03	4.99	2×10^{-4}	0.001	86.67%	5.00 (± 3.93)
Both	Group	12.47	4.64	4×10^{-4}	0.002		
<i>Model: Stroop_CWScore ~ Session + (1 Subject)</i>							
Older	Session	4.17	2.93	0.024	0.035	85.71%	4.00 (± 3.87)
Younger	Session	5.88	4.14	0.004	0.026	87.50%	5.88 (± 4.02)
Untrained	Session	2.25	0.98	0.358		62.50%	2.25 (± 6.48)
<i>Model: Stroop_CWScore ~ Group</i>							
Both	Pre	11.62	4.61	4×10^{-4}			
Both	Post	13.16	3.94	0.002			

Table S.5: Statistical models of AFLT performance. Results of statistical models used to assess each AFLT performance measure. Group post-hoc analyses were only performed in the presence of a significant Session ("SessionPost") main effect and included an untrained group of younger adults. Prevalence (Prev.) represents the percentage of subjects (either across or within groups) who showed an improvement in the AFLT measure, based on the direction of their slopes. For most measures, improvement corresponds to positive slopes; however, for interferences, negative slopes indicate better performance. The mean and standard deviation (SD) of the slopes are also provided. Correction for multiple comparisons were not computed, as this test was used to assess the specificity of the transfer effects on the auditory modality. Significant results ($p < 0.05$) are highlighted in bold and results referenced in Results (Section 3.1.4) are shaded in purple.

Group	Effect	Estimate	t value	p value	Prev.	Mean ($\pm$ SD)
<i>Model: AFLT_LearningGain ~ Session * Group + (1 Subject)</i>						
Both	Session	0.26	0.96	0.353	26.67%	-0.21 ($\pm$ 0.85)
Both	Group	0.23	0.80	0.428		
Both	Session:Group	-0.86	-2.25	0.041		
<i>Model: AFLT_LearningGain ~ Session + (1 Subject)</i>						
Older	Session	0.27	0.89	0.651	57.14%	0.23 ($\pm$ 0.84)
Younger	Session	-0.60	-2.47	0.043	0%	-0.60 ($\pm$ 0.68)
Untrained	Session	0.66	1.08	0.317	50%	0.66 ($\pm$ 1.73)
<i>Model: AFLT_TotalScore ~ Session + Group + (1 Subject)</i>						
Both	Session	2.81	1.79	0.094	62.50%	2.81 ($\pm$ 6.28)
Both	Group	21.69	4.02	0.001		
<i>Model: AFLT_DelayedRecallIndex ~ Session + Group + (1 Subject)</i>						
Both	Session	0.02	1.02	0.322	46.67%	0.03 ($\pm$ 0.10)
Both	Group	0.13	3.65	0.003		
<i>Model: AFLT_Retroactive_Interference ~ Session + Group + (1 Subject)</i>						
Both	Session	-0.06	-1.75	0.092	53.33%	-0.04 ($\pm$ 0.11)
Both	Group	-0.17	-4.60	8×10^{-5}		
<i>Model: AFLT_Proactive_Interference ~ Session + Group + (1 Subject)</i>						
Both	Session	0.10	1.00	0.332	40%	0.09 ($\pm$ 0.39)
Both	Group	-0.48	-4.04	0.001		

Table S.6: Correlation between cognitive measures and training performance. Results of statistical models used to assess the relationship between cognitive measures that were deemed significant, and the average level reached per day. A single data point was obtained per subject, using the slopes of the performance in the task and the difference between Post and Pre sessions on the cognitive measures. Coefficients of determination (R^2) were calculated as described in [Section 2.10.1](#). No significant results ($p < 0.05$) were found. R^2 values higher than 0.2 are highlighted in bold and comparisons referenced in Results ([Section 3.1.4](#)) are shaded in purple.

Group	Effect	Estimate	t value	p value	R^2
<i>Model: diff_RAVLT_LearningGain ~ slope_AvgLevel</i>					
Older	slope_AvgLevel	2.85	2.44	0.050	0.46
Younger	slope_AvgLevel	-0.40	-0.36	0.732	0.02
<i>Model: diff_RAVLT_Proactive_Interference ~ slope_AvgLevel</i>					
Older	slope_AvgLevel	-0.02	-0.02	0.988	< 0.01
Younger	slope_AvgLevel	0.50	0.74	0.486	0.07
<i>Model: diff_Stroop_CWScore ~ slope_AvgLevel</i>					
Older	slope_AvgLevel	15.47	0.98	0.371	0.14
Younger	slope_AvgLevel	-9.77	-1.85	0.113	0.33

Table S.7: Statistical models of auditory M100 peak amplitude. Results of statistical models used to assess the effect of training and age on the maximum M100 amplitude in the auditory cortex. Visual cortex was evaluated during the same time period to determine the specificity of observed auditory changes. Post-hoc analyses were conducted to evaluate each group separately. Prevalence (Prev.) represents the percentage of subjects (either across or within groups) that showed an M100 amplitude increase, as defined by a positive slope. The mean and standard deviation (SD) of the slopes are also provided. Significant results ($p < 0.05$) are highlighted in bold and results referenced in Results (Section 3.2.2) are shaded in purple.

Group	Hem.	Effect	Estimate	t value	p value	Prev.	Mean ($\pm$ SD)
<i>Model: MaxAmp_M100_auditory_Left ~ Day * Group + (1 + Day Subject)</i>							
Both	Left	Day	0.13	1.37	0.180		
Both	Left	Group	-4.26	-1.98	0.067		
Both	Left	Day:Group	-0.17	-1.37	0.177		
<i>Model: MaxAmp_M100_auditory_Left ~ Day + Group + (1 + Day Subject)</i>							
Both	Left	Day	-0.01	-0.21	0.835	43.75%	4×10^{-4} (± 0.29)
Both	Left	Group	-5.63	-2.98	0.010		
<i>Model: MaxAmp_M100_auditory_Left ~ Day + (1 + Day Subject)</i>							
Older	Left	Day	0.01	0.08	0.939	37.50%	0.04 (± 0.38)
Younger	Left	Day	-0.04	-0.55	0.592	50%	-0.04 (± 0.19)
<i>Model: MaxAmp_M100_auditory_Right ~ Day * Group + (1 + Day Subject)</i>							
Both	Right	Day	0.40	3.39	0.002	62.50%	0.24 (± 0.59)
Both	Right	Group	0.37	0.18	0.860		
Both	Right	Day:Group	-0.52	-3.26	0.002		
<i>Model: MaxAmp_M100_auditory_Right ~ Day + (1 + Day Subject)</i>							
Older	Right	Day	0.41	3.16	0.007	100%	0.60 (± 0.65)
Younger	Right	Day	-0.12	-1.21	0.238	25%	-0.12 (± 0.17)
<i>Model: MaxAmp_M100_auditory_Left ~ Day * Age + (1 + Day Subject)</i>							
-	Left	Day	-0.04	-0.25	0.801		
-	Left	Age	0.09	1.80	0.092		
-	Left	Day:Age	2×10^{-3}	0.58	0.563		
<i>Model: MaxAmp_M100_auditory_Left ~ Day + Age + (1 + Day Subject)</i>							
-	Left	Day	0.04	0.56	0.577		
-	Left	Age	0.10	1.98	0.068		

Continued on next page

Table S.7: Statistical models of auditory M100 peak amplitude. (Continued)

Group	Hem.	Effect	Estimate	<i>t</i> value	<i>p</i> value	Prev.	Mean (± SD)
<i>Model: MaxAmp_M100_**auditory_Right** ~ Day * Age + (1 + Day Subject)</i>							
-	Right	Day	-0.24	-1.34	0.190		
-	Right	Age	-0.02	-0.37	0.718		
-	Right	Day:Age	0.01	2.27	0.031		
<i>Model: MaxAmp_M100_**visual** ~ Day * Group + (1 + Day Subject)</i>							
Both	-	Day	0.05	1.50	0.156	50%	5×10^{-4} (±0.11)
Both	-	Group	1.07	1.21	0.247		
Both	-	Day:Group	-0.11	-2.19	0.046		
<i>Model: MaxAmp_M100_**visual** ~ Day + (1 + Day Subject)</i>							
Older	-	Day	0.06	1.65	0.143	75%	0.06 (±0.09)
Younger	-	Day	-0.06	-1.52	0.173	25%	-0.06 (±0.10)
<i>Model: MaxAmp_M100_**visual** ~ Day * Age + (1 + Day Subject)</i>							
-	-	Day	-0.08	-1.38	0.190		
-	-	Age	-0.02	-1.18	0.257		
-	-	Day:Age	2×10^{-3}	1.51	0.155		
<i>Model: MaxAmp_M100_**visual** ~ Day + Age + (1 + Day Subject)</i>							
-	-	Day	-2×10^{-3}	-0.08	0.935		
-	-	Age	-1×10^{-3}	-0.09	0.928		

Table S.8: Statistical models of laterality and hemispheric differences in auditory M100 amplitude. Results of statistical models used to assess the effect of training and age on laterality on the maximum M100 amplitude in the auditory cortex. Post-hoc analyses were conducted to evaluate each group separately. Prevalence (Prev.) represents the percentage of subjects (either across or within groups) that showed the specified effect through either an increase in the laterality index throughout days, as defined by a positive slope (less activation on the right), or higher activation on the right hemisphere, as defined by a negative laterality index. The mean and standard deviation (SD) of the slopes (Day) or laterality (Hemisphere R) are also provided. To examine the 3-way interaction between hemisphere, group and training day, multiple models were computed, and only the one with the lowest AIC was chosen. Significant results ($p < 0.05$) are highlighted in bold and results referenced in Results (Section 3.2.2) are shaded in purple.

Group	Effect	Est.	t value	p value	Prev.	Mean ($\pm$ SD)
<i>Model: MaxAmp_M100_auditory_Laterality ~ Day * Group + (1 + Day Subject)</i>						
Both	Day	-0.01	-1.54	0.145		
Both	Group	-0.19	-1.54	0.146		
Both	Day:Group	0.01	0.94	0.362		
<i>Model: MaxAmp_M100_auditory_Laterality ~ Day + Group + (1 + Day Subject)</i>						
Both	Day	-4×10^{-3}	-1.24	0.232	43.75%	-4×10^{-3} (± 0.01)
Both	Group	-0.12	-1.21	0.246		
<i>Model: MaxAmp_M100_auditory_Laterality ~ Day + (1 + Day Subject)</i>						
Older	Day	-0.01	-1.55	0.143	25%	-7×10^{-3} (± 0.01)
Younger	Day	-1×10^{-3}	-0.21	0.836	62.50%	-1×10^{-3} (± 0.01)
<i>Model: MaxAmp_M100_auditory ~ Day * Group * Hemisphere + (1 Subject) [AIC = 715.11]</i>						
<i>Model: MaxAmp_M100_auditory ~ Day * Hemisphere + Group + (1 Subject) [AIC = 719.09]</i>						
<i>Model: MaxAmp_M100_auditory ~ Day * Group + Hemisphere + (1 Subject) [AIC = 714.45]</i>						
<i>Model: MaxAmp_M100_auditory ~ Day + Group + Hemisphere + (1 Subject) [AIC = 716.34]</i>						
<i>Model: MaxAmp_M100_auditory ~ Day + Group * Hemisphere + (1 Subject) [AIC = 713.12]</i>						
Both	Day	0.06	0.78	0.436		
Both	Group	-5.33	-3.21	0.004		
Both	Hemisphere R	2.77	2.83	0.006	75%	-0.18 (± 0.21)
Both	Group:Hemisphere	2.28	1.67	0.099		

Continued on next page

Table S.8: Statistical models of laterality and hemispheric differences in auditory M100 amplitude.
(Continued)

Group	Effect	Est.	<i>t</i> value	<i>p</i> value	Prev.	Mean (± SD)
<i>Model: MaxAmp_M100_</i> auditory ~ Day + Hemisphere + (1 Subject)						
Older	Day	0.27	1.91	0.062		
Older	Hemisphere R	2.77	2.40	0.020	75%	-0.11 (±0.23)
Younger	Day	-0.12	-1.45	0.154		
Younger	Hemisphere R	5.05	7.15	2×10⁻⁹	75%	-0.25 (±0.18)

Table S.9: Statistical models of auditory Cue peak amplitude. Results of statistical models used to assess the effect of training and age on the maximum M100 amplitude (50 to 150 ms after Cue) in response to the Cue in the auditory cortex. Post-hoc analyses were conducted to evaluate each group separately. Prevalence (Prev.) represents the percentage of subjects (either across or within groups) that showed the specified effect through either an M100 amplitude increase throughout days, as defined by a positive slope; or higher activation on the right hemisphere, as defined by a negative laterality index. The mean and standard deviation (SD) of the slopes (Day) or laterality (Hemisphere R) are also provided. Significant results ($p < 0.05$) are highlighted in bold and results referenced in Results (Section 3.2.3) are shaded in purple.

Group	Hem.	Effect	Est.	t value	p value	Prev.	Mean ($\pm$ SD)
<i>Model: MaxAmp_Cue_ auditory_Left ~ Day * Group + (1 + Day Subject)</i>							
Both	Left	Day	0.05	0.88	0.386		
Both	Left	Group	0.98	0.54	0.598		
Both	Left	Day:Group	-0.12	-1.44	0.159		
<i>Model: MaxAmp_Cue_ auditory_Left ~ Day + Group + (1 + Day Subject)</i>							
Both	Left	Day	0.01	0.35	0.726	50%	2×10^{-3} (± 0.13)
Both	Left	Group	-0.23	-0.15	0.885		
<i>Model: MaxAmp_Cue_ auditory_Right ~ Day * Group + (1 + Day Subject)</i>							
Both	Right	Day	0.13	2.30	0.030		
Both	Right	Group	3.03	2.09	0.054		
Both	Right	Day:Group	-0.11	-1.38	0.181		
<i>Model: MaxAmp_Cue_ auditory_Right ~ Day + Group + (1 + Day Subject)</i>							
Both	Right	Day	0.08	1.84	0.077	68.75%	0.08 (± 0.16)
Both	Right	Group	3.24	2.26	0.039		
<i>Model: MaxAmp_Cue_ auditory_Right ~ Day + (1 + Day Subject)</i>							
Older	Right	Day	0.13	1.94	0.089	62.50%	0.14 (± 0.19)
Younger	Right	Day	0.02	0.33	0.746	75%	0.02 (± 0.11)
<i>Model: MaxAmp_Cue_ auditory ~ Day + Group * Hemisphere + (1 Subject)</i>							
Both	-	Day	0.06	1.13	0.261		
Both	-	Group	-0.12	-0.09	0.931		
Both	-	Hemisphere R	-0.55	-0.85	0.396	56.25%	-0.07 (± 0.36)
Both	-	Group:Hem.	2.68	2.99	0.003		

Continued on next page

Table S.9: Statistical models of auditory Cue peak amplitude. (Continued)

Group	Hem.	Effect	Est.	<i>t</i> value	<i>p</i> value	Prev.	Mean ($\pm$ SD)
<i>Model: MaxAmp_Cue_</i> auditory $\sim$ Day + Hemisphere + (1 Subject)							
Older	–	Day	0.12	1.71	0.094		
Older	–	Hemisphere R	-0.55	-0.94	0.352	50%	0.05 ($\pm$ 0.36)
Younger	–	Day	0.01	0.08	0.938		
Younger	–	Hemisphere R	2.13	3.17	0.002	62.50%	-0.19 ($\pm$ 0.33)

Table S.10: Statistical models of auditory baseline average amplitude. Results of statistical models used to assess the effect of training and age group on the baseline average amplitude (-500 to 0 ms before Cue onset) in the auditory cortex. Post-hoc analyses were conducted to evaluate each group separately. Prevalence (Prev.) represents the percentage of subjects (either across or within groups) that showed the specified effect through either an M100 amplitude increase throughout days or an increase in the laterality index throughout days (less activation on the right), as defined by positive slopes; or higher activation on the right hemisphere, as defined by a negative laterality index. The mean and standard deviation (SD) of the slopes (Day) or laterality (Hem. R) are also provided. Significant results ($p < 0.05$) are highlighted in bold and results referenced in Results (Section 3.2.4) are shaded in purple.

Group	Hem.	Effect	Est.	t value	p value	Prev.	Mean ($\pm$ SD)
<i>Model: AvgAmp_Baseline_ auditory_Left ~ Day * Group + (1 + Day Subject)</i>							
Both	Left	Day	7×10^{-4}	0.45	0.652	37.50%	-2×10^{-3} ($\pm 4 \times 10^{-3}$)
Both	Left	Group	0.10	1.73	0.105		
Both	Left	Day:Grp	-0.01	-2.83	0.007		
<i>Model: AvgAmp_Baseline_ auditory_Left ~ Day + (1 + Day Subject)</i>							
Old	Left	Day	5×10^{-4}	0.34	0.739	50%	5×10^{-4} ($\pm 2 \times 10^{-3}$)
Young	Left	Day	-0.01	-3.16	0.007	25%	-5×10^{-3} ($\pm 4 \times 10^{-3}$)
<i>Model: AvgAmp_Baseline_ auditory_Left ~ Day * Age + (1 + Day Subject)</i>							
-	Left	Day	-0.01	-3.60	0.001		
-	Left	Age	-2×10^{-3}	-1.58	0.136		
-	Left	Day:Age	1×10^{-4}	2.80	0.008		
<i>Model: AvgAmp_Baseline_ auditory_Right ~ Day * Group + (1 + Day Subject)</i>							
Both	Right	Day	-2×10^{-3}	-1.21	0.235		
Both	Right	Group	0.03	1.20	0.248		
Both	Right	Day:Grp	6×10^{-4}	0.29	0.770		
<i>Model: AvgAmp_Baseline_ auditory_Right ~ Day + Group + (1 + Day Subject)</i>							
Both	Right	Day	-1×10^{-3}	-1.45	0.157	37.50%	-1×10^{-3} ($\pm 4 \times 10^{-3}$)
Both	Right	Group	0.03	1.24	0.234		
<i>Model: AvgAmp_Baseline_ auditory_Laterality ~ Day * Group + (1 + Day Subject)</i>							
Both	-	Day	0.01	1.69	0.099	43.75%	1×10^{-3} (± 0.01)
Both	-	Group	0.11	1.01	0.330		
Both	-	Day:Grp	-0.01	-2.23	0.032		

Continued on next page

Table S.10: Statistical models of auditory baseline average amplitude. (Continued)

Group	Hem.	Effect	Est.	t value	p value	Prev.	Mean ($\pm$ SD)
<i>Model: AvgAmp_Baseline_ auditory_Laterality $\sim$ Day + (1 + Day Subject)</i>							
Old	–	Day	0.01	1.50	0.189	50%	7×10^{-3} (± 0.02)
Young	–	Day	-0.01	-1.53	0.141	37.50%	-5×10^{-3} ($\pm 7 \times 10^{-3}$)
<i>Model: AvgAmp_Baseline_ auditory $\sim$ Day + Group + Hemisphere + (1 Subject)</i>							
Both	–	Day	-2×10^{-3}	-1.62	0.108		
Both	–	Group	0.04	1.46	0.166		
Both	–	Hem. R	-0.01	-0.60	0.549	56.25%	-3×10^{-3} (± 0.21)
<i>Model: AvgAmp_Baseline_ auditory $\sim$ Day + Hemisphere + (1 Subject)</i>							
Old	–	Day	-10×10^{-4}	-0.67	0.504		
Old	–	Hem. R	2×10^{-3}	0.13	0.896	62.50%	-0.01 (± 0.18)
Young	–	Day	-4×10^{-3}	-1.46	0.150		
Young	–	Hem. R	-0.02	-0.75	0.456	50%	6×10^{-3} (± 0.25)

Table S.11: Statistical models of auditory preM100 average amplitude. Results of statistical models used to assess the effect of training and age group on the average preM100 amplitude (-300 to 0 ms before Stimulus onset) in the auditory cortex. Significant results ($p < 0.05$) are highlighted in bold. Prevalence (Prev.) represents the percentage of subjects (either across or within groups) that showed the specified effect through either an increase in the average preM100 amplitude throughout days, as defined by a positive slope; or higher activation on the right hemisphere, as defined by a negative laterality index. The mean and standard deviation (SD) of the slopes (Day) or laterality (Hem. R) are also provided. See [Section 3.2.4](#) for interpretation and plots.

Group	Hem.	Effect	Estimate	<i>t</i> value	<i>p</i> value	Prev.	Mean ($\pm$ SD)
<i>Model: AvgAmp_preM100_auditory_Left ~ Day * Group + (1 + Day Subject)</i>							
Both	Left	Day	0.07	2.68	0.017		
Both	Left	Group	-0.30	-0.46	0.651		
Both	Left	Day:Group	-0.07	-1.96	0.070		
<i>Model: AvgAmp_preM100_auditory_Left ~ Day + Group + (1 + Day Subject)</i>							
Both	Left	Day	0.03	1.59	0.134	68.75%	0.04 (± 0.09)
Both	Left	Group	-0.83	-1.44	0.172		
<i>Model: AvgAmp_preM100_auditory_Left ~ Day + (1 + Day Subject)</i>							
Older	Left	Day	0.06	2.08	0.081	87.50%	0.09 (± 0.11)
Younger	Left	Day	-2×10^{-4}	-0.01	0.990	50%	-2×10^{-4} (± 0.05)
<i>Model: AvgAmp_preM100_auditory_Right ~ Day * Group + (1 + Day Subject)</i>							
Both	Right	Day	0.08	2.48	0.026		
Both	Right	Group	0.22	0.61	0.556		
Both	Right	Day:Group	-0.09	-1.99	0.066		
<i>Model: AvgAmp_preM100_auditory_Right ~ Day + Group + (1 + Day Subject)</i>							
Both	Right	Day	0.03	1.40	0.182	62.50%	0.01 (± 0.14)
Both	Right	Group	-0.18	-0.59	0.565		
<i>Model: AvgAmp_preM100_auditory_Right ~ Day + (1 + Day Subject)</i>							
Older	Right	Day	0.08	2.20	0.062	87.50%	0.08 (± 0.10)
Younger	Right	Day	-0.01	-0.32	0.755	37.50%	-0.05 (± 0.16)
<i>Model: AvgAmp_preM100_auditory ~ Day + Group + Hemisphere + (1 Subject)</i>							
Both	–	Day	0.03	1.59	0.114		
Both	–	Group	-0.66	-1.88	0.081		
Both	–	Hem. R	-0.27	-1.59	0.115	31.25%	0.18 (± 1.50)

Table S.12: Statistical models of auditory later component average amplitude. Results of statistical models used to assess the effect of training and age group on the average amplitude of the later component (200 to 500 ms after Stimulus onset) in the auditory cortex. Prevalence (Prev.) represents the percentage of subjects (either across or within groups) that showed the specified effect through either an increase in the average activation during the later component throughout days, as defined by a positive slope; or higher activation on the right hemisphere, as defined by a negative laterality index. The mean and standard deviation (SD) of the slopes (Day) or laterality (Hem. R) are also provided. Significant results ($p < 0.05$) are highlighted in bold and results referenced in [Section 3.2.5](#) are shaded in purple.

Rsp.	Group	Hem.	Effect	Est.	<i>t</i>	<i>p</i>	Prev.	Mean ($\pm$ SD)
<i>Model: AvgAmp_LaterComp_auditory_Left ~ Day + Group + (1 + Day Subject)</i>								
Hit	Both	L	Day	9×10^{-5}	5×10^{-3}	0.996	50%	0.03 (± 0.16)
Hit	Both	L	Group	0.20	0.56	0.585		
WH	Both	L	Day	0.01	0.21	0.837	50%	0.01 (± 0.10)
WH	Both	L	Group	0.12	0.35	0.734		
<i>Model: AvgAmp_LaterComp_auditory_Right ~ Day + Group + (1 + Day Subject)</i>								
Hit	Both	R	Day	2×10^{-3}	0.13	0.894	56.25%	-0.001 (± 0.06)
Hit	Both	R	Group	0.12	0.44	0.665		
WH	Both	R	Day	-0.02	-1.02	0.315	43.75%	-0.02 (± 0.09)
WH	Both	R	Group	0.35	0.93	0.365		
<i>Model: AvgAmp_LaterComp_auditory_Right ~ Day * Group + (1 + Day Subject)</i>								
WH	Both	R	Day	0.02	0.55	0.588	43.75%	-0.02 (± 0.09)
WH	Both	R	Group	0.66	1.57	0.133		
WH	Both	R	Day:Grp	-0.08	-1.74	0.092		
<i>Model: AvgAmp_LaterComp_auditory_Right ~ Day + (1 + Day Subject)</i>								
WH	Older	R	Day	0.02	0.55	0.594	62.50%	0.02 (± 0.09)
WH	Young	R	Day	-0.06	-1.95	0.070	25%	-0.06 (± 0.08)
<i>Model: AvgAmp_LaterComp_auditory ~ Day + Group + Hemisphere + (1 Subject)</i>								
Hit	Both	–	Day	-0.01	-0.60	0.551		
Hit	Both	–	Group	0.10	0.33	0.749		
Hit	Both	–	Hem. R	0.22	1.84	0.068	68.75%	-0.10 (± 0.25)
WH	Both	–	Day	-2×10^{-3}	-0.14	0.892		
WH	Both	–	Group	0.08	0.24	0.815		
WH	Both	–	Hem. R	0.54	3.65	4×10^{-4}	75%	-0.11 (± 0.16)

Continued on next page

Table S.12: Statistical models of auditory later component average amplitude. (Continued)

Rsp.	Group	Hem.	Effect	Est.	<i>t</i>	<i>p</i>	Prev.	Mean (± SD)
<i>Model: AvgAmp_LaterComp_</i> auditory ~ Day + Hemisphere + (1 Subject)								
WH	Older	–	Day	0.04	1.62	0.111		
WH	Older	–	Hem. R	0.44	1.99	0.052	87.50%	-0.10 (±0.19)
WH	Young	–	Day	-0.04	-1.94	0.057		
WH	Young	–	Hem. R	0.64	3.35	0.001	62.50%	-0.11 (±0.15)

Table S.13: Regressions and correlations between auditory measures and behavior performance. Results of statistical models used to assess the relationship between auditory neural correlates that were deemed significantly related to the training progression, and the behavioral and cognitive measures identified on [Section 3.1](#). Models between auditory measures and the average level used all available data points, while models between auditory measures and cognitive measures used a single data point per subject. Coefficients of determination (R^2) were calculated as described in [Section 2.10.1](#). For main and interaction effects (*Day*, *Day:Group*), the R^2 values represent the marginal R squared of the reduced model (R^2_{red}). No significant results ($p < 0.05$) were found, but some trends were observed ($p < 0.1$). R^2 values higher than 0.2 are highlighted in bold and comparisons referenced in Results ([Section 3.2.6](#)) are shaded in purple.

Group	Effect	Estimate	t value	p value	R^2
<i>Model: AvgLevel ~ Day * Group + MaxAmp_M100_auditory_Right + (1 + Day Subject)</i>					
Both	Day:Group	0.27	3.08	0.007	0.61
Both	MaxAmp_M100_auditory_Right	-0.05	-0.97	0.340	< 0.01
Older	Day	0.15	2.96	0.010	0.21
Older	MaxAmp_M100_auditory_Right	0.04	0.68	0.503	0.02
<i>Model: AvgLevel ~ Day * Group + AvgAmp_Baseline_auditory_Left + (1 + Day Subject)</i>					
Both	Day:Group	0.27	3.15	0.007	0.59
Both	AvgAmp_Baseline_auditory_Left	4.38	1.48	0.154	0.02
Younger	Day	0.46	6.00	3×10^{-4}	0.36
Younger	AvgAmp_Baseline_auditory_Left	8.11	2.25	0.063	0.14
<i>Model: diff_RAVLT_LearningGain ~ slope_MaxAmp_M100_auditory_Right</i>					
Older	slope_MaxAmp_M100_auditory_Right	1.43	2.15	0.075	0.40
<i>Model: diff_RAVLT_Proactive_Interference ~ slope_MaxAmp_M100_auditory_Right</i>					
Older	slope_MaxAmp_M100_auditory_Right	-0.26	-0.38	0.720	0.02
<i>Model: diff_Stroop_CWScore ~ slope_MaxAmp_M100_auditory_Right</i>					
Older	slope_MaxAmp_M100_auditory_Right	5.79	0.69	0.519	0.07
Younger	slope_MaxAmp_M100_auditory_Right	-3.40	-0.35	0.737	0.02
<i>Model: diff_Stroop_CWScore ~ slope_AvgAmp_Baseline_auditory_Left</i>					
Older	slope_AvgAmp_Baseline_auditory_Left	363.05	0.91	0.404	0.12
Younger	slope_AvgAmp_Baseline_auditory_Left	499.87	1.36	0.223	0.21
<i>Model: slope_MaxAmp_M100_auditory_Right ~ Day01_RAVLT_LearningGain</i>					
Older	Day01_RAVLT_LearningGain	-0.22	-1.13	0.302	0.15
<i>Model: slope_MaxAmp_M100_auditory_Right ~ Day01_RAVLT_Proactive_Interference</i>					
Older	Day01_RAVLT_Interference_Proactive	0.06	0.17	0.872	< 0.01

Continued on next page

Table S.13: Regressions and correlations between auditory measures and behavior performance.
(Continued)

Group	Effect	Estimate	<i>t</i> value	<i>p</i> value	<i>R</i> ²
<i>Model: slope_MaxAmp_M100_auditory_Right ~ Day01_Stroop_CWScore</i>					
Older	Day01_Stroop_CWScore	0.01	0.22	0.834	< 0.01
Younger	Day01_Stroop_CWScore	-0.01	-1.03	0.343	0.13
<i>Model: slope_AvgAmp_Baseline_auditory_Left ~ Day01_Stroop_CWScore</i>					
Older	Day01_Stroop_CWScore	4×10^{-4}	0.77	0.473	0.08
Younger	Day01_Stroop_CWScore	10×10^{-5}	0.41	0.698	0.02

Table S.14: Statistical models of dorsal attention network average preM100 activity. Results of statistical models used to assess the effect of training and age on the averaged preM100 amplitude in the dorsal attention network (DAN). Post-hoc analyses were conducted to evaluate each group separately. Prevalence (Prev.) represents the percentage of participants (either across or within groups) who exhibited higher preM100 activation across days, as defined by a positive slope. The mean and standard deviation (SD) of the slopes are also provided. When the model corresponded to regressions, the R squared is presented instead. Significant results ($p < 0.05$) and R^2 values higher than 0.2 are highlighted in bold and results referenced in Section 3.3.2 are shaded in purple.

Group	Hem.	Effect	Estimate	t value	p value	Prev./ R^2	Mean ($\pm$ SD)
<i>Model: AvgAmp_preM100_DAN_Left ~ Day * Group + (1 + Day Subject)</i>							
Both	Left	Day	0.03	1.92	0.063		
Both	Left	Group	-0.12	-0.64	0.532		
Both	Left	Day:Group	-3×10^{-3}	-0.17	0.868		
<i>Model: AvgAmp_preM100_DAN_Left ~ Day + Group + (1 + Day Subject)</i>							
Both	Left	Day	0.02	2.47	0.019	75%	0.02 (± 0.03)
Both	Left	Group	-0.18	-1.03	0.320	75%	0.02 (± 0.03)
<i>Model: AvgAmp_preM100_DAN_Left ~ Day + (1 + Day Subject)</i>							
Older	Left	Day	0.02	1.57	0.163	62.50%	0.02 (± 0.03)
Younger	Left	Day	0.02	1.65	0.120	87.50%	0.02 (± 0.03)
<i>Model: AvgAmp_preM100_DAN_Left ~ Day * Age + (1 + Day Subject)</i>							
Both	Left	Day	0.02	1.16	0.257		
Both	Left	Age	2×10^{-3}	0.36	0.720		
Both	Left	Day:Age	3×10^{-5}	0.07	0.945		
<i>Model: AvgAmp_preM100_DAN_Left ~ Day + Age + (1 + Day Subject)</i>							
Both	Left	Day	0.02	2.47	0.018		
Both	Left	Age	3×10^{-3}	0.82	0.425		
<i>Model: AvgAmp_preM100_DAN_Right ~ Day * Group + (1 + Day Subject)</i>							
Both	Right	Day	0.07	5.49	1×10^{-4}	56.25%	0.02 (± 0.06)
Both	Right	Group	0.48	2.89	0.012		
Both	Right	Day:Group	-0.10	-5.32	1×10^{-4}		
<i>Model: AvgAmp_preM100_DAN_Right ~ Day + (1 + Day Subject)</i>							
Older	Right	Day	0.07	5.46	0.002	87.50%	0.06 (± 0.05)
Younger	Right	Day	-0.03	-2.24	0.058	25%	-0.03 (± 0.03)

Continued on next page

Table S.14: Statistical models of dorsal attention network average preM100 activity. (Continued)

Group	Hem.	Effect	Estimate	t value	p value	Prev./R ²	Mean (± SD)
<i>Model: AvgAmp_preM100_DAN_Right ~ Day * Age + (1 + Day Subject)</i>							
Both	Right	Day	-0.07	-3.23	0.007		
Both	Right	Age	-0.01	-2.63	0.020		
Both	Right	Day:Age	2×10^{-3}	4.79	4×10^{-4}		
<i>Model: AvgAmp_preM100_DAN_Laterality ~ Day * Group + (1 + Day Subject)</i>							
Both	–	Day	-0.02	-1.24	0.235	50%	6×10^{-3} (±0.05)
Both	–	Group	-0.39	-1.28	0.222		
Both	–	Day:Group	0.05	2.16	0.048		
<i>Model: AvgAmp_preM100_DAN_Laterality ~ Day + (1 + Day Subject)</i>							
Older	–	Day	-0.02	-1.28	0.243	25%	-0.02 (±0.04)
Younger	–	Day	0.03	1.67	0.140	75%	0.03 (±0.05)
<i>Model: AvgAmp_preM100_DAN_Laterality ~ Day * Age + (1 + Day Subject)</i>							
Both	–	Day	0.06	2.47	0.027	50%	6×10^{-3} (±0.05)
Both	–	Age	0.01	1.24	0.236		
Both	–	Day:Age	-1×10^{-3}	-2.52	0.024		
<i>Model: AvgLevel ~ Day + AvgAmp_preM100_DAN_Right + (1 + Day Subject)</i>							
Older	Right	Day	0.14	2.29	0.034	0.21	
Older	Right	DAN R	0.25	0.38	0.705	< 0.01	
<i>Model: AvgLevel ~ Day * Age + AvgAmp_preM100_DAN_Laterality + (1 + Day Subject)</i>							
Both	–	Day:Age	-0.01	-4.09	0.001	0.65	
Both	–	DAN Lat.	0.19	0.44	0.660	< 0.01	

Table S.15: Regressions between auditory M100 amplitude and preM100 DAN activity. Results of linear mixed effects models assessing the relationship between auditory M100 amplitude and preM100 DAN activity, accounting for the influence of training day. Coefficients of determination (R^2) were calculated as described in [Section 2.10.1](#). For main and interaction effects (*Day*, *Group*, *Day:Group*), the R^2 values represent the marginal R squared of the reduced model (R^2_{red}). Significant results ($p < 0.05$) and R^2 values higher than 0.2 are highlighted in bold and comparisons referenced in Results ([Section 3.3.3](#)) are shaded in purple.

Group	Effect	Estimate	<i>t</i> value	<i>p</i> value	R^2
<i>Model: MaxAmp_M100_auditory_Right ~ AvgAmp_preM100_DAN_Right</i>					
Both	AvgAmp_preM100_DAN_Right	4.02	3.35	0.001	0.16
Older	AvgAmp_preM100_DAN_Right	4.91	2.84	0.008	0.22
Younger	AvgAmp_preM100_DAN_Right	0.85	0.55	0.586	< 0.01
<i>Model: MaxAmp_M100_auditory_Right ~ Day * Group + AvgAmp_preM100_DAN_Right + (1 + Day Subject)</i>					
Both	Day:Group	-0.44	-2.41	0.021	0.16
Both	AvgAmp_preM100_DAN_Right	1.08	0.95	0.347	< 0.01
Older	Day	0.07	0.33	0.746	0.09
Older	AvgAmp_preM100_DAN_Right	5.27	2.65	0.014	0.15
Younger	Day	-0.12	-1.23	0.234	0.02
Younger	AvgAmp_preM100_DAN_Right	-0.69	-0.53	0.603	< 0.01
<i>Model: MaxAmp_M100_auditory_Left ~ Day + Group + AvgAmp_preM100_DAN_Right + (1 + Day Subject)</i>					
Both	Day	-0.08	-1.02	0.326	0.29
Both	Group	-5.05	-2.73	0.017	0.29
Both	AvgAmp_preM100_DAN_Right	2.23	2.48	0.017	0.04
Older	Day	-0.12	-0.71	0.482	< 0.01
Older	AvgAmp_preM100_DAN_Right	3.59	2.08	0.051	0.13
Younger	Day	-0.12	-1.19	0.274	0.02
Younger	AvgAmp_preM100_DAN_Right	1.07	0.91	0.372	0.01

Continued on next page

Table S.15: Regressions between auditory M100 amplitude and preM100 DAN activity. (Continued)

Group	Effect	Estimate	t value	p value	R ²
<i>Model: MaxAmp_M100_auditory_Right ~ Day * Group + AvgAmp_preM100_DAN_Left + (1 + Day Subject)</i>					
Both	Day:Group	-0.56	-3.42	0.002	0.18
Both	AvgAmp_preM100_DAN_Left	1.46	1.48	0.145	0.01
Older	Day	0.34	2.15	0.058	0.11
Older	AvgAmp_preM100_DAN_Left	3.23	1.94	0.065	0.07
Younger	Day	-0.12	-1.14	0.268	0.02
Younger	AvgAmp_preM100_DAN_Left	0.02	0.01	0.990	< 0.01
<i>Model: MaxAmp_M100_auditory_Left ~ Day + Group + AvgAmp_preM100_DAN_Left + (1 + Day Subject)</i>					
Both	Day	-0.12	-1.49	0.145	0.30
Both	Group	-5.68	-2.65	0.019	0.30
Both	AvgAmp_preM100_DAN_Left	1.64	1.85	0.071	< 0.01
Older	Day	-0.04	-0.31	0.758	< 0.01
Older	AvgAmp_preM100_DAN_Left	1.57	0.99	0.332	0.02
Younger	Day	-0.18	-1.68	0.132	0.02
Younger	AvgAmp_preM100_DAN_Left	1.78	1.91	0.070	0.05
<i>Model: MaxAmp_M100_auditory_Right ~ Day * Group + AvgAmp_preM100_auditory_Right + (1 + Day Subject)</i>					
Both	Day:Group	-0.52	-3.18	0.003	0.16
Both	AvgAmp_preM100_auditory_Right	-0.01	-0.03	0.979	< 0.01
Older	Day	0.45	3.19	0.007	0.09
Older	AvgAmp_preM100_auditory_Right	-0.54	-0.63	0.534	< 0.01
Younger	Day	-0.12	-1.19	0.249	0.02
Younger	AvgAmp_preM100_auditory_Right	0.01	0.02	0.988	< 0.01

Continued on next page

Table S.15: Regressions between auditory M100 amplitude and preM100 DAN activity. (Continued)

Group		Effect	Estimate	<i>t</i> value	<i>p</i> value	<i>R</i> ²
<i>Model: MaxAmp_M100_auditory_Left ~ Day + Group + AvgAmp_preM100_auditory_Left + (1 + Day Subject)</i>						
Both	Day		-0.02	-0.32	0.752	0.32
Both	Group		-5.09	-2.51	0.025	0.32
Both	AvgAmp_preM100_auditory_Left		0.40	0.97	0.338	< 0.01
Older	Day		0.02	0.14	0.888	< 0.01
Older	AvgAmp_preM100_auditory_Left		-0.13	-0.24	0.815	< 0.01
Younger	Day		-0.04	-0.49	0.639	< 0.01
Younger	AvgAmp_preM100_auditory_Left		0.42	0.73	0.473	0.03

Table S.16: Mediation analysis of training effects on auditory M100 amplitude via preM100 DAN activity in older adults. For each model, the mediator and outcome models are specified, detailing the relationship of the treatment variable (training day) with the mediator and outcome variables. The average causal mediation effect (ACME), average direct effect (ADE), total effect, and proportion mediated are reported along with their respective p -values. Significant results ($p < 0.05$) are highlighted in bold, and estimates referenced in Results (Section 3.3.3) are shaded in purple.

Group	Effect	Estimate	p value
Mediator: AvgAmp_preM100_DAN_Right			
Mediator model: $\text{AvgAmp_preM100_DAN_Right} \sim \text{Day} + (1 + \text{Day} \mid \text{Subject})$			
Outcome: MaxAmp_M100_auditory_Right			
Outcome model: $\text{MaxAmp_M100_auditory_Right} \sim \text{Day} + \text{AvgAmp_preM100_DAN_Right} + (1 + \text{Day} \mid \text{Subject})$			
Treatment: Day			
Older	ACME	0.38	0.010
Older	ADE	0.04	0.834
Older	Total Effect	0.42	0.002
Older	Proportion Mediated	0.91	0.012
Mediator: AvgAmp_preM100_DAN_Right			
Mediator model: $\text{AvgAmp_preM100_DAN_Right} \sim \text{Day} + (1 + \text{Day} \mid \text{Subject})$			
Outcome: MaxAmp_M100_auditory_Left			
Outcome model: $\text{MaxAmp_M100_auditory_Left} \sim \text{Day} + \text{AvgAmp_preM100_DAN_Right} + (1 + \text{Day} \mid \text{Subject})$			
Treatment: Day			
Older	ACME	0.25	0.038
Older	ADE	-0.11	0.490
Older	Total Effect	0.13	0.296
Older	Proportion Mediated	1.32	0.330

Continued on next page

Table S.16: Mediation analysis of training effects on auditory M100 amplitude via preM100 DAN activity in older adults. (Continued)

Group	Effect	Estimate	p value
Mediator: <i>AvgAmp_preM100_DAN_Left</i>			
Mediator model: <i>AvgAmp_preM100_DAN_Left</i> ~ <i>Day</i> + (1 + <i>Day</i> <i>Subject</i>)			
Outcome: <i>MaxAmp_M100_auditory_Right</i>			
Outcome model: <i>MaxAmp_M100_auditory_Right</i> ~ <i>Day</i> + <i>AvgAmp_preM100_DAN_Left</i> + (1 + <i>Day</i> <i>Subject</i>)			
Treatment: <i>Day</i>			
Older	ACME	0.14	0.106
Older	ADE	0.32	0.040
Older	Total Effect	0.46	0.004
Older	Proportion Mediated	0.28	0.110
Mediator: <i>AvgAmp_preM100_auditory_Right</i>			
Mediator model: <i>AvgAmp_preM100_auditory_Right</i> ~ <i>Day</i> + (1 + <i>Day</i> <i>Subject</i>)			
Outcome: <i>MaxAmp_M100_auditory_Right</i>			
Outcome model: <i>MaxAmp_M100_auditory_Right</i> ~ <i>Day</i> + <i>AvgAmp_preM100_auditory_Right</i> + (1 + <i>Day</i> <i>Subject</i>)			
Treatment: <i>Day</i>			
Older	ACME	-0.02	0.812
Older	ADE	0.44	0.004
Older	Total Effect	0.42	0.004
Older	Proportion Mediated	-0.02	0.812

Table S.17: Statistical models of baseline alpha oscillations in auditory cortex and DAN. Results of statistical models assessing training-related changes in baseline alpha (α). Linear mixed-effects models were used to examine whether spontaneous alpha oscillatory activity during the baseline period (-500 to -25 ms before cue onset) changed with training in the auditory cortices (AC) and dorsal attention network (DAN) in both hemispheres (L: left, R: right). Both response types (Hits and withholds/WH) were analyzed. Prevalence (Prev.) represents the percentage of participants across groups who exhibited higher oscillatory activity across days, as defined by a positive slope. The mean and standard deviation (SD) of the slopes are also provided. See [Section 3.3.4](#) for interpretation.

<i>f</i>	ROI	Resp.	Group	Effect	Est.	<i>t</i>	<i>p</i>	Prev.	Mean ($\pm$ SD)
<i>Model: Alpha_Baseline_auditory_Left ~ Day + Group + (1 Subject)</i>									
α	AC L	Hit	Both	Day	9×10^{-4}	1.01	0.320	62.50%	9×10^{-4} ($\pm 3 \times 10^{-3}$)
α	AC L	Hit	Both	Group	-0.01	-0.14	0.889		
α	AC L	WH	Both	Day	5×10^{-4}	0.64	0.528	62.50%	2×10^{-4} ($\pm 4 \times 10^{-3}$)
α	AC L	WH	Both	Group	-2×10^{-3}	-0.03	0.973		
<i>Model: Alpha_Baseline_auditory_Right ~ Day + Group + (1 Subject)</i>									
α	AC R	Hit	Both	Day	7×10^{-4}	0.93	0.358	56.25%	2×10^{-3} ($\pm 7 \times 10^{-3}$)
α	AC R	Hit	Both	Group	0.01	0.32	0.752		
α	AC R	WH	Both	Day	5×10^{-5}	0.09	0.931	43.75%	4×10^{-5} ($\pm 2 \times 10^{-3}$)
α	AC R	WH	Both	Group	-9×10^{-4}	-0.02	0.987		
<i>Model: Alpha_Baseline_DAN_Left ~ Day + Group + (1 Subject)</i>									
α	DAN L	Hit	Both	Day	9×10^{-4}	0.61	0.542	43.75%	4×10^{-5} ($\pm 9 \times 10^{-3}$)
α	DAN L	Hit	Both	Group	0.04	0.43	0.676		
α	DAN L	WH	Both	Day	2×10^{-3}	1.32	0.195	53.33%	2×10^{-3} ($\pm 6 \times 10^{-3}$)
α	DAN L	WH	Both	Group	0.04	0.42	0.683		
<i>Model: Alpha_Baseline_DAN_Right ~ Day + Group + (1 Subject)</i>									
α	DAN R	Hit	Both	Day	1×10^{-3}	0.80	0.427	37.50%	1×10^{-3} ($\pm 7 \times 10^{-3}$)
α	DAN R	Hit	Both	Group	0.08	0.97	0.351		
α	DAN R	WH	Both	Day	1×10^{-3}	1.05	0.301	62.50%	3×10^{-3} ($\pm 7 \times 10^{-3}$)
α	DAN R	WH	Both	Group	0.08	0.81	0.433		

Table S.18: Statistical analysis of pre-stimulus alpha and theta power dynamics in auditory cortex and DAN. Results of statistical models used to investigate preparatory training-related changes in alpha (α) and theta (θ) oscillations. Linear mixed-effects models were used to assess whether pre-stimulus oscillatory activity (-525 to -125 ms before stimulus onset) was associated with the observed mediation of auditory M100 activation by preM100 DAN activity in older adults. Analyses were conducted separately for each hemisphere (L: left, R: right) and response (Rsp) type (Hits and withholds/WH) in both, the auditory cortex (AC) and the dorsal attention network (DAN). Prevalence (Prev) represents the percentage of participants (either across or within groups) who exhibited higher oscillatory activity across days, as defined by a positive slope. The mean and standard deviation (SD) of the slopes are also provided. When the model corresponded to regressions, the R squared is presented instead. Significant results ($p < 0.05$) and R^2 values higher than 0.2 are highlighted in bold and results referenced in [Section 3.3.4](#) (alpha) and [Section 3.3.5](#) (theta) are shaded in purple. See [Figure 3.12](#) for time-frequency representations and [Figure 3.13](#) for individual data points.

f	ROI	Rsp	Group	Effect	Est	t	p	p_{FDR}	Prev/ R^2	Mean ($\pm$ SD)
<i>Model: Alpha_PreStim_auditory_Left ~ Day + Group + (1 Subject)</i>										
α	AC L	Hit	Both	Day	0.16	0.71	0.484		56.25%	0.04 ($\pm$ 1.19)
α	AC L	Hit	Both	Group	4.22	0.91	0.377			
α	AC L	WH	Both	Day	0.64	3.53	0.001		81.25%	0.71 ($\pm$ 0.92)
α	AC L	WH	Both	Group	2.96	0.60	0.558			
α	AC L	WH	Old	Day	0.46	1.44	0.165	0.604	75%	0.61 ($\pm$ 1.23)
α	AC L	WH	Young	Day	0.80	4.38	2×10^{-4}	0.001	87.50%	0.81 ($\pm$ 0.52)
<i>Model: Alpha_PreStim_auditory_Right ~ Day + Group + (1 Subject)</i>										
α	AC R	Hit	Both	Day	-0.04	-0.12	0.903		56.25%	-0.05 ($\pm$ 1.97)
α	AC R	Hit	Both	Group	-2.27	-0.46	0.654			
α	AC R	WH	Both	Day	0.24	1.33	0.189		62.50%	0.29 ($\pm$ 0.78)
α	AC R	WH	Both	Group	0.31	0.05	0.957			
<i>Model: Alpha_PreStim_DAN_Left ~ Day + Group + (1 Subject)</i>										
α	DAN L	Hit	Both	Day	0.19	0.56	0.578		56.25%	0.17 ($\pm$ 1.58)
α	DAN L	Hit	Both	Group	8.90	2.11	0.053			
α	DAN L	WH	Both	Day	0.60	2.72	0.009		81.25%	0.69 ($\pm$ 1.24)
α	DAN L	WH	Both	Group	5.84	1.62	0.128			
α	DAN L	WH	Old	Day	0.55	1.46	0.161	0.323	75%	0.74 ($\pm$ 1.76)
α	DAN L	WH	Young	Day	0.65	2.38	0.026	0.103	87.50%	0.65 ($\pm$ 0.42)
<i>Model: Alpha_PreStim_DAN_Right ~ Day + Group + (1 Subject)</i>										
α	DAN R	Hit	Both	Day	0.22	0.64	0.524		56.25%	0.01 ($\pm$ 1.66)
α	DAN R	Hit	Both	Group	0.41	0.09	0.928			

Continued on next page

Table S.18: Statistical analysis of pre-stimulus alpha and theta power dynamics in auditory cortex and DAN. (Continued)

<i>f</i>	ROI	Rsp	Group	Effect	Est	<i>t</i>	<i>p</i>	<i>p</i> _{FDR}	Prev/ <i>R</i> ²	Mean (± SD)
<i>Model: Alpha_PreStim_DAN_Right ~ Day * Group + (1 Subject)</i>										
α	DAN R	WH	Both	Day	-0.53	-1.63	0.110		50%	0.16 (±1.11)
α	DAN R	WH	Both	Group	-2.17	-0.36	0.725			
α	DAN R	WH	Both	Day:Grp	1.09	2.48	0.017			
α	DAN R	WH	Old	Day	-0.52	-1.59	0.127	0.323	12.50%	-0.23 (±1.26)
α	DAN R	WH	Young	Day	0.55	1.90	0.070	0.140	87.50%	0.55 (±0.83)
<i>Model: Theta_PreStim_auditory_Left ~ Day + Group + (1 Subject)</i>										
θ	AC L	Hit	Both	Day	1.00	2.56	0.014		62.50%	1.00 (±1.69)
θ	AC L	Hit	Both	Group	4.72	0.81	0.428			
θ	AC L	WH	Both	Day	0.31	1.18	0.245		68.75%	0.27 (±1.02)
θ	AC L	WH	Both	Group	-0.20	-0.04	0.966			
<i>Model: Theta_PreStim_auditory_Right ~ Day + Group + (1 Subject)</i>										
θ	AC R	Hit	Both	Day	0.42	1.28	0.207		56.25%	0.38 (±1.16)
θ	AC R	Hit	Both	Group	8.65	1.72	0.107			
θ	AC R	WH	Both	Day	0.14	0.61	0.545		56.25%	0.04 (±0.99)
θ	AC R	WH	Both	Group	3.05	0.62	0.543			
<i>Model: Theta_PreStim_DAN_Left ~ Day + Group + (1 Subject)</i>										
θ	DAN L	Hit	Both	Day	0.18	0.68	0.502		62.50%	0.08 (±1.12)
θ	DAN L	Hit	Both	Group	8.73	2.65	0.019			
θ	DAN L	WH	Both	Day	0.08	0.50	0.619		46.67%	0.11 (±0.71)
θ	DAN L	WH	Both	Group	4.85	1.53	0.148			
<i>Model: Theta_PreStim_DAN_Right ~ Day + Group + (1 Subject)</i>										
θ	DAN R	Hit	Both	Day	0.21	0.73	0.466		56.25%	0.17 (±1.08)
θ	DAN R	Hit	Both	Group	3.57	0.98	0.344			
<i>Model: Theta_PreStim_DAN_Right ~ Day * Group + (1 Subject)</i>										
θ	DAN R	WH	Both	Day	-0.60	-2.61	0.013		37.50%	-0.14 (±0.84)
θ	DAN R	WH	Both	Group	1.17	0.25	0.805			
θ	DAN R	WH	Both	Day:Grp	0.74	2.36	0.023			
θ	DAN R	WH	Old	Day	-0.61	-2.59	0.018		12.50%	-0.43 (±0.83)
θ	DAN R	WH	Young	Day	0.13	0.63	0.534		62.50%	0.14 (±0.81)

Continued on next page

Table S.18: Statistical analysis of pre-stimulus alpha and theta power dynamics in auditory cortex and DAN. (Continued)

<i>f</i>	ROI	Rsp	Group	Effect	Est	<i>t</i>	<i>p</i>	<i>p</i> _{FDR}	Prev/ <i>R</i> ²	Mean (± SD)
<i>Model: MaxAmp_M100_auditory_Right ~ Day * Group + Theta_PreStim_DAN_Right + (1 + Day Subject)</i>										
-	-	WH	Both	Day:Grp	-0.55	-3.83	4 × 10⁻⁴		0.18	
-	-	WH	Both	θ DAN R	-0.08	-1.50	0.139		0.03	
-	-	WH	Old	Day	0.43	3.80	0.001		0.14	
-	-	WH	Old	θ DAN R	-0.05	-0.68	0.502		0.01	
<i>Model: AvgAmp_preM100_DAN_Right ~ Day * Group + Theta_PreStim_DAN_Right + (1 + Day Subject)</i>										
-	-	WH	Both	Day:Grp	-0.09	-4.67	5 × 10⁻⁴		0.24	
-	-	WH	Both	θ DAN R	0.01	1.44	0.157		0.03	
-	-	WH	Old	Day	0.06	4.93	1 × 10⁻⁴		0.25	
-	-	WH	Old	θ DAN R	0.01	1.31	0.203		0.04	
<i>Model: AvgLevel ~ Day + Alpha_PreStim_auditory_Left + (1 + Day Subject)</i>										
-	-	WH	Young	α AC L	0.10	2.48	0.021	0.064	0.04	
<i>Model: AvgLevel ~ Day + Alpha_PreStim_DAN_Left + (1 + Day Subject)</i>										
-	-	WH	Young	α DAN L	0.01	0.35	0.732	0.732	< 0.01	
<i>Model: AvgLevel ~ Day + Alpha_PreStim_DAN_Right + (1 + Day Subject)</i>										
-	-	WH	Young	α DAN R	-0.05	-1.47	0.157	0.235	0.01	
<i>Model: AvgLevel ~ Day + Theta_PreStim_DAN_Right + (1 + Day Subject)</i>										
-	-	WH	Old	θ DAN R	-0.01	-0.31	0.760		< 0.01	

Table S.19: Statistical analysis of task-related post-stimulus alpha and theta oscillatory activity in auditory cortex and DAN. Results of statistical models assessing task-related changes in post-stimulus alpha (α) and theta (θ) oscillatory activity. Linear mixed-effects models were used to examine whether training influenced post-stimulus (225 to 725 ms after stimulus onset) alpha and theta power in the auditory cortex (AC) and dorsal attention network (DAN) across hemispheres (L: left, R: right), given their role in attentional modulation and distractor suppression. Analyses were conducted separately for Hits (targets) and Withholds (WH, distractors) to account for expected differences in stimulus processing. Prevalence (Prev) represents the percentage of participants (either across or within groups) who exhibited increased oscillatory activity across days, as defined by a positive slope. The mean (μ) and standard deviation (SD) of the slopes are also provided. When the model corresponded to regressions, the R squared is presented instead. Significant results ($p < 0.05$) and R^2 values above 0.2 are highlighted in bold, and results referenced in [Section 3.3.4](#) (alpha) and [Section 3.3.5](#) (theta) are shaded in purple. See [Figure 3.12](#) for time-frequency representations and [Figure 3.14](#) for individual data points.

<i>f</i>	ROI	Rsp	Group	Effect	Est	<i>t</i>	<i>p</i>	<i>p</i> _{FDR}	Prev/ <i>R</i> ²	μ ($\pm$ SD)
<i>Model: Alpha_PostStim_auditory_Left ~ Day + Group + (1 Subject)</i>										
α	AC L	Hit	Both	Day	0.52	2.28	0.028		62.50%	0.46 ($\pm$ 1.00)
α	AC L	Hit	Both	Group	17.61	2.19	0.046			
α	AC L	Hit	Old	Day	0.33	0.96	0.346	0.462	62.50%	0.22 ($\pm$ 1.19)
α	AC L	Hit	Young	Day	0.70	2.25	0.034	0.046	62.50%	0.70 ($\pm$ 0.79)
<i>Model: Alpha_PostStim_auditory_Left ~ Day * Group + (1 Subject)</i>										
α	AC L	WH	Both	Day	0.35	0.76	0.451		68.75%	1.31 ($\pm$ 1.79)
α	AC L	WH	Both	Group	3.47	0.37	0.714			
α	AC L	WH	Both	Day:Grp	1.77	2.71	0.010			
α	AC L	WH	Old	Day	0.35	0.73	0.472	0.472	50%	0.30 ($\pm$ 1.39)
α	AC L	WH	Young	Day	2.13	4.81	0.0001	0.0004	87.50%	2.31 ($\pm$ 1.63)
<i>Model: Alpha_PostStim_auditory_Right ~ Day * Group + (1 Subject)</i>										
α	AC R	Hit	Both	Day	-0.58	-1.41	0.165		43.75%	0.26 ($\pm$ 1.29)
α	AC R	Hit	Both	Group	-4.96	-0.46	0.648			
α	AC R	Hit	Both	Day:Grp	1.65	2.92	0.006			
α	AC R	Hit	Old	Day	-0.58	-1.29	0.212	0.424	12.50%	-0.55 ($\pm$ 0.59)
α	AC R	Hit	Young	Day	1.08	3.07	0.006	0.012	75%	1.07 ($\pm$ 1.30)
<i>Model: Alpha_PostStim_auditory_Right ~ Day + Group + (1 Subject)</i>										
α	AC R	WH	Both	Day	0.53	2.45	0.019		62.50%	0.61 ($\pm$ 1.10)
α	AC R	WH	Both	Group	13.02	1.56	0.141			
α	AC R	WH	Old	Day	0.55	1.96	0.065	0.260	62.50%	0.57 ($\pm$ 0.86)
α	AC R	WH	Young	Day	0.52	1.57	0.132	0.132	62.50%	0.65 ($\pm$ 1.35)

Continued on next page

Table S.19: Statistical analysis of task-related post-stimulus alpha and theta oscillatory activity in auditory cortex and DAN. (Continued)

<i>f</i>	ROI	Rsp	Group	Effect	Est	<i>t</i>	<i>p</i>	<i>p</i> _{FDR}	Prev/ <i>R</i> ²	μ ($\pm$ SD)
<i>Model: Alpha_PostStim_DAN_Left ~ Day + Group + (1 Subject)</i>										
α	DAN L	Hit	Both	Day	0.58	2.28	0.028		68.75%	0.55 ($\pm$ 1.07)
α	DAN L	Hit	Both	Group	24.78	3.20	0.006			
α	DAN L	Hit	Old	Day	0.32	0.87	0.396	0.971	50%	0.27 ($\pm$ 1.12)
α	DAN L	Hit	Young	Day	0.82	2.33	0.029	0.029	87.50%	0.82 ($\pm$ 1.01)
<i>Model: Alpha_PostStim_DAN_Left ~ Day * Group + (1 Subject)</i>										
α	DAN L	WH	Both	Day	0.02	0.04	0.967		75%	0.75 ($\pm$ 1.50)
α	DAN L	WH	Both	Group	12.94	1.66	0.108			
α	DAN L	WH	Both	Day:Grp	1.51	2.31	0.026			
α	DAN L	WH	Old	Day	0.02	0.04	0.971	0.971	50%	-0.05 ($\pm$ 1.58)
α	DAN L	WH	Young	Day	1.53	3.53	0.002	0.008	100%	1.54 ($\pm$ 0.95)
<i>Model: Alpha_PostStim_DAN_Right ~ Day * Group + (1 Subject)</i>										
α	DAN R	Hit	Both	Day	-0.03	-0.07	0.942		68.75%	0.50 ($\pm$ 1.32)
α	DAN R	Hit	Both	Group	7.92	0.79	0.437			
α	DAN R	Hit	Both	Day:Grp	1.07	1.82	0.077			
α	DAN R	Hit	Old	Day	-0.02	-0.06	0.952	0.971	62.50%	-0.04 ($\pm$ 1.08)
α	DAN R	Hit	Young	Day	1.04	2.44	0.023	0.029	75%	1.04 ($\pm$ 1.38)
α	DAN R	WH	Both	Day	0.02	0.07	0.947		68.75%	0.70 ($\pm$ 1.47)
α	DAN R	WH	Both	Group	13.38	1.55	0.136			
α	DAN R	WH	Both	Day:Grp	1.08	2.17	0.036			
α	DAN R	WH	Old	Day	0.03	0.08	0.941	0.971	50%	0.08 ($\pm$ 1.25)
α	DAN R	WH	Young	Day	1.10	3.11	0.006	0.011	87.50%	1.32 ($\pm$ 1.48)
<i>Model: Theta_PostStim_auditory_Left ~ Day + Group + (1 Subject)</i>										
θ	AC L	Hit	Both	Day	1.09	2.45	0.019		75%	0.98 ($\pm$ 1.88)
θ	AC L	Hit	Both	Group	-1.40	-0.17	0.866			
θ	AC L	Hit	Old	Day	1.02	1.34	0.196	0.595	75%	0.78 ($\pm$ 2.06)
θ	AC L	Hit	Young	Day	1.15	2.12	0.045	0.076	75%	1.17 ($\pm$ 1.80)
θ	AC L	WH	Both	Day	0.41	1.18	0.244		56.25%	0.54 ($\pm$ 1.69)
θ	AC L	WH	Both	Group	-8.21	-0.94	0.365			

Continued on next page

Table S.19: Statistical analysis of task-related post-stimulus alpha and theta oscillatory activity in auditory cortex and DAN. (Continued)

<i>f</i>	ROI	Rsp	Group	Effect	Est	<i>t</i>	<i>p</i>	<i>p</i> _{FDR}	Prev/ <i>R</i> ²	μ ($\pm$ SD)
<i>Model: Theta_PostStim_auditory_Right</i> ~ <i>Day</i> * <i>Group</i> + (1 <i>Subject</i>)										
θ	AC R	Hit	Both	Day	-0.18	-0.33	0.741		62.50%	1.23 ($\pm$ 3.61)
θ	AC R	Hit	Both	Group	-9.22	-0.87	0.392			
θ	AC R	Hit	Both	Day:Grp	1.45	1.83	0.074			
θ	AC R	Hit	Old	Day	-0.18	-0.32	0.751	0.751	50%	-0.24 ($\pm$ 0.96)
θ	AC R	Hit	Young	Day	1.27	2.32	0.030	0.076	75%	2.71 ($\pm$ 4.70)
<i>Model: Theta_PostStim_auditory_Right</i> ~ <i>Day</i> + <i>Group</i> + (1 <i>Subject</i>)										
θ	AC R	WH	Both	Day	0.67	2.18	0.035		56.25%	0.61 ($\pm$ 1.41)
θ	AC R	WH	Both	Group	-4.14	-0.53	0.602			
θ	AC R	WH	Old	Day	0.48	1.07	0.298	0.595	50%	0.24 ($\pm$ 1.35)
θ	AC R	WH	Young	Day	0.85	2.00	0.057	0.076	62.50%	0.98 ($\pm$ 1.47)
<i>Model: Theta_PostStim_DAN_Left</i> ~ <i>Day</i> * <i>Group</i> + (1 <i>Subject</i>)										
θ	DAN L	Hit	Both	Day	-0.65	-1.51	0.139		56.25%	0.09 ($\pm$ 1.65)
θ	DAN L	Hit	Both	Group	-3.04	-0.35	0.727			
θ	DAN L	Hit	Both	Day:Grp	1.54	2.55	0.014			
θ	DAN L	Hit	Old	Day	-0.65	-1.52	0.145	0.145	25%	-0.77 ($\pm$ 1.30)
θ	DAN L	Hit	Young	Day	0.90	2.10	0.047	0.047	87.50%	0.95 ($\pm$ 1.57)
<i>Model: Theta_PostStim_DAN_Left</i> ~ <i>Day</i> + <i>Group</i> + (1 <i>Subject</i>)										
θ	DAN L	WH	Both	Day	0.13	0.56	0.576		56.25%	0.07 ($\pm$ 1.00)
θ	DAN L	WH	Both	Group	5.63	0.93	0.367			
<i>Model: Theta_PostStim_DAN_Right</i> ~ <i>Day</i> * <i>Group</i> + (1 <i>Subject</i>)										
θ	DAN R	Hit	Both	Day	-0.84	-1.98	0.055		56.25%	-0.29 ($\pm$ 1.70)
θ	DAN R	Hit	Both	Group	-3.86	-0.41	0.684			
θ	DAN R	Hit	Both	Day:Grp	1.61	2.61	0.012			
θ	DAN R	Hit	Old	Day	-0.84	-1.72	0.100	0.145	37.50%	-0.93 ($\pm$ 1.37)
θ	DAN R	Hit	Young	Day	0.78	2.11	0.047	0.047	75%	0.34 ($\pm$ 1.84)
<i>Model: Theta_PostStim_DAN_Right</i> ~ <i>Day</i> + <i>Group</i> + (1 <i>Subject</i>)										
θ	DAN R	WH	Both	Day	0.19	0.84	0.404		50%	0.12 ($\pm$ 1.14)
θ	DAN R	WH	Both	Group	7.42	1.08	0.297			
<i>Model: AvgLevel</i> ~ <i>Day</i> + Alpha_PostStim_auditory_Left + (1 + <i>Day</i> <i>Subject</i>)										
-	-	Hit	Young	α AC L	0.01	0.51	0.614		< 0.01	
-	-	WH	Young	α AC L	0.02	1.17	0.258		< 0.01	

Continued on next page

Table S.19: Statistical analysis of task-related post-stimulus alpha and theta oscillatory activity in auditory cortex and DAN. (Continued)

<i>f</i>	ROI	Rsp	Group	Effect	Est	<i>t</i>	<i>p</i>	<i>p</i> _{FDR}	Prev/ <i>R</i> ²	μ ($\pm$ SD)
<i>Model: AvgLevel ~ Day + Alpha_PostStim_auditory_Right + (1 + Day Subject)</i>										
–	–	Hit	Young	α AC R	0.02	1.03	0.312		< 0.01	
<i>Model: AvgLevel ~ Day + Alpha_PostStim_DAN_Left + (1 + Day Subject)</i>										
–	–	Hit	Young	α DAN L	0.04	1.30	0.205		0.02	
–	–	WH	Young	α DAN L	-0.002	-0.11	0.914		< 0.01	
<i>Model: AvgLevel ~ Day + Alpha_PostStim_DAN_Right + (1 + Day Subject)</i>										
–	–	Hit	Young	α DAN R	0.03	1.22	0.233		< 0.01	
–	–	WH	Young	α DAN R	0.01	0.33	0.747		< 0.01	
<i>Model: AvgLevel ~ Day + Theta_PostStim_auditory_Left + (1 + Day Subject)</i>										
–	–	Hit	Young	θ AC L	-0.02	-1.03	0.313		< 0.01	
<i>Model: AvgLevel ~ Day + Theta_PostStim_auditory_Right + (1 + Day Subject)</i>										
–	–	Hit	Young	θ AC R	-0.01	-0.72	0.475		< 0.01	
–	–	WH	Young	θ AC R	0.01	0.22	0.828		< 0.01	
<i>Model: AvgLevel ~ Day + Theta_PostStim_DAN_Left + (1 + Day Subject)</i>										
–	–	Hit	Young	θ DAN L	-0.02	-0.62	0.538		< 0.01	
<i>Model: AvgLevel ~ Day + Theta_PostStim_DAN_Right + (1 + Day Subject)</i>										
–	–	Hit	Young	θ DAN R	-0.002	-0.07	0.942		< 0.01	

Table S.20: Statistical models of DAN–auditory coherence and its relationship to training-related changes. Results of statistical models examining pre-stimulus coherence (1–20 Hz) between the right dorsal attention network (DAN) and right auditory cortex (AC), and its relationship to training-related changes in auditory M100 amplitude, preM100 DAN activation, and average performance level. Each group was evaluated separately. Prevalence (Prev.) represents the percentage of participants within each group who exhibited higher coherence across days, as defined by a positive slope. The mean and standard deviation (SD) of the slopes are also provided. In regression models, the R squared is presented instead. Significant results ($p < 0.05$) and R^2 values higher than 0.2 are highlighted in bold and results referenced in [Section 3.3.6](#) are shaded in purple. See [Figure 3.15](#) for individual data points.

Group	Effect	Estimate	t value	p value	R^2	Prev.	Mean ($\pm$ SD)
<i>Model: Coherence_preM100_DAN-Right_auditory-Right $\sim$ Day + (1 Subject)</i>							
Older	Day	0.75	2.42	0.025		75%	0.63 ($\pm$ 1.07)
Younger	Day	0.19	0.57	0.575		75%	0.04 ($\pm$ 1.14)
<i>Model: MaxAmp_M100_ auditory-Right $\sim$ Day + Coherence_preM100_DAN-Right_auditory-Right + (1 + Day Subject)</i>							
Older	Day	0.44	3.01	0.010	0.11		
Older	Coherence	0.03	0.37	0.716	< 0.01		
<i>Model: AvgAmp_preM100_ DAN-Right $\sim$ Day + Coherence_preM100_DAN-Right_auditory-Right + (1 + Day Subject)</i>							
Older	Day	0.06	5.01	2×10^{-4}	0.27		
Older	Coherence	0.01	1.94	0.064	0.03		
<i>Model: AvgLevel $\sim$ Day + Coherence_preM100_DAN-Right_auditory-Right + (1 + Day Subject)</i>							
Older	Day	0.17	3.70	0.002	0.21		
Older	Coherence	-0.01	-0.47	0.644	< 0.01		

Table S.21: Statistical models of ventral attention network average preM100 activity and its relationship to auditory cortex and training. Results of statistical models used to assess the effect of training and age on the averaged preM100 amplitude in the ventral attention network (VAN). Post-hoc analyses were conducted to evaluate each group separately. Prevalence (Prev.) represents the percentage of participants (either across or within groups) who exhibited higher preM100 activation across days, as defined by a positive slope. The mean and standard deviation (SD) of the slopes are also provided. When the model corresponded to regressions, the R^2 is presented instead. Significant results ($p < 0.05$) and R^2 values higher than 0.2 are highlighted in bold and results referenced in [Section 3.3.7](#) are shaded in purple.

Group	Hem.	Effect	Est.	t	p	R^2	Prev.	Mean ($\pm$ SD)
<i>Model: AvgAmp_preM100_VAN_Left ~ Day * Group + (1 + Day Subject)</i>								
Both	L	Day	0.08	3.93	0.002		68.75%	0.05 ($\pm$ 0.06)
Both	L	Group	-0.13	-0.61	0.552			
Both	L	Day:Grp	-0.06	-2.10	0.056			
<i>Model: AvgAmp_preM100_VAN_Left ~ Day + Group + (1 + Day Subject)</i>								
Both	L	Day	0.05	3.06	0.008		68.75%	0.05 ($\pm$ 0.06)
Both	L	Group	-0.38	-2.30	0.038			
<i>Model: AvgAmp_preM100_VAN_Left ~ Day + (1 + Day Subject)</i>								
Old	L	Day	0.07	3.13	0.019		87.50%	0.08 ($\pm$ 0.06)
Young	L	Day	0.02	1.21	0.245		50%	0.02 ($\pm$ 0.04)
<i>Model: AvgAmp_preM100_VAN_Left ~ Day * Age + (1 + Day Subject)</i>								
Both	L	Day	3×10^{-3}	0.10	0.920		68.75%	0.05 ($\pm$ 0.06)
Both	L	Age	3×10^{-3}	0.62	0.546			
Both	L	Day:Age	1×10^{-3}	1.58	0.138			
<i>Model: AvgAmp_preM100_VAN_Left ~ Day + Age + (1 + Day Subject)</i>								
Both	L	Day	0.05	3.12	0.007		68.75%	0.05 ($\pm$ 0.06)
Both	L	Age	0.01	1.70	0.110			
<i>Model: AvgAmp_preM100_VAN_Right ~ Day * Group + (1 + Day Subject)</i>								
Both	R	Day	0.07	3.83	0.002		81.25%	0.04 ($\pm$ 0.06)
Both	R	Group	0.20	0.63	0.536			
Both	R	Day:Grp	-0.06	-2.33	0.035			
<i>Model: AvgAmp_preM100_VAN_Right ~ Day + (1 + Day Subject)</i>								
Old	R	Day	0.07	3.49	0.010		87.50%	0.07 ($\pm$ 0.06)
Young	R	Day	0.01	0.66	0.528		75%	0.01 ($\pm$ 0.04)

Continued on next page

Table S.21: Statistical models of ventral attention network average preM100 activity and its relationship to auditory cortex and training. (Continued)

Group	Hem.	Effect	Est.	<i>t</i>	<i>p</i>	<i>R</i> ²	Prev.	Mean (± SD)
<i>Model: AvgAmp_preM100_VAN_Right ~ Day + Group + (1 + Day Subject)</i>								
Both	R	Day	0.04	2.71	0.016		81.25%	0.04 (±0.06)
Both	R	Group	-0.30	-1.26	0.228			
<i>Model: AvgAmp_preM100_VAN_Right ~ Day * Age + (1 Subject)</i>								
Both	R	Day	-0.02	-0.94	0.352		81.25%	0.04 (±0.05)
Both	R	Age	-0.01	-1.13	0.272			
Both	R	Day:Age	2×10^{-3}	3.67	0.001			
<i>Model: AvgAmp_preM100_VAN_Laterality ~ Day + Group + (1 + Day Subject)</i>								
Both	–	Day	1×10^{-3}	0.10	0.924		43.75%	1×10^{-3} (±0.05)
Both	–	Group	0.06	0.29	0.777			
<i>Model: MaxAmp_M100_auditory_Right ~ Day + AvgAmp_preM100_VAN_Left + (1 + Day Subject)</i>								
Old	–	Day	0.33	1.80	0.091	0.11		
Old	–	VAN L	1.68	1.16	0.257	0.02		
<i>Model: MaxAmp_M100_auditory_Right ~ Day + AvgAmp_preM100_VAN_Left + AvgAmp_preM100_DAN_Right + (1 + Day Subject)</i>								
Old	–	Day	0.10	0.48	0.634	0.11		
Old	–	VAN L	0.26	0.17	0.867	< 0.01		
Old	–	DAN R	5.10	2.24	0.034	0.15		
<i>Model: MaxAmp_M100_auditory_Right ~ Day + AvgAmp_preM100_VAN_Right + (1 + Day Subject)</i>								
Old	–	Day	0.23	1.10	0.285	0.09		
Old	–	VAN R	2.09	1.08	0.292	0.03		
<i>Model: MaxAmp_M100_auditory_Right ~ Day + AvgAmp_preM100_VAN_Right + AvgAmp_preM100_DAN_Right + (1 + Day Subject)</i>								
Old	–	Day	0.11	0.52	0.612	0.09		
Old	–	VAN R	-1.26	-0.55	0.586	< 0.01		
Old	–	DAN R	6.14	2.40	0.026	0.15		

Continued on next page

Table S.21: Statistical models of ventral attention network average preM100 activity and its relationship to auditory cortex and training. (Continued)

Group	Hem.	Effect	Est.	<i>t</i>	<i>p</i>	<i>R</i> ²	Prev.	Mean (± SD)
<i>Model: AvgLevel ~ Day + AvgAmp_preM100_VAN_Left + (1 + Day Subject)</i>								
Old	L	Day	0.15	2.59	0.019	0.21		
Old	L	VAN L	0.19	0.42	0.677	< 0.01		
<i>Model: AvgLevel ~ Day + AvgAmp_preM100_VAN_Right + (1 + Day Subject)</i>								
Old	R	Day	0.16	2.85	0.011	0.21		
Old	R	VAN R	-0.03	-0.07	0.948	< 0.01		

Table S.22: Demographic predictors of task performance. Results of linear models used to explore whether demographic factors predicted individual differences in training-related changes in task performance. Only combinations that showed significant relationships in the initial models (individual slopes across days $\sim$ demographic + group), either across both groups or within the age group that exhibited training-related effects in the corresponding outcome, are included. For each case, both the initial and updated models with the relevant demographic variable added as a covariate are displayed. Group-specific estimates are presented where applicable. Significant results ($p < 0.05$) and R^2 values greater than 0.2 are highlighted in bold, and results referenced in [Section 3.4.2](#) are shaded in purple. For the models where the training-related effect on average level was originally reported, see [Table S.1](#).

Group	Effect	Estimate	t value	p value	R^2
<i>Model: slope_AvgLevel $\sim$ PTA_{std} + Group</i>					
Both	PTA _{std}	-0.01	-0.96	0.357	0.42
Older	PTA _{std}	-0.01	-4.27	0.005	0.72
Younger	PTA _{std}	0.01	0.26	0.805	< 0.01
<i>Model: AvgLevel $\sim$ Day * Group + PTA_{std} + (1 + Day Subject)</i>					
Both	Day:Group	0.25	2.87	0.012	0.59
Both	PTA _{std}	-0.16	-2.35	0.036	0.07
Older	Day	0.16	3.55	0.007	0.21
Older	PTA _{std}	-0.17	-5.00	0.003	0.42
<i>Model: slope_AvgLevel $\sim$ PTA_{full} + Group</i>					
Both	PTA _{full}	-0.01	-1.23	0.241	0.44
Older	PTA _{full}	-0.01	-3.93	0.008	0.69
Younger	PTA _{full}	2×10^{-3}	0.05	0.962	< 0.01
<i>Model: AvgLevel $\sim$ Day * Group + PTA_{full} + (1 + Day Subject)</i>					
Both	Day:Group	0.29	3.50	0.003	0.62
Both	PTA _{full}	-0.08	-1.69	0.119	0.04
Older	Day	0.16	3.67	0.006	0.21
Older	PTA _{full}	-0.11	-4.01	0.012	0.37
<i>Model: slope_AvgLevel $\sim$ PTA_{high}</i>					
Both	PTA _{high}	-5×10^{-3}	-1.16	0.265	0.44
Older	PTA _{high}	-5×10^{-3}	-3.23	0.018	0.60
Younger	PTA _{high}	5×10^{-4}	0.02	0.987	< 0.01

Continued on next page

Table S.22: Demographic predictors of task performance. (Continued)

Group	Effect	Estimate	<i>t</i> value	<i>p</i> value	<i>R</i> ²
<i>Model: AvgLevel ~ Day * Group + PTA_{high} + (1 + Day Subject)</i>					
Both	Day:Group	0.29	3.53	0.003	0.62
Both	PTA _{high}	-0.03	-1.12	0.287	0.01
Older	Day	0.16	3.84	0.006	0.21
Older	PTA _{high}	-0.05	-2.58	0.057	0.26

Table S.23: Demographic predictors of training-related changes in cognitive tests. Results of linear models used to explore whether demographic factors predicted individual differences in training-related changes in cognitive tests. Only combinations that showed significant relationships in the initial models (individual slopes across days $\sim$ demographic + group), either across both groups or within the age group that exhibited training-related effects in the corresponding outcome, are included. For each case, both the initial and updated models with the relevant demographic variable added as a covariate are displayed. Group-specific estimates are presented where applicable. Significant results ($p < 0.05$) and R^2 values greater than 0.2 are highlighted in bold, and results referenced in [Section 3.4.2](#) are shaded in purple. For the models where the training-related effects on cognitive tests were originally reported, see [Tables S.3](#) and [S.4](#).

Group	Effect	Estimate	<i>t</i> value	<i>p</i> value	R^2
<i>Model: diff_RAVLT_LearningGain $\sim$ PTA_{std} + Group</i>					
Both	PTA _{std}	-0.05	-2.15	0.051	0.31
Older	PTA _{std}	-0.05	-2.70	0.036	0.51
Younger	PTA _{std}	-0.08	-1.13	0.301	0.15
<i>Model: RAVLT_LearningGain $\sim$ Session + Group + PTA_{std} + (1 Subject)</i>					
Both	Session	0.36	2.58	0.016	0.22
Both	Group	-0.21	-1.11	0.278	0.22
Both	PTA _{std}	-0.01	-0.42	0.679	< 0.01
Older	Session	0.61	4.00	0.005	0.46
Older	PTA _{std}	-2×10^{-4}	-0.01	0.989	< 0.01
Younger	Session	0.09	0.46	0.655	0.01
Younger	PTA _{std}	-0.02	-0.83	0.421	0.05
<i>Model: diff_Stroop_CWScore $\sim$ AWP_{current} + Group</i>					
Both	AWP _{current}	-0.20	-0.31	0.764	0.14
Older	AWP _{current}	1.75	3.61	0.022	0.72
Younger	AWP _{current}	-1.25	-1.63	0.154	0.28
<i>Model: Stroop_CWScore $\sim$ Session + Group + AWP_{current} + (1 Subject)</i>					
Both	Session	4.64	4.55	0.001	0.55
Both	Group	12.44	3.85	0.003	0.55
Both	AWP _{current}	2×10^{-3}	2×10^{-3}	0.999	< 0.01
Older	Session	3.00	2.37	0.064	0.14
Older	AWP _{current}	0.62	0.55	0.610	0.02
Younger	Session	5.88	4.14	0.004	0.15
Younger	AWP _{current}	-0.33	-0.21	0.838	< 0.01

Table S.24: Demographic predictors of training-related changes in auditory processing. Results of linear models used to explore whether demographic factors predicted individual differences in training-related changes in auditory responses. Only combinations that showed significant relationships in the initial models (individual slopes across days $\sim$ demographic + group), either across both groups or within the age group that exhibited training-related effects in the corresponding outcome, are included. For each case, both the initial and updated models with the relevant demographic variable added as a covariate are displayed. Group-specific estimates are presented where applicable. Significant results ($p < 0.05$) and R^2 values greater than 0.2 are highlighted in bold, and results referenced in [Section 3.4.2](#) are shaded in purple. For the models where the training-related effect on auditory responses were originally reported, see [Table S.7](#).

Group	Effect	Estimate	t value	p value	R^2
<i>Model: slope_MaxAmp_M100_auditory_Right $\sim$ PTA_{std} + Group</i>					
Both	PTA _{std}	-0.02	-2.79	0.015	0.80
Older	PTA _{std}	-0.02	-2.84	0.029	0.54
Younger	PTA _{std}	-0.02	-0.88	0.412	0.10
<i>Model: MaxAmp_M100_auditory_Right $\sim$ Day * Group + PTA_{std} + (1 + Day Subject)</i>					
Both	Day:Group	-0.51	-3.26	0.002	0.16
Both	PTA _{std}	-0.16	-0.81	0.431	< 0.01
Older	Day	0.40	3.14	0.005	0.09
Older	PTA _{std}	-0.30	-1.15	0.295	0.08
Younger	Day	-0.12	-1.20	0.243	0.02
Younger	PTA _{std}	0.33	1.18	0.282	0.10
<i>Model: slope_MaxAmp_M100_auditory_Right $\sim$ PTA_{full} + Group</i>					
Both	PTA _{full}	-0.02	-2.92	0.012	0.80
Older	PTA _{full}	-0.01	-2.68	0.036	0.51
Younger	PTA _{full}	-0.04	-1.75	0.131	0.30
<i>Model: MaxAmp_M100_auditory_Right $\sim$ Day * Group + PTA_{full} + (1 + Day Subject)</i>					
Both	Day:Group	-0.51	-3.26	0.002	0.16
Both	PTA _{full}	-0.17	-1.28	0.224	0.04
Older	Day	0.40	3.13	0.006	0.09
Older	PTA _{full}	-0.19	-1.10	0.314	0.07
Younger	Day	-0.12	-1.21	0.241	0.02
Younger	PTA _{full}	0.23	0.47	0.654	0.02

Continued on next page

Table S.24: Demographic predictors of training-related changes in auditory processing. (Continued)

Group	Effect	Estimate	<i>t</i> value	<i>p</i> value	<i>R</i> ²
<i>Model: slope_MaxAmp_M100_auditory_Right ~ PTA_{high} + Group</i>					
Both	PTA _{high}	-0.01	-2.78	0.016	0.79
Older	PTA _{high}	-0.01	-2.35	0.057	0.44
Younger	PTA _{high}	-0.04	-3.27	0.017	0.60
<i>Model: MaxAmp_M100_auditory_Right ~ Day * Group + PTA_{high} + (1 + Day Subject)</i>					
Both	Day:Group	-0.51	-3.25	0.002	0.16
Both	PTA _{high}	-0.11	-1.41	0.180	0.05
Older	Day	0.40	3.12	0.006	0.09
Older	PTA _{high}	-0.10	-1.00	0.356	0.06
Younger	Day	-0.12	-1.21	0.241	0.02
Younger	PTA _{high}	-0.40	-1.30	0.240	0.12

Table S.25: Demographic predictors of training-related changes in the dorsal attention network. Results of linear models used to explore whether demographic factors predicted individual differences in training-related changes in dorsal attention network (DAN). Only combinations that showed significant relationships in the initial models (individual slopes across days ~ demographic + group), either across both groups or within the age group that exhibited training-related effects in the corresponding outcome, are included. For each case, both the initial and updated models with the relevant demographic variable added as a covariate are displayed. Group-specific estimates are presented where applicable. Significant results ($p < 0.05$) and R^2 values greater than 0.2 are highlighted in bold, and results referenced in [Section 3.4.2](#) are shaded in purple. For the models where the training-related effect on DAN responses were originally reported, see [Table S.14](#).

Group	Effect	Estimate	t value	p value	R^2
<i>Model: slope_AvgAmp_preM100_DAN_Right ~ Education years + Group</i>					
Both	Education	0.01	2.79	0.015	0.56
Older	Education	0.01	2.35	0.057	0.44
Younger	Education	0.01	1.54	0.174	0.25
<i>Model: AvgAmp_preM100_DAN_Right ~ Day * Group + Education years + (1 + Day Subject)</i>					
Both	Day:Group	-0.10	-5.43	1×10^{-4}	0.27
Both	Education	0.05	1.90	0.077	0.09
Older	Day	0.07	5.45	0.002	0.27
Older	Education	0.06	1.58	0.164	0.13
Younger	Day	-0.03	-2.25	0.058	0.14
Younger	Education	0.02	0.63	0.550	< 0.01
<i>Model: slope_AvgAmp_preM100_DAN_Right ~ Musical Education + Group</i>					
Both	Musical Education	-4×10^{-3}	-1.13	0.283	0.31
Older	Musical Education	-0.04	-3.63	0.022	0.73
Younger	Musical Education	-3×10^{-3}	-0.73	0.493	0.07
<i>Model: AvgAmp_preM100_DAN_Right ~ Day * Group + Musical Education + (1 + Day Subject)</i>					
Both	Day:Group	-0.09	-4.25	0.001	0.20
Both	Musical Education	-5×10^{-3}	-0.20	0.845	< 0.01
Older	Day	0.06	3.56	0.020	0.17
Older	Musical Education	-2×10^{-3}	-0.01	0.992	< 0.01

Continued on next page

Table S.25: Demographic predictors of training-related changes in the dorsal attention network.
(Continued)

Group	Effect	Estimate	<i>t</i> value	<i>p</i> value	<i>R</i> ²
<i>Model: slope_AvgAmp_preM100_DAN_Right ~ Musicality Index + Group</i>					
Both	Musicality Index	-2×10^{-4}	-0.43	0.676	0.25
Older	Musicality Index	-0.01	-4.02	0.016	0.76
Younger	Musicality Index	-1×10^{-4}	-0.25	0.812	< 0.01
<i>Model: AvgAmp_preM100_DAN_Right ~ Day * Group + Musicality Index + (1 + Day Subject)</i>					
Both	Day:Group	-0.09	-4.26	0.001	0.20
Both	Musicality Index	-2×10^{-3}	-0.63	0.544	< 0.01
Older	Day	0.06	3.53	0.021	0.17
Older	Musicality Index	0.01	0.27	0.799	< 0.01

Table S.26: Demographic predictors of training-related changes in pre-stimulus oscillations. Results of linear models used to explore whether demographic factors predicted individual differences in training-related changes in pre-stimulus oscillatory activity. Only combinations that showed significant relationships in the initial models (individual slopes across days ~ demographic + group), either across both groups or within the age group that exhibited training-related effects in the corresponding outcome, are included. For each case, both the initial and updated models with the relevant demographic variable added as a covariate are displayed. Group-specific estimates are presented where applicable. Significant results ($p < 0.05$) and R^2 values greater than 0.2 are highlighted in bold, and results referenced in [Section 3.4.2](#) are shaded in purple. For the models where the training-related effects on alpha and theta pre-stimulus power were originally reported, see [Table S.18](#).

Response	Group	Effect	Estimate	<i>t</i> value	<i>p</i> value	R^2
<i>Model: slope_Alpha_PreStim_auditory_Left ~ Language Proficiency Index + Group</i>						
WH	Both	LPI	-0.86	-2.52	0.026	0.30
WH	Older	LPI	-1.04	-2.21	0.069	0.41
WH	Younger	LPI	-0.28	-0.54	0.610	0.04
<i>Model: Alpha_PreStim_auditory_Left ~ Day + Group + Language Proficiency Index + (1 Subject)</i>						
WH	Both	Day	0.64	3.52	0.001	0.07
WH	Both	LPI	7.20	1.90	0.080	0.13
WH	Older	Day	0.46	1.43	0.167	0.02
WH	Older	LPI	6.82	1.22	0.267	0.11
WH	Younger	Day	0.80	4.37	3×10^{-4}	0.15
WH	Younger	LPI	8.46	1.53	0.180	0.15
<i>Model: slope_Theta_PreStim_DAN_Right ~ Musical Education + Group</i>						
WH	Both	Musical Education	0.10	2.42	0.034	0.47
WH	Older	Musical Education	0.09	0.48	0.659	0.04
WH	Younger	Musical Education	0.10	2.03	0.089	0.37
<i>Model: Theta_PreStim_DAN_Right ~ Day * Group + Musical Education + (1 Subject)</i>						
WH	Both	Day:Group	0.63	2.22	0.033	0.22
WH	Both	Musical Education	0.37	0.63	0.542	< 0.01
WH	Older	Day	-0.75	-2.90	0.011	0.08
WH	Older	Musical Education	-3.62	-1.00	0.375	0.12
WH	Younger	Day	-0.13	-0.83	0.415	< 0.01
WH	Younger	Musical Education	0.53	1.09	0.318	0.11

Continued on next page

Table S.26: Demographic predictors of training-related changes in pre-stimulus oscillations.
(Continued)

Response	Group	Effect	Estimate	<i>t</i> value	<i>p</i> value	<i>R</i> ²
<i>Model: slope_Theta_PreStim_DAN_Right ~ Musicality Index + Group</i>						
WH	Both	Musicality Index	0.02	3.04	0.011	0.56
WH	Older	Musicality Index	0.03	0.59	0.588	0.06
WH	Younger	Musicality Index	0.02	2.64	0.039	0.50
<i>Model: Theta_PreStim_DAN_Right ~ Day * Group + Musicality Index + (1 Subject)</i>						
WH	Both	Day:Group	0.63	2.22	0.033	0.22
WH	Both	Musicality Index	0.02	0.20	0.842	< 0.01
WH	Older	Day	-0.75	-2.90	0.011	0.08
WH	Older	Musicality Index	-0.99	-0.95	0.398	0.11
WH	Younger	Day	-0.13	-0.83	0.414	< 0.01
WH	Younger	Musicality Index	0.02	0.36	0.733	0.01

Table S.27: Demographic predictors of training-related changes in post-stimulus oscillatory activity. Results of linear models used to explore whether demographic factors predicted individual differences in training-related changes in post-stimulus oscillations. Only combinations that showed significant relationships in the initial models (individual slopes across days ~ demographic + group), either across both groups or within the age group that exhibited training-related effects in the corresponding outcome, are included. For each case, both the initial and updated models with the relevant demographic variable added as a covariate are displayed. Group-specific estimates are presented where applicable. Significant results ($p < 0.05$) and R^2 values greater than 0.2 are highlighted in bold, and results referenced in [Section 3.4.2](#) are shaded in purple. For the models where the training-related effects on alpha and theta pre-stimulus power were originally reported, see [Table S.19](#).

Response	Group	Effect	Estimate	t value	p value	R^2
<i>Model: slope_Alpha_PostStim_auditory_Right ~ Language Proficiency Index + Group</i>						
Hit	Both	LPI	0.98	2.62	0.021	0.53
Hit	Older	LPI	0.44	1.80	0.121	0.32
Hit	Younger	LPI	2.70	4.07	0.007	0.70
<i>Model: Alpha_PostStim_auditory_Right ~ Day * Group + Language Proficiency Index + (1 Subject)</i>						
Hit	Both	Day:Group	1.65	2.92	0.006	0.05
Hit	Both	LPI	2.02	0.23	0.818	< 0.01
Hit	Older	Day	-0.58	-1.28	0.213	0.01
Hit	Older	LPI	5.15	0.46	0.664	0.02
Hit	Younger	Day	1.07	3.07	0.006	0.06
Hit	Younger	LPI	-7.96	-0.51	0.627	0.02
<i>Model: slope_Alpha_PostStim_auditory_Left ~ Musical Education + Group</i>						
WH	Both	Musical Education	0.17	2.13	0.059	0.57
WH	Older	Musical Education	0.19	0.35	0.742	0.02
WH	Younger	Musical Education	0.17	3.01	0.030	0.60
<i>Model: Alpha_PostStim_auditory_Left ~ Day * Group + Musical Education + (1 Subject)</i>						
WH	Both	Day:Group	2.24	3.05	0.004	0.22
WH	Both	Musical Education	-0.11	-0.10	0.923	< 0.01
WH	Older	Day	-0.11	-0.17	0.864	< 0.01
WH	Older	Musical Education	-0.68	-0.11	0.918	< 0.01
WH	Younger	Day	2.13	4.80	1 × 10⁻⁴	0.21
WH	Younger	Musical Education	-0.09	-0.08	0.943	< 0.01

Continued on next page

Table S.27: Demographic predictors of training-related changes in post-stimulus oscillatory activity. (Continued)

Response	Group	Effect	Estimate	<i>t</i> value	<i>p</i> value	<i>R</i> ²
<i>Model: slope_Alpha_PostStim_auditory_Left ~ PTA_{std} + Group</i>						
WH	Both	PTA _{std}	0.13	2.49	0.028	0.51
WH	Older	PTA _{std}	0.15	2.83	0.030	0.53
WH	Younger	PTA _{std}	0.05	0.40	0.706	0.03
<i>Model: Alpha_PostStim_auditory_Left ~ Day * Group + PTA_{std} + (1 Subject)</i>						
WH	Both	Day:Group	1.77	2.71	0.010	0.22
WH	Both	PTA _{std}	0.19	0.23	0.825	< 0.01
WH	Older	Day	0.35	0.73	0.474	< 0.01
WH	Older	PTA _{std}	0.34	0.33	0.755	0.01
WH	Younger	Day	2.13	4.81	1×10⁻⁴	0.21
WH	Younger	PTA _{std}	-0.33	-0.19	0.854	< 0.01
<i>Model: slope_Alpha_PostStim_auditory_Right ~ Education years + Group</i>						
WH	Both	Education	-0.24	-2.32	0.039	0.32
WH	Older	Education	-0.29	-3.14	0.020	0.58
WH	Younger	Education	-0.16	-0.73	0.497	0.08
<i>Model: Alpha_PostStim_auditory_Right ~ Day + Group + Education years + (1 Subject)</i>						
WH	Both	Day	0.53	2.45	0.019	0.13
WH	Both	Education	1.40	0.97	0.351	0.04
WH	Older	Day	0.54	1.94	0.067	0.01
WH	Older	Education	4.41	2.97	0.025	0.46
WH	Younger	Day	0.52	1.55	0.137	0.02
WH	Younger	Education	-2.75	-1.63	0.153	0.21

Continued on next page

Table S.27: Demographic predictors of training-related changes in post-stimulus oscillatory activity. (Continued)

Response	Group	Effect	Estimate	<i>t</i> value	<i>p</i> value	<i>R</i> ²
<i>Model: slope_Alpha_PostStim_auditory_Right ~ AWP_{current} + Group</i>						
WH	Both	AWP _{current}	0.55	3.09	0.011	0.45
WH	Older	AWP _{current}	0.41	2.29	0.106	0.57
WH	Younger	AWP _{current}	0.60	2.37	0.055	0.45
<i>Model: Alpha_PostStim_auditory_Right ~ Day + Group + AWP_{current} + (1 Subject)</i>						
WH	Both	Day	0.42	1.83	0.075	0.07
WH	Both	AWP _{current}	-2.30	-0.77	0.458	0.02
WH	Older	Day	0.27	0.95	0.359	< 0.01
WH	Older	AWP _{current}	-4.84	-0.78	0.479	0.07
WH	Younger	Day	0.53	1.57	0.132	0.02
WH	Younger	AWP _{current}	-0.93	-0.29	0.782	< 0.01
<i>Model: slope_Alpha_PostStim_DAN_Left ~ PTA_{std} + Group</i>						
WH	Both	PTA _{std}	0.14	3.21	0.008	0.70
WH	Older	PTA _{std}	0.14	2.76	0.040	0.56
WH	Younger	PTA _{std}	0.16	1.60	0.162	0.27
<i>Model: Alpha_PostStim_DAN_Left ~ Day * Group + PTA_{std} + (1 Subject)</i>						
WH	Both	Day:Group	1.52	2.33	0.024	0.39
WH	Both	PTA _{std}	1.00	1.68	0.115	0.05
WH	Older	Day	4×10 ⁻³	0.01	0.993	< 0.01
WH	Older	PTA _{std}	1.20	2.08	0.082	0.24
WH	Younger	Day	1.53	3.53	0.002	0.15
WH	Younger	PTA _{std}	0.26	0.18	0.866	< 0.01

Continued on next page

Table S.27: Demographic predictors of training-related changes in post-stimulus oscillatory activity. (Continued)

Response	Group	Effect	Estimate	<i>t</i> value	<i>p</i> value	<i>R</i> ²
<i>Model: slope_Alpha_PostStim_DAN_Left ~ PTA_{full} + Group</i>						
WH	Both	PTA _{full}	0.09	2.67	0.020	0.65
WH	Older	PTA _{full}	0.08	2.51	0.054	0.51
WH	Younger	PTA _{full}	0.24	1.46	0.196	0.23
<i>Model: Alpha_PostStim_DAN_Left ~ Day * Group + PTA_{full} + (1 Subject)</i>						
WH	Both	Day:Group	1.51	2.31	0.026	0.39
WH	Both	PTA _{full}	0.81	1.97	0.070	0.08
WH	Older	Day	0.02	0.03	0.975	< 0.01
WH	Older	PTA _{full}	0.85	2.47	0.048	0.29
WH	Younger	Day	1.53	3.53	0.002	0.15
WH	Younger	PTA _{full}	-0.22	-0.09	0.930	< 0.01
<i>Model: slope_Alpha_PostStim_DAN_Left ~ PTA_{high} + Group</i>						
WH	Both	PTA _{high}	0.05	2.27	0.042	0.61
WH	Older	PTA _{high}	0.05	2.18	0.081	0.44
WH	Younger	PTA _{high}	0.12	0.93	0.390	0.11
<i>Model: Alpha_PostStim_DAN_Left ~ Day * Group + PTA_{high} + (1 Subject)</i>						
WH	Both	Day:Group	1.50	2.29	0.027	0.39
WH	Both	PTA _{high}	0.50	2.12	0.053	0.09
WH	Older	Day	0.03	0.07	0.947	< 0.01
WH	Older	PTA _{high}	0.54	2.99	0.023	0.35
WH	Younger	Day	1.53	3.53	0.002	0.15
WH	Younger	PTA _{high}	-0.81	-0.51	0.630	< 0.01

Continued on next page

Table S.27: Demographic predictors of training-related changes in post-stimulus oscillatory activity. (Continued)

Response	Group	Effect	Estimate	<i>t</i> value	<i>p</i> value	<i>R</i> ²
<i>Model: slope_Alpha_PostStim_DAN_Right ~ AWP_{current} + Group</i>						
WH	Both	AWP _{current}	0.62	3.55	0.005	0.62
WH	Older	AWP _{current}	0.11	0.43	0.699	0.04
WH	Younger	AWP _{current}	0.78	4.01	0.007	0.70
<i>Model: Alpha_PostStim_DAN_Right ~ Day * Group + AWP_{current} + (1 Subject)</i>						
WH	Both	Day:Group	1.38	2.70	0.011	0.26
WH	Both	AWP _{current}	-1.62	-0.55	0.593	< 0.01
WH	Older	Day	-0.27	-0.76	0.459	< 0.01
WH	Older	AWP _{current}	-5.45	-0.97	0.386	0.13
WH	Younger	Day	1.10	3.09	0.006	0.08
WH	Younger	AWP _{current}	0.45	0.13	0.897	< 0.01

Table S.28: Demographic predictors of training-related changes in ventral attention network. Results of linear models used to explore whether demographic factors predicted individual differences in training-related changes in ventral attention network (VAN). Only combinations that showed significant relationships in the initial models (individual slopes across days ~ demographic + group), either across both groups or within the age group that exhibited training-related effects in the corresponding outcome, are included. For each case, both the initial and updated models with the relevant demographic variable added as a covariate are displayed. Group-specific estimates are presented where applicable. Significant results ($p < 0.05$) and R^2 values greater than 0.2 are highlighted in bold, and results referenced in [Section 3.4.2](#) are shaded in purple. For the models where the training-related effect on VAN responses were originally reported, see [Table S.21](#).

Hem.	Group	Effect	Estimate	t value	p value	R^2
<i>Model: slope_AvgAmp_preM100_VAN_Right ~ Language Proficiency Index + Group</i>						
Right	Both	LPI	-0.05	-2.56	0.024	0.50
Right	Older	LPI	-0.04	-1.82	0.118	0.32
Right	Younger	LPI	-0.06	-1.68	0.145	0.29
<i>Model: AvgAmp_preM100_VAN_Right ~ Day * Group + Language Proficiency Index + (1 + Day Subject)</i>						
Right	Both	Day:Group	-0.06	-2.44	0.029	0.16
Right	Both	LPI	-0.49	-2.75	0.017	0.14
Right	Older	Day	0.07	3.45	0.010	0.25
Right	Older	LPI	-0.38	-2.09	0.080	0.12
Right	Younger	Day	0.01	0.44	0.672	< 0.01
Right	Younger	LPI	-0.80	-1.96	0.097	0.21

*Roads go ever on and on,
Over rock and under tree,
By caves where never sun has shone,
By streams that never find the sea;*

*Over snow by winter sown,
And through the merry flowers of June,
Over grass and over stone,
And under mountains in the moon.*

*Roads go ever on and on,
Under cloud and under star;
Yet feet that wandering have gone
Turn at last to home afar.*

— J.R.R. Tolkien (1937)

References

- Abdul-Kareem, I. A. and Sluming, V. (2008). Heschl gyrus and its included primary auditory cortex: Structural MRI studies in healthy and diseased subjects. *Journal of Magnetic Resonance Imaging*, 28(2):287–299. <https://doi.org/10.1002/jmri.21445>
- Adcock, R. A., Dale, C., Fisher, M., Aldebot, S., Genevsky, A., Simpson, G. V., Nagarajan, S., and Vinogradov, S. (2009). When top-down meets bottom-up: Auditory training enhances verbal memory in schizophrenia. *Schizophrenia Bulletin*, 35(6):1132–1141. <https://doi.org/10.1093/schbul/sbp068>
- Addante, R. J., Watrous, A. J., Yonelinas, A. P., Ekstrom, A. D., and Ranganath, C. (2011). Prestimulus theta activity predicts correct source memory retrieval. *Proceedings of the National Academy of Sciences*, 108(26):10702–10707. <https://doi.org/10.1073/pnas.1014528108>
- Ahissar, M., Nahum, M., Nelken, I., and Hochstein, S. (2009). Reverse hierarchies and sensory learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1515):285–299. <https://doi.org/10.1098/rstb.2008.0253>
- Ahlfors, S. P., Han, J., Belliveau, J. W., and Hämäläinen, M. S. (2010). Sensitivity of MEG and EEG to source orientation. *Brain Topography*, 23:227–232. <https://doi.org/10.1007/s10548-010-0154-x>
- Ahveninen, J., Huang, S., Belliveau, J. W., Chang, W.-T., and Hämäläinen, M. (2013). Dynamic oscillatory processes governing cued orienting and allocation of auditory attention. *Journal of Cognitive Neuroscience*, 25(11):1926–1943. https://doi.org/10.1162/jocn_a_00452
- Alain, C., Moussard, A., Singer, J., Lee, Y., Bidelman, G. M., and Moreno, S. (2019). Music and visual art training modulate brain activity in older adults. *Frontiers in Neuroscience*, 13:182. <https://doi.org/10.3389/fnins.2019.00182>

- Alain, C. and Snyder, J. S. (2008). Age-related differences in auditory evoked responses during rapid perceptual learning. *Clinical Neurophysiology*, 119(2):356–366. <https://doi.org/10.1016/j.clinph.2007.10.024>
- Alain, C., Zendel, B. R., Hutka, S., and Bidelman, G. M. (2014). Turning down the noise: The benefit of musical training on the aging auditory brain. *Hearing Research*, 308:162–173. <https://doi.org/10.1016/j.heares.2013.06.008>
- Alavash, M. and Obleser, J. (2024). Brain network interconnectivity dynamics explain metacognitive differences in listening behavior. *The Journal of Neuroscience*, 44(31):e2322232024. <https://doi.org/10.1523/JNEUROSCI.2322-23.2024>
- Albouy, P., Benjamin, L., Morillon, B., and Zatorre, R. J. (2020). Distinct sensitivity to spectrotemporal modulation supports brain asymmetry for speech and melody. *Science*, 367:1043–1047. <https://doi.org/10.1126/science.aaz3468>
- Albouy, P., Martinez-Moreno, Z. E., Hoyer, R. S., Zatorre, R. J., and Baillet, S. (2022). Supramodality of neural entrainment: Rhythmic visual stimulation causally enhances auditory working memory performance. *Science Advances*, 8(8):eabj9782. <https://doi.org/10.1126/sciadv.abj9782>
- Albouy, P., Weiss, A., Baillet, S., and Zatorre, R. J. (2017). Selective entrainment of theta oscillations in the dorsal stream causally enhances auditory working memory performance. *Neuron*, 94:193–206. <https://doi.org/10.1016/j.neuron.2017.03.015>
- Alho, K., Salmi, J., Koistinen, S., Salonen, O., and Rinne, T. (2015). Top-down controlled and bottom-up triggered orienting of auditory attention to pitch activate overlapping brain networks. *Brain Research*, 1626:136–145. <https://doi.org/10.1016/j.brainres.2014.12.050>
- Allen, L., Scott, J., Brand, A., Hlava, M., and Altman, M. (2014). Publishing: Credit where credit is due. *Nature*, 508(7496):312–313. <https://doi.org/10.1038/508312a>
- Amieva, H., Ouvrard, C., Giulioli, C., Meillon, C., Rullier, L., and Dartigues, J.-F. (2015). Self-reported hearing loss, hearing aids, and cognitive decline in elderly adults: A 25-year study. *Journal of the American Geriatrics Society*, 63(10):2099–2104. <https://doi.org/10.1111/jgs.13649>
- Amitay, S., Hawkey, D. J. C., and Moore, D. R. (2005). Auditory frequency discrimination learning is affected by stimulus variability. *Perception & Psychophysics*, 67(4):691–698. <https://doi.org/10.3758/BF03193525>

- Anderson, B. (2011). There is no such thing as attention. *Frontiers in Psychology*, 2:246. <https://doi.org/10.3389/fpsyg.2011.00246>
- Anderson, S., White-Schwoch, T., Choi, H. J., and Kraus, N. (2013a). Training changes processing of speech cues in older adults with hearing loss. *Frontiers in Systems Neuroscience*, 7:97. <https://doi.org/10.3389/fnsys.2013.00097>
- Anderson, S., White-Schwoch, T., Choi, H. J., and Kraus, N. (2014). Partial maintenance of auditory-based cognitive training benefits in older adults. *Neuropsychologia*, 62:286–296. <https://doi.org/10.1016/j.neuropsychologia.2014.07.034>
- Anderson, S., White-Schwoch, T., Parbery-Clark, A., and Kraus, N. (2013b). Reversal of age-related neural timing delays with training. *Proceedings of the National Academy of Sciences*, 110(11):4357–4362. <https://doi.org/10.1073/pnas.1213555110>
- Andoh, J. and Zatorre, R. J. (2011). Interhemispheric connectivity influences the degree of modulation of TMS-induced effects during auditory processing. *Frontiers in Psychology*, 2:161. <https://doi.org/10.3389/fpsyg.2011.00161>
- Andoh, J. and Zatorre, R. J. (2013). Mapping interhemispheric connectivity using functional MRI after transcranial magnetic stimulation on the human auditory cortex. *NeuroImage*, 79:162–171. <https://doi.org/10.1016/j.neuroimage.2013.04.078>
- Angenstein, N. (2024). Asymmetries and hemispheric interaction in the auditory system of elderly people. *Frontiers in Neuroimaging*, 2:1320989. <https://doi.org/10.3389/fnimg.2023.1320989>
- Ansado, J., Monchi, O., Ennabil, N., Faure, S., and Joannette, Y. (2012). Load-dependent posterior–anterior shift in aging in complex visual selective attention situations. *Brain Research*, 1454:14–22. <https://doi.org/10.1016/j.brainres.2012.02.061>
- Antolovic, K., Higby, E., and Obler, L. K. (2023). Mechanisms of cognitive aging in multilingualism. In J. Cabrelli, A. Chaouch-Orozco, J. González Alonso, S. M. Pereira Soares, E. Puig-Mayenco, and J. Rothman (Eds.), *The Cambridge Handbook of Third Language Acquisition*, Cambridge Handbooks in Language and Linguistics (Chapter 23, pp. 606–632). Cambridge University Press. <https://doi.org/10.1017/9781108957823.024>

- Arif, Y., Spooner, R. K., Wiesman, A. I., Embury, C. M., Proskovec, A. L., and Wilson, T. W. (2020). Modulation of attention networks serving reorientation in healthy aging. *Aging*, 12(13):12582–12597. <https://doi.org/10.18632/aging.103515>
- Arredondo, M. M., Hu, X.-S., Satterfield, T., and Kovelman, I. (2017). Bilingualism alters children's frontal lobe functioning for attentional control. *Developmental Science*, 20(3):e12377. <https://doi.org/10.1111/desc.12377>
- Awh, E., Belopolsky, A. V., and Theeuwes, J. (2012). Top-down versus bottom-up attentional control: A failed theoretical dichotomy. *Trends in Cognitive Sciences*, 16(8):437–443. <https://doi.org/10.1016/j.tics.2012.06.010>
- Baillet, S. (2010). The dowser in the fields: Searching for MEG sources. In P. Hansen, M. Kringelbach, and R. Salmelin (Eds.), *MEG: An Introduction to Methods* (Chapter 5, pp. 83–123). Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780195307238.003.0005>
- Baillet, S. (2017). Magnetoencephalography for brain electrophysiology and imaging. *Nature Neuroscience*, 20(3):327–339. <https://doi.org/10.1038/nn.4504>
- Baillet, S., Mosher, J. C., and Leahy, R. M. (2001). Electromagnetic brain mapping. *IEEE Signal Processing Magazine*, 18(6):14–30. <https://doi.org/10.1109/79.962275>
- Balboni, I., Rampinini, A., Kepinska, O., Berthele, R., and Golestani, N. (2025). *Brain activation for language and its relationship to cognitive and linguistic measures*. bioRxiv. <https://doi.org/10.1101/2024.12.31.630909>
- Bandettini, P. A. (2009). What's new in neuroimaging methods? *Annals of the New York Academy of Sciences*, 1156:260–293. <https://doi.org/10.1111/j.1749-6632.2009.04420.x>
- Bandettini, P. A. (2012). Twenty years of functional MRI: The science and the stories. *NeuroImage*, 62:575–588. <https://doi.org/10.1016/j.neuroimage.2012.04.026>
- Bandettini, P. A., Wong, E. C., Hinks, R. S., Tikofsky, R. S., and Hyde, J. S. (1992). Time course EPI of human brain function during task activation. *Magnetic Resonance in Medicine*, 25(2):390–397. <https://doi.org/10.1002/mrm.1910250220>
- Barnes, G. R., Furlong, P. L., Singh, K. D., and Hillebrand, A. (2006). A verifiable solution to the MEG inverse problem. *NeuroImage*, 31(2):623–626. <https://doi.org/10.1016/j.neuroimage.2005.12.036>

- Bartolomeo, P. and Seidel Malkinson, T. (2019). Hemispheric lateralization of attention processes in the human brain. *Current Opinion in Psychology*, 29:90–96. <https://doi.org/10.1016/j.copsyc.2018.12.023>
- Barton, K. (2023). *MuMIn: Multi-Model Inference* [R package version 1.47.5]. The Comprehensive R Archive Network. <https://cran.r-project.org/package=MuMIn>
- Bastos, A. M. and Schoffelen, J.-M. (2016). A tutorial review of functional connectivity analysis methods and their interpretational pitfalls. *Frontiers in Systems Neuroscience*, 9:175. <https://doi.org/10.3389/fnsys.2015.00175>
- Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1):1–48. <https://doi.org/10.18637/jss.v067.i01>
- Baum, S. and Titone, D. (2014). Moving toward a neuroplasticity view of bilingualism, executive control, and aging. *Applied Psycholinguistics*, 35(5):857–894. <https://doi.org/10.1017/S0142716414000174>
- BCBS FEP (2024, January). *Federal employee program utilization management guideline 005. Hearing aids*. Blue Cross and Blue Shield's Federal Employee Program. https://www.fepblue.org/-/media/PDFs/MedicalPolicies/2024/January/UMGuidelines/FEPUMGuideline005HearingAids2024benefitupdate_PMPCCorrection.pdf
- BCBS FEP (2025, April). *Federal employee program utilization management guideline 005. Hearing aids*. Blue Cross and Blue Shield's Federal Employee Program. https://www.fepblue.org/-/media/PDFs/Medical-Policies/2025/March/Medical-Policies/Remove-and-Replace/FEP-UM-Guideline-005-Hearing-Aids-2025_.pdf
- Behrmann, M., Geng, J. J., and Shomstein, S. (2004). Parietal cortex and attention. *Current Opinion in Neurobiology*, 14:212–217. <https://doi.org/10.1016/j.conb.2004.03.012>
- Bellis, T. J., Nicol, T., and Kraus, N. (2000). Aging affects hemispheric asymmetry in the neural representation of speech sounds. *The Journal of Neuroscience*, 20(2):791–797. <https://doi.org/10.1523/JNEUROSCI.20-02-00791.2000>
- Bendixen, A., Schroger, E., and Winkler, I. (2009). I heard that coming: Event-related potential evidence for stimulus-driven prediction in the auditory system. *Journal of Neuroscience*, 29(26):8447–8451. <https://doi.org/10.1523/JNEUROSCI.1493-09.2009>

- Benedek, M., Schickel, R. J., Jauk, E., Fink, A., and Neubauer, A. C. (2014). Alpha power increases in right parietal cortex reflects focused internal attention. *Neuropsychologia*, 56:393–400. <https://doi.org/10.1016/j.neuropsychologia.2014.02.010>
- Benjamini, Y. and Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 57(1):289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>
- Berken, J. A., Chai, X., Chen, J.-K., Gracco, V. L., and Klein, D. (2016). Effects of early and late bilingualism on resting-state functional connectivity. *The Journal of Neuroscience*, 36(4):1165–1172. <https://doi.org/10.1523/JNEUROSCI.1960-15.2016>
- Berlangeri, M., Danelli, L., Bottini, G., Sberna, M., and Paulesu, E. (2013). Reassessing the HAROLD model: Is the hemispheric asymmetry reduction in older adults a special case of compensatory-related utilisation of neural circuits? *Experimental Brain Research*, 224(3):393–410. <https://doi.org/10.1007/s00221-012-3319-x>
- Bertoli, S. and Bodmer, D. (2016). Effects of age and task difficulty on ERP responses to novel sounds presented during a speech-perception-in-noise test. *Clinical Neurophysiology*, 127:360–368. <https://doi.org/10.1016/j.clinph.2015.02.055>
- Bieber, R. E. and Gordon-Salant, S. (2021). Improving older adults' understanding of challenging speech: Auditory training, rapid adaptation and perceptual learning. *Hearing Research*, 402:108054. <https://doi.org/10.1016/j.heares.2020.108054>
- Biermann, S. and Heil, P. (2000). Parallels between timing of onset responses of single neurons in cat and of evoked magnetic fields in human auditory cortex. *Journal of Neurophysiology*, 84(5):2426–2439. <https://doi.org/10.1152/jn.2000.84.5.2426>
- Bigler, E. D. (2017). Structural neuroimaging in neuropsychology: History and contemporary applications. *Neuropsychology*, 31(8):934–953. <https://doi.org/10.1037/neu0000418>
- Bonnefond, M. and Jensen, O. (2012). Alpha oscillations serve to protect working memory maintenance against anticipated distracters. *Current Biology*, 22(20):1969–1974. <https://doi.org/10.1016/j.cub.2012.08.029>
- Boothroyd, A. (2007). Adult aural rehabilitation: What is it and does it work? *Trends in Amplification*, 11(2):63–71. <https://doi.org/10.1177/1084713807301073>

- Boto, E., Holmes, N., Leggett, J., Roberts, G., Shah, V., Meyer, S. S., Muñoz, L. D., Mullinger, K. J., Tierney, T. M., Bestmann, S., Barnes, G. R., Bowtell, R., and Brookes, M. J. (2018). Moving magnetoencephalography towards real-world applications with a wearable system. *Nature*, 555(7698):657–661. <https://doi.org/10.1038/nature26147>
- Brand, A., Allen, L., Altman, M., Hlava, M., and Scott, J. (2015). Beyond authorship: Attribution, contribution, collaboration, and credit. *Learned Publishing*, 28(2):151–155. <https://doi.org/10.1087/20150211>
- Braver, T. S., Gray, J. R., and Burgess, G. C. (2007). Explaining the many varieties of working memory variation: Dual mechanisms of cognitive control. In A. Conway, C. Jarrold, M. Kane, A. Miyake, and J. Towse (Eds.), *Variation in Working Memory* (Chapter 4, pp. 76–106). Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780195168648.003.0004>
- Braver, T. S., Paxton, J. L., Locke, H. S., and Barch, D. M. (2009). Flexible neural mechanisms of cognitive control within human prefrontal cortex. *Proceedings of the National Academy of Sciences*, 106(18):7351–7356. <https://doi.org/10.1073/pnas.0808187106>
- Braver, T. S. and West, R. (2008). Working memory, executive control, and aging. In F. I. M. Craik and T. A. Salthouse (Eds.), *The Handbook of Aging and Cognition* (Chapter 7, pp. 311–372). Psychology Press (3rd ed.). <https://doi.org/10.4324/9780203837665>
- Brehmer, Y., Kalpouzos, G., Wenger, E., and Lövdén, M. (2014). Plasticity of brain and cognition in older adults. *Psychological Research*, 78(6):790–802. <https://doi.org/10.1007/s00426-014-0587-z>
- Brehmer, Y., Shing, Y. L., Heekeren, H. R., Lindenberger, U., and Bäckman, L. (2016). Training-induced changes in subsequent-memory effects: No major differences among children, younger adults, and older adults. *NeuroImage*, 131:214–225. <https://doi.org/10.1016/j.neuroimage.2015.11.074>
- Brehmer, Y., Westerberg, H., and Bäckman, L. (2012). Working-memory training in younger and older adults: Training gains, transfer, and maintenance. *Frontiers in Human Neuroscience*, 6:63. <https://doi.org/10.3389/fnhum.2012.00063>
- Brenowitz, W. D., Kaup, A. R., Lin, F. R., and Yaffe, K. (2019). Multiple sensory impairment is associated with increased risk of dementia among black and white older adults.

- The Journals of Gerontology: Series A*, 74(6):890–896. <https://doi.org/10.1093/geron/gly264>
- Brewster, K. K., Hu, M.-C., Zilcha-Mano, S., Stein, A., Brown, P. J., Wall, M. M., Roose, S. P., Golub, J. S., and Rutherford, B. R. (2021). Age-related hearing loss, late-life depression, and risk for incident dementia in older adults. *The Journals of Gerontology: Series A*, 76(5):827–834. <https://doi.org/10.1093/geron/glaa242>
- Brilliant, Yaar-Soffer, Y., Herrmann, C. S., Henkin, Y., and Kral, A. (2024). Theta and alpha oscillatory signatures of auditory sensory and cognitive loads during complex listening. *NeuroImage*, 289:120546. <https://doi.org/10.1016/j.neuroimage.2024.120546>
- Brookes, M. J., Woolrich, M. W., and Price, D. (2019). An introduction to MEG connectivity measurements. In S. Supek and C. J. Aine (Eds.), *Magnetoencephalography: From Signals to Dynamic Cortical Networks* (pp. 433–470). Springer International Publishing (2nd ed.). https://doi.org/10.1007/978-3-030-00087-5_16
- Brown, D. (June 28, 1984). “*I was dumb now I speak*” [Newspaper article: Google News Archive]. In *Times Daily*, pp. 13A, Column 2.
- Brummett, R. E., Talbot, J. M., and Charuhas, P. (1988). Potential hearing loss resulting from MR imaging. *Radiology*, 169(2):539–540. <https://doi.org/10.1148/radiology.169.2.3175004>
- Bugos, J. A., Bidelman, G. M., Moreno, S., Shen, D., Lu, J., and Alain, C. (2022). Music and visual art training increase auditory-evoked theta oscillations in older adults. *Brain Sciences*, 12:1300. <https://doi.org/10.3390/brainsci12101300>
- Bürki, C. N., Ludwig, C., Chicherio, C., and de Ribaupierre, A. (2014). Individual differences in cognitive plasticity: An investigation of training curves in younger and older adults. *Psychological Research*, 78(6):821–835. <https://doi.org/10.1007/s00426-014-0559-3>
- Buzsáki, G., Anastassiou, C. A., and Koch, C. (2012). The origin of extracellular fields and currents—EEG, ECoG, LFP and spikes. *Nature Reviews Neuroscience*, 13(6):407–420. <https://doi.org/10.1038/nrn3241>
- CAA (2017). *Presbycusis* (Fact sheet). Canadian Academy of Audiology. https://canadianaudiology.ca/wp-content/uploads/2016/11/CAA-Fact_PresbycusisJP_2017.pdf

- Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging*, 17(1):85–100. <https://doi.org/10.1037/0882-7974.17.1.85>
- Cai, R., Richardson, B. D., and Caspary, D. M. (2016). Responses to predictable versus random temporally complex stimuli from single units in auditory thalamus: Impact of aging and anesthesia. *The Journal of Neuroscience*, 36(41):10696–10706. <https://doi.org/10.1523/JNEUROSCI.1454-16.2016>
- Campbell, J. and Sharma, A. (2013). Compensatory changes in cortical resource allocation in adults with hearing loss. *Frontiers in Systems Neuroscience*, 7:71. <https://doi.org/10.3389/fnsys.2013.00071>
- Camus, A. (1953). *Retour à Tipasa*. In *L'Été*. <https://edder.org/literatura/tipasa2.pdf>
- Cappell, K. A., Gmeindl, L., and Reuter-Lorenz, P. A. (2010). Age differences in prefrontal recruitment during verbal working memory maintenance depend on memory load. *Cortex*, 46(4):462–473. <https://doi.org/10.1016/j.cortex.2009.11.009>
- Castiglione, A., Benatti, A., Velardita, C., Favaro, D., Padoan, E., Severi, D., Pagliaro, M., Bovo, R., Vallesi, A., Gabelli, C., and Martini, A. (2016). Aging, cognitive decline and hearing loss: Effects of auditory rehabilitation and training with hearing aids and cochlear implants on cognitive function and depression among older adults. *Audiology and Neurotology*, 21(Suppl. 1):21–28. <https://doi.org/10.1159/000448350>
- Catani, M., Robertsson, N., Beyh, A., Huynh, V., de Santiago Requejo, F., Howells, H., Barrett, R. L. C., Aiello, M., Cavaliere, C., Dyrby, T. B., Krug, K., Ptito, M., D'Arceuil, H., Forkel, S. J., and Dell'Acqua, F. (2017). Short parietal lobe connections of the human and monkey brain. *Cortex*, 97:339–357. <https://doi.org/10.1016/j.cortex.2017.10.022>
- Cazzoli, D., Kaufmann, B. C., Paladini, R. E., Müri, R. M., Nef, T., and Nyffeler, T. (2021). Anterior insula and inferior frontal gyrus: Where ventral and dorsal visual attention systems meet. *Brain Communications*, 3(1):fcaa220. <https://doi.org/10.1093/braincomms/fcaa220>
- Chan, J. S., Wibral, M., Stawowsky, C., Brandl, M., Helbling, S., Naumer, M. J., Kaiser, J., and Wollstadt, P. (2021). Predictive coding over the lifespan: Increased reliance on perceptual priors in older adults—A magnetoencephalography and dynamic

- causal modeling study. *Frontiers in Aging Neuroscience*, 13:631599. <https://doi.org/10.3389/fnagi.2021.631599>
- Chen, J. E. and Glover, G. H. (2015). Functional magnetic resonance imaging methods. *Neuropsychology Review*, 25:289–313. <https://doi.org/10.1007/s11065-015-9294-9>
- Chen, X., Liang, Y., Deng, Y., Li, J., Chen, S., Wang, C., and Luo, P. (2013). Age-associated reduction of asymmetry in human central auditory function: A 1H-magnetic resonance spectroscopy study. *Neural Plasticity*, 2013:735290. <https://doi.org/10.1155/2013/735290>
- Cheng, Y., Jia, G., Zhang, Y., Hao, H., Shan, Y., Yu, L., Sun, X., Zheng, Q., Kraus, N., Merzenich, M. M., and Zhou, X. (2017). Positive impacts of early auditory training on cortical processing at an older age. *Proceedings of the National Academy of Sciences*, 114(24):6364–6369. <https://doi.org/10.1073/pnas.1707086114>
- Cheng, Z., Chen, P., and Yan, J. (2025). A review of state-of-the-art resolution improvement techniques in SPECT imaging. *European Journal of Nuclear Medicine and Molecular Imaging Physics*, 12:9. <https://doi.org/10.1186/s40658-025-00724-9>
- Chennu, S., Noreika, V., Gueorguiev, D., Blenkmann, A., Kochen, S., Ibanez, A., Owen, A. M., and Bekinschtein, T. A. (2013). Expectation and attention in hierarchical auditory prediction. *Journal of Neuroscience*, 33(27):11194–11205. <https://doi.org/10.1523/JNEUROSCI.0114-13.2013>
- Cheslock, M. and Jesus, O. D. (Updated: August, 2023). *Presbycusis*. StatPearls [Internet]. <https://www.ncbi.nlm.nih.gov/books/NBK559220/>
- Choi, H. J., Lee, D. Y., Seo, E. H., Jo, M. K., Sohn, B. K., Choe, Y. M., Byun, M. S., Kim, J. W., Kim, S. G., Yoon, J. C., Jhoo, J. H., Kim, K. W., and Woo, J. I. (2014). A normative study of the digit span in an educationally diverse elderly population. *Psychiatry Investigation*, 11:39. <https://doi.org/10.4306/pi.2014.11.1.39>
- Christensen, H., Anstey, K. J., Leach, L. S., and Mackinnon, A. J. (2008). Intelligence, education, and the brain reserve hypothesis. In F. I. M. Craik and T. A. Salthouse (Eds.), *The Handbook of Aging and Cognition* (Chapter 4, pp. 133–188). Psychology Press (3rd ed.). <https://doi.org/10.4324/9780203837665>
- Chung-Fat-Yim, A., Hayakawa, S., and Marian, V. (2023). Multilingualism and cognitive control in the brain. In J. Cabrelli, A. Chaouch-Orozco, J. González Alonso, S. M.

- Pereira Soares, E. Puig-Mayenco, and J. Rothman (Eds.), *The Cambridge Handbook of Third Language Acquisition*, Cambridge Handbooks in Language and Linguistics (Chapter 20, pp. 519–554). Cambridge University Press. <https://doi.org/10.1017/9781108957823.021>
- Cisneros-Franco, J. M., Ouellet, L., Kamal, B., and de Villers-Sidani, E. (2018). A brain without brakes: Reduced inhibition is associated with enhanced but dysregulated plasticity in the aged rat auditory cortex. *eNeuro*, 5(4):ENEURO.0051–18.2018. <https://doi.org/10.1523/ENEURO.0051-18.2018>
- Cisneros-Franco, J. M., Voss, P., Thomas, M. E., and de Villers-Sidani, E. (2020). Critical periods of brain development. In A. Gallagher, C. Bulteau, D. Cohen, and J. L. Michaud (Eds.), *Neurocognitive Development: Normative Development*, Vol. 173(S.III) of *Handbook of Clinical Neurology* (Chapter 8, pp. 75–88). Elsevier. <https://doi.org/10.1016/B978-0-444-64150-2.00009-5>
- Clements, G. M., Bowie, D. C., Gyurkovics, M., Low, K. A., Fabiani, M., and Gratton, G. (2021). Spontaneous alpha and theta oscillations are related to complementary aspects of cognitive control in younger and older adults. *Frontiers in Human Neuroscience*, 15:621620. <https://doi.org/10.3389/fnhum.2021.621620>
- Coffey, E. B. J., Herholz, S. C., Chepesiuk, A. M. P., Baillet, S., and Zatorre, R. J. (2016). Cortical contributions to the auditory frequency-following response revealed by MEG. *Nature Communications*, 7:11070. <https://doi.org/10.1038/ncomms11070>
- Cohen, D. (1968). Magnetoencephalography: Evidence of magnetic fields produced by alpha-rhythm currents. *Science*, 161:784–786. <https://doi.org/10.1126/science.161.3843.784>
- Cohen, M. X. (2014). *Analyzing neural time series data: Theory and practice* (1st ed.). Issues in Clinical and Cognitive Neuropsychology. The MIT Press. <https://doi.org/10.7551/mitpress/9609.001.0001>
- Cohen, M. X. and Gulbinaite, R. (2014). Five methodological challenges in cognitive electrophysiology. *NeuroImage*, 85:702–710. <https://doi.org/10.1016/j.neuroimage.2013.08.010>
- Colby, S., Clayards, M., and Baum, S. (2018). The role of lexical status and individual differences for perceptual learning in younger and older adults. *Journal of Speech,*

- Language, and Hearing Research*, 61(8):1855–1874. https://doi.org/10.1044/2018_JSLHR-S-17-0392
- Corbetta, M. and Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3:201–215. <https://doi.org/10.1038/nrn755>
- Coste, C. P. and Kleinschmidt, A. (2016). Cingulo-opercular network activity maintains alertness. *NeuroImage*, 128:264–272. <https://doi.org/10.1016/j.neuroimage.2016.01.026>
- Côté, J. (2022). *Development of a novel neuroimaging method to probe the auditory system and its age-related changes* [Doctoral dissertation, McGill University]. <https://escholarship.mcgill.ca/concern/theses/gh93h459z>
- Criscuolo, A. and Brattico, E. (2023). Fundamentals of electroencephalography and magnetoencephalography. In M. Grimaldi, E. Brattico, and Y. Shtyrov (Eds.), *Language Electrified: Principles, Methods, and Future Perspectives of Investigation*, Vol. 202 of *Neuromethods* (Chapter 6, pp. 163–194). Humana Press. https://doi.org/10.1007/978-1-0716-3263-5_6
- Cummins, T. D. R. and Finnigan, S. (2007). Theta power is reduced in healthy cognitive aging. *International Journal of Psychophysiology*, 66:10–17. <https://doi.org/10.1016/j.ijpsycho.2007.05.008>
- Dahlin, E., Nyberg, L., Bäckman, L., and Neely, A. S. (2008). Plasticity of executive functioning in young and older adults: Immediate training gains, transfer, and long-term maintenance. *Psychology and Aging*, 23(4):720–730. <https://doi.org/10.1037/a0014296>
- Daigneault, S., Braun, C. M. J., and Whitaker, H. A. (1992). Early effects of normal aging on perseverative and non-perseverative prefrontal measures. *Developmental Neuropsychology*, 8(1):99–114. <https://doi.org/10.1080/87565649209540518>
- Dale, A. M., Fischl, B., and Sereno, M. I. (1999). Cortical surface-based analysis: I. Segmentation and surface reconstruction. *NeuroImage*, 9(2):179–194. <https://doi.org/10.1006/nimg.1998.0395>
- Dale, C. L., Brown, E. G., Fisher, M., Herman, A. B., Dowling, A. F., Hinkley, L. B., Subramaniam, K., Nagarajan, S. S., and Vinogradov, S. (2016). Auditory cortical

- plasticity drives training-induced cognitive changes in schizophrenia. *Schizophrenia Bulletin*, 42(1):220–228. <https://doi.org/10.1093/schbul/sbv087>
- Damoiseaux, J. S. (2017). Effects of aging on functional and structural brain connectivity. *NeuroImage*, 160:32–40. <https://doi.org/10.1016/j.neuroimage.2017.01.077>
- Das, P. and Steyvers, M. (2023). Older adults catch up to younger adults on cognitive tasks after extended training. *Collabra: Psychology*, 9(1). <https://doi.org/10.1525/collabra.88156>
- Davis, H., Davis, P. A., Loomis, A. L., Harvey, E. N., and Hobart, G. (1939). Electrical reactions of the human brain to auditory stimulation during sleep. *Journal of Neurophysiology*, 2(6):500–514. <https://doi.org/10.1152/jn.1939.2.6.500>
- Davis, S. W., Dennis, N. A., Daselaar, S. M., Fleck, M. S., and Cabeza, R. (2008). Qué PASA? The posterior–anterior shift in aging. *Cerebral Cortex*, 18(5):1201–1209. <https://doi.org/10.1093/cercor/bhm155>
- Dawson, C. (2022). *ggprism: A 'ggplot2' extension inspired by 'GraphPad Prism'* [R package version 1.0.4]. The Comprehensive R Archive Network. <https://cran.r-project.org/package=ggprism>
- De Blasio, F. M. and Barry, R. J. (2018). Prestimulus delta and theta contributions to equiprobable Go/NoGo processing in healthy ageing. *International Journal of Psychophysiology*, 130:40–52. <https://doi.org/10.1016/j.ijpsycho.2018.05.005>
- de Schotten, M. T., Dell'Acqua, F., Forkel, S. J., Simmons, A., Vergani, F., Murphy, D. G. M., and Catani, M. (2011). A lateralized brain network for visuospatial attention. *Nature Neuroscience*, 14(10):1245–1246. <https://doi.org/10.1038/nn.2905>
- de Souza, A. C. S., Yehia, H. C., Sato, M.-a., and Callan, D. (2013). Brain activity underlying auditory perceptual learning during short period training: Simultaneous fMRI and EEG recording. *BMC Neuroscience*, 14:8. <https://doi.org/10.1186/1471-2202-14-8>
- de Villers-Sidani, E., Alzghoul, L., Zhou, X., Simpson, K. L., Lin, R. C. S., and Merzenich, M. M. (2010). Recovery of functional and structural age-related changes in the rat primary auditory cortex with operant training. *Proceedings of the National Academy of Sciences*, 107(31):13900–13905. <https://doi.org/10.1073/pnas.1007885107>

- Delhommeau, K., Micheyl, C., Jouvent, R., and Collet, L. (2002). Transfer of learning across durations and ears in auditory frequency discrimination. *Perception & Psychophysics*, 64(3):426–436. <https://doi.org/10.3758/BF03194715>
- Deng, Y., Choi, I., and Shinn-Cunningham, B. (2020). Topographic specificity of alpha power during auditory spatial attention. *NeuroImage*, 207:116360. <https://doi.org/10.1016/j.neuroimage.2019.116360>
- Deng, Y., Reinhart, R. M. G., Choi, I., and Shinn-Cunningham, B. G. (2019). Causal links between parietal alpha activity and spatial auditory attention. *eLife*, 8:e51184. <https://doi.org/10.7554/eLife.51184>
- Deoni, S. C. L., Burton, P., Beauchemin, J., Cano-Lorente, R., De Both, M. D., Johnson, M., Ryan, L., and Huentelman, M. J. (2023). Neuroimaging and verbal memory assessment in healthy aging adults using a portable low-field MRI scanner and a web-based platform: Results from a proof-of-concept population-based cross-section study. *Brain Structure and Function*, 228(2):493–509. <https://doi.org/10.1007/s00429-022-02595-7>
- Deoni, S. C. L., Medeiros, P., Deoni, A. T., Burton, P., Beauchemin, J., D'Sa, V., Boskamp, E., By, S., McNulty, C., Mileski, W., Welch, B. E., and Huentelman, M. (2022). Development of a mobile low-field MRI scanner. *Scientific Reports*, 12:5690. <https://doi.org/10.1038/s41598-022-09760-2>
- Dillon, C. F., Gu, Q., Hoffman, H. J., and Ko, C. W. (2010). *Vision, hearing, balance, and sensory impairment in Americans aged 70 years and over: United States, 1999-2006*. (DHHS Publication no. (PHS) 2010-1209). In *NCHS data brief*, Vol. 31. U.S. Department of Health & Human Services, Centers for Disease Control and Prevention, National Center for Health Statistics. <https://doi.org/https://www.cdc.gov/nchs/data/databriefs/db31.pdf>
- Dittinger, E., Scherer, J., Jäncke, L., Besson, M., and Elmer, S. (2019). Testing the influence of musical expertise on novel word learning across the lifespan using a cross-sectional approach in children, young adults and older adults. *Brain and Language*, 198:104678. <https://doi.org/10.1016/j.bandl.2019.104678>
- Doesburg, S. M., Green, J. J., McDonald, J. J., and Ward, L. M. (2012). Theta modulation of inter-regional gamma synchronization during auditory attention control. *Brain Research*, 1431:77–85. <https://doi.org/10.1016/j.brainres.2011.11.005>

- Dosher, B. and Lu, Z.-L. (2017). Visual perceptual learning and models. *Annual Review of Vision Science*, 3:343–363. <https://doi.org/10.1146/annurev-vision-102016-061249>
- Eckert, M. A., Cute, S. L., Vaden, K. I., Kuchinsky, S. E., and Dubno, J. R. (2012). Auditory cortex signs of age-related hearing loss. *Journal of the Association for Research in Otolaryngology*, 13(5):703–713. <https://doi.org/10.1007/s10162-012-0332-5>
- Eggermont, J. J. (2019). A primer on auditory evoked potentials and magnetic fields. In *The Auditory Brain and Age-Related Hearing Impairment* (pp. 255–268). Elsevier. <https://doi.org/10.1016/B978-0-12-815304-8.00021-9>
- Espinoza-Varas, B. and Jang, H. (2006). Aging impairs the ability to ignore irrelevant information in frequency discrimination tasks. *Experimental Aging Research*, 32(2):209–226. <https://doi.org/10.1080/03610730600554008>
- Fedorenko, E., Ivanova, A. A., and Regev, T. I. (2024). The language network as a natural kind within the broader landscape of the human brain. *Nature Reviews Neuroscience*, 25(5):289–312. <https://doi.org/10.1038/s41583-024-00802-4>
- Fehr, T., Wiechert, J., and Erhard, P. (2014). Variability in color-choice Stroop performance within and across EEG and MRI laboratory contexts. *Attention, Perception, & Psychophysics*, 76(8):2495–2507. <https://doi.org/10.3758/s13414-014-0745-9>
- Feindel, W. (1977). Wilder Penfield: His legacy to neurology. To praise an absent friend. *Canadian Medical Association journal*, 116(12):1365–7. <https://pmc.ncbi.nlm.nih.gov/articles/PMC1879308/>
- Ferguson, M., Maidment, D., Henshaw, H., and Heffernan, E. (2019). Evidence-based interventions for adult aural rehabilitation: That was then, this is now. *Seminars in Hearing*, 40(1):68–84. <https://doi.org/10.1055/s-0038-1676784>
- Ferguson, M. A. and Henshaw, H. (2015). Auditory training can improve working memory, attention, and communication in adverse conditions for adults with hearing loss. *Frontiers in Psychology*, 6:556. <https://doi.org/10.3389/fpsyg.2015.00556>
- Fernández-Rubio, G., Olsen, E. R., Klarlund, M., Mallon, O., Carlomagno, F., Vuust, P., Kringelbach, M. L., Brattico, E., and Bonetti, L. (2024). Investigating the impact of age on auditory short-term, long-term, and working memory. *Psychology of Music*, 52(2):187–198. <https://doi.org/10.1177/03057356231183404>

- Fischer, M. E., Cruickshanks, K. J., Schubert, C. R., Pinto, A. A., Carlsson, C. M., Klein, B. E. K., Klein, R., and Tweed, T. S. (2016). Age-related sensory impairments and risk of cognitive impairment. *Journal of the American Geriatrics Society*, 64(10):1981–1987. <https://doi.org/10.1111/jgs.14308>
- Fischer, M. H. F., Zibrandtsen, I. C., Høgh, P., and Musaeus, C. S. (2023). Systematic review of EEG coherence in Alzheimer's disease. *Journal of Alzheimer's Disease*, 91:1261–1272. <https://doi.org/10.3233/JAD-220508>
- Fischl, B., Salat, D. H., Busa, E., Albert, M., Dieterich, M., Haselgrove, C., van der Kouwe, A., Killiany, R., Kennedy, D., Klaveness, S., Montillo, A., Makris, N., Rosen, B., and Dale, A. M. (2002). Whole brain segmentation: Automated labeling of neuroanatomical structures in the human brain. *Neuron*, 33(3):341–355. [https://doi.org/10.1016/S0896-6273\(02\)00569-X](https://doi.org/10.1016/S0896-6273(02)00569-X)
- Fisher, M., Holland, C., Merzenich, M. M., and Vinogradov, S. (2009). Using neuroplasticity-based auditory training to improve verbal memory in schizophrenia. *American Journal of Psychiatry*, 166(7):805–811. <https://doi.org/10.1176/appi.ajp.2009.08050757>
- Fisher, M., Holland, C., Subramaniam, K., and Vinogradov, S. (2010). Neuroplasticity-based cognitive training in schizophrenia: An interim report on the effects 6 months later. *Schizophrenia Bulletin*, 36(4):869–879. <https://doi.org/10.1093/schbul/sbn170>
- Fisher, M., Loewy, R., Carter, C., Lee, A., Ragland, J. D., Niendam, T., Schlosser, D., Pham, L., Miskovich, T., and Vinogradov, S. (2015). Neuroplasticity-based auditory training via laptop computer improves cognition in young individuals with recent onset schizophrenia. *Schizophrenia Bulletin*, 41(1):250–258. <https://doi.org/10.1093/schbul/sbt232>
- Fitzgerald, M. B. and Wright, B. A. (2011). Perceptual learning and generalization resulting from training on an auditory amplitude-modulation detection task. *The Journal of the Acoustical Society of America*, 129(2):898–906. <https://doi.org/10.1121/1.3531841>
- Fitzhugh, M. C., Hemesath, A., Schaefer, S. Y., Baxter, L. C., and Rogalsky, C. (2019). Functional connectivity of Heschl's gyrus associated with age-related hearing loss: A resting-state fMRI study. *Frontiers in Psychology*, 10:2485. <https://doi.org/10.3389/fpsyg.2019.02485>

- Flegal, K. E., Ragland, J. D., and Ranganath, C. (2019). Adaptive task difficulty influences neural plasticity and transfer of training. *NeuroImage*, 188:111–121. <https://doi.org/10.1016/j.neuroimage.2018.12.003>
- Fonov, V., Evans, A. C., Botteron, K., Almli, C. R., McKinstry, R. C., and Collins, D. L. (2011). Unbiased average age-appropriate atlases for pediatric studies. *NeuroImage*, 54:313–327. <https://doi.org/10.1016/j.neuroimage.2010.07.033>
- Fonov, V. S., Evans, A. C., McKinstry, R. C., Almli, C. R., and Collins, D. L. (2009). Unbiased nonlinear average age-appropriate brain templates from birth to adulthood. *NeuroImage*, 47(Suppl. 1):S102. [https://doi.org/10.1016/S1053-8119\(09\)70884-5](https://doi.org/10.1016/S1053-8119(09)70884-5)
- Fontolan, L., Morillon, B., Liegeois-Chauvel, C., and Giraud, A.-L. (2014). The contribution of frequency-specific activity to hierarchical information processing in the human auditory cortex. *Nature Communications*, 5:4694. <https://doi.org/10.1038/ncomms5694>
- Fostick, L., Taitelbaum-Swead, R., Kreitler, S., Zokraut, S., and Billig, M. (2020). Auditory training to improve speech perception and self-efficacy in aging adults. *Journal of Speech, Language, and Hearing Research*, 63(4):1270–1281. https://doi.org/10.1044/2019_JSLHR-19-00355
- Foxe, J. J. and Snyder, A. C. (2011). The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Frontiers in Psychology*, 2:154. <https://doi.org/10.3389/fpsyg.2011.00154>
- Freedman, L., Zivan, M., Farah, R., and Horowitz-Kraus, T. (2020). Greater functional connectivity within the cingulo-opercular and ventral attention networks is related to better fluent reading: A resting-state functional connectivity study. *NeuroImage: Clinical*, 26:102214. <https://doi.org/10.1016/j.nicl.2020.102214>
- Freigang, C., Schmidt, L., Wagner, J., Eckardt, R., Steinhagen-Thiessen, E., Ernst, A., and Rübsamen, R. (2011). Evaluation of central auditory discrimination abilities in older adults. *Frontiers in Aging Neuroscience*, 3(6):1–11. <https://doi.org/10.3389/fnagi.2011.00006>
- Frey, J. N., Mainy, N., Lachaux, J.-P., Müller, N., Bertrand, O., and Weisz, N. (2014). Selective modulation of auditory cortical alpha activity in an audiovisual spatial attention task. *The Journal of Neuroscience*, 34(19):6634–6639. <https://doi.org/10.1523/JNEUROSCI.4813-13.2014>

- Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360:815–836. <https://doi.org/10.1098/rstb.2005.1622>
- Gates, G. A. and Hoffman, H. (2011). *What the numbers mean: An epidemiological perspective on hearing*. In *Statistics and Epidemiology*. National Institute on Deafness and Other Communication Disorders, National Institutes of Health. <https://www.nidcd.nih.gov/health/statistics/what-numbers-mean-epidemiological-perspective-hearing>
- Gates, G. A. and Mills, J. H. (2005). Presbycusis. *The Lancet*, 366:1111–1120. [https://doi.org/10.1016/S0140-6736\(05\)67423-5](https://doi.org/10.1016/S0140-6736(05)67423-5)
- Geerligs, L., Maurits, N. M., Renken, R. J., and Lorist, M. M. (2014). Reduced specificity of functional connectivity in the aging brain during task performance. *Human Brain Mapping*, 35:319–330. <https://doi.org/10.1002/hbm.22175>
- Gilbert, D. K. and Rogers, W. A. (1996). Age-related differences in perceptual learning. *Human Factors: The Journal of the Human Factors and Ergonomics Society*, 38(3):417–424. <https://doi.org/10.1518/001872096778701953>
- Glick, H. A. and Sharma, A. (2020). Cortical neuroplasticity and cognitive function in early-stage, mild-moderate hearing loss: Evidence of neurocognitive benefit from hearing aid use. *Frontiers in Neuroscience*, 14:93. <https://doi.org/10.3389/fnins.2020.00093>
- Goh, J. O. S. (2011). Functional dedifferentiation and altered connectivity in older adults: Neural accounts of cognitive aging. *Aging and disease*, 2(1):30–48. <https://pmc.ncbi.nlm.nih.gov/articles/PMC3066008/>
- Gourévitch, B., Martin, C., Postal, O., and Eggermont, J. J. (2020). Oscillations in the auditory system and their possible role. *Neuroscience & Biobehavioral Reviews*, 113:507–528. <https://doi.org/10.1016/j.neubiorev.2020.03.030>
- Gracia-Tabuenca, Z., Barbeau, E. B., Kousaie, S., Chen, J.-K., Chai, X., and Klein, D. (2024). Enhanced efficiency in the bilingual brain through the inter-hemispheric cortico-cerebellar pathway in early second language acquisition. *Communications Biology*, 7:1298. <https://doi.org/10.1038/s42003-024-06965-1>
- Grady, C. L., Maisog, J. M., Horwitz, B., Ungerleider, L. G., Mentis, M. J., Salerno, J. A., Pietrini, P., Wagner, E., and Haxby, J. V. (1994). Age-related changes in cortical

- blood flow activation during visual processing of faces and location. *The Journal of Neuroscience*, 14(3):1450–1462. <https://doi.org/10.1523/JNEUROSCI.14-03-01450.1994>
- Grassi, M., Meneghetti, C., Toffalini, E., and Borella, E. (2017). Auditory and cognitive performance in elderly musicians and nonmusicians. *PLoS ONE*, 12(11):e0187881. <https://doi.org/10.1371/journal.pone.0187881>
- Green, C. S. and Bavelier, D. (2008). Exercising your brain: A review of human brain plasticity and training-induced learning. *Psychology and Aging*, 23(4):692–701. <https://doi.org/10.1037/a0014345>
- Gresele, A. D. P., Garcia, M. V., Torres, E. M. O., Santos, S. N. d. S., and Costa, M. J. (2013). Bilingualism and auditory processing abilities: Performance of adults in dichotic listening tests. *CoDAS*, 25(6):506–512. <https://doi.org/10.1590/S2317-17822014000100003>
- Gross, J., Baillet, S., Barnes, G. R., Henson, R. N., Hillebrand, A., Jensen, O., Jerbi, K., Litvak, V., Maess, B., Oostenveld, R., Parkkonen, L., Taylor, J. R., van Wassenhove, V., Wibral, M., and Schoffelen, J.-M. (2013). Good practice for conducting and reporting MEG research. *NeuroImage*, 65:349–363. <https://doi.org/10.1016/j.neuroimage.2012.10.001>
- Guéguin, M., Le Bouquin-Jeannès, R., Faucon, G., Chauvel, P., and Liégeois-Chauvel, C. (2007). Evidence of functional connectivity between auditory cortical areas revealed by amplitude modulation sound processing. *Cerebral Cortex*, 17:304–313. <https://doi.org/10.1093/cercor/bhj148>
- Gutschalk, A. (2014). MEG auditory research. In S. Supek and C. J. Aine (Eds.), *Magnetoencephalography: From Signals to Dynamic Cortical Networks* (pp. 679–711). Springer International Publishing (1st ed.). https://doi.org/10.1007/978-3-642-33045-2_32
- Gutschalk, A. (2019). MEG auditory research. In S. Supek and C. J. Aine (Eds.), *Magnetoencephalography: From Signals to Dynamic Cortical Networks* (pp. 907–941). Springer International Publishing (2nd ed.). https://doi.org/10.1007/978-3-030-00087-5_32
- Hahn, A., Reed, M. B., Vraga, C., Godbersen, G. M., Klug, S., Komorowski, A., Falb, P., Nics, L., Traub-Weidinger, T., Hacker, M., and Lanzenberger, R. (2023). High-temporal

- resolution functional PET/MRI reveals coupling between human metabolic and hemodynamic brain response. *European Journal of Nuclear Medicine and Molecular Imaging*, 51:1310–1322. <https://doi.org/10.1007/s00259-023-06542-4>
- Hall, E. L., Robson, S. E., Morris, P. G., and Brookes, M. J. (2014). The relationship between MEG and fMRI. *NeuroImage*, 102:80–91. <https://doi.org/10.1016/j.neuroimage.2013.11.005>
- Harada, C. N., Natelson Love, M. C., and Triebel, K. L. (2013). Normal cognitive aging. *Clinics in Geriatric Medicine*, 29:737–752. <https://doi.org/10.1016/j.cger.2013.07.002>
- Hari, R. and Puce, A. (2023). *MEG–EEG Primer* (2nd ed.). Oxford University Press. <https://doi.org/10.1093/med/9780197542187.001.0001>
- Harris, A. M., Dux, P. E., Jones, C. N., and Mattingley, J. B. (2017). Distinct roles of theta and alpha oscillations in the involuntary capture of goal-directed attention. *NeuroImage*, 152:171–183. <https://doi.org/10.1016/j.neuroimage.2017.03.008>
- Hedden, T. and Gabrieli, J. D. E. (2004). Insights into the ageing mind: A view from cognitive neuroscience. *Nature Reviews Neuroscience*, 5(2):87–96. <https://doi.org/10.1038/nrn1323>
- Hedrich, T., Pellegrino, G., Kobayashi, E., Lina, J. M., and Grova, C. (2017). Comparison of the spatial resolution of source imaging techniques in high-density EEG and MEG. *NeuroImage*, 157:531–544. <https://doi.org/10.1016/j.neuroimage.2017.06.022>
- Heidari, A., Moossavi, A., Yadegari, F., Bakhshi, E., and Ahadi, M. (2020). Effect of vowel auditory training on the speech-in-noise perception among older adults with normal hearing. *Iranian Journal of Otorhinolaryngology*, 32(4, Serial No. 111):229–236. <https://doi.org/10.22038/ijorl.2019.33433.2110>
- Helfrich, R. F. and Knight, R. T. (2019). Cognitive neurophysiology: Event-related potentials. In K. H. Levin and P. Chauvel (Eds.), *Clinical Neurophysiology: Basis and Technical Aspects*, Vol. 160(S.III) of *Handbook of Clinical Neurology* (Chapter 36, pp. 543–558). Elsevier. <https://doi.org/10.1016/B978-0-444-64032-1.00036-9>
- Henderson, D., Bichoutar, I., Moxham, B., Faidherbe, V., Plaisant, O., and Guédon, A. (2023). Descriptive and functional anatomy of the Heschl gyrus: Historical review, manual labelling and current perspectives. *Surgical and Radiologic Anatomy*, 45:337–350. <https://doi.org/10.1007/s00276-023-03114-x>

- Herrmann, B., Maess, B., Henry, M. J., Obleser, J., and Johnsrude, I. S. (2023). Neural signatures of task-related fluctuations in auditory attention and age-related changes. *NeuroImage*, 268:119883. <https://doi.org/10.1016/j.neuroimage.2023.119883>
- Holman, C. and de Villers-Sidani, E. (2014). Indestructible plastic: the neuroscience of the new aging brain. *Frontiers in Human Neuroscience*, 8:219. <https://doi.org/10.3389/fnhum.2014.00219>
- Hommel, B., Chapman, C. S., Cisek, P., Neyedli, H. F., Song, J.-H., and Welsh, T. N. (2019). No one knows what attention is. *Attention, Perception, & Psychophysics*, 81:2288–2303. <https://doi.org/10.3758/s13414-019-01846-w>
- Hsiao, F.-J., Chen, W.-T., Wang, P.-N., Cheng, C.-H., and Lin, Y.-Y. (2014). Temporo-frontal functional connectivity during auditory change detection is altered in Alzheimer's disease. *Human Brain Mapping*, 35:5565–5577. <https://doi.org/10.1002/hbm.22570>
- Hsiao, F.-J., Cheng, C.-H., Liao, K.-K., and Lin, Y.-Y. (2010). Cortico-cortical phase synchrony in auditory mismatch processing. *Biological Psychology*, 84:336–345. <https://doi.org/10.1016/j.biopsycho.2010.03.019>
- Hsiao, F.-J., Wu, Z.-A., Ho, L.-T., and Lin, Y.-Y. (2009). Theta oscillation during auditory change detection: An MEG study. *Biological Psychology*, 81:58–66. <https://doi.org/10.1016/j.biopsycho.2009.01.007>
- Hsu, Y.-F., Waszak, F., Strömmer, J., and Hämäläinen, J. A. (2021). Human brain ages with hierarchy-selective attenuation of prediction errors. *Cerebral Cortex*, 31(4):2156–2168. <https://doi.org/10.1093/cercor/bhaa352>
- Iemi, L., Chaumon, M., Crouzet, S. M., and Busch, N. A. (2017). Spontaneous neural oscillations bias perception by modulating baseline excitability. *The Journal of Neuroscience*, 37(4):807–819. <https://doi.org/10.1523/JNEUROSCI.1432-16.2016>
- Irvine, D. R. F. (2018). Auditory perceptual learning and changes in the conceptualization of auditory cortex. *Hearing Research*, 366:3–16. <https://doi.org/10.1016/j.heares.2018.03.011>
- Jääskeläinen, I. P. and Ahveninen, J. (2014). Auditory-cortex short-term plasticity induced by selective attention. *Neural Plasticity*, 2014(216731):1–11. <https://doi.org/10.1155/2014/216731>

- Jamadar, S. D. (2020). The CRUNCH model does not account for load-dependent changes in visuospatial working memory in older adults. *Neuropsychologia*, 142:107446. <https://doi.org/10.1016/j.neuropsychologia.2020.107446>
- James, W. (1890). Attention. In *The principles of psychology*, Vol. I (Chapter XI, pp. 402–458). Classics in the History of Psychology, internet resource by C. D. Green. <https://psychclassics.yorku.ca/James/Principles/prin11.htm>
- Jäncke, L., Mirzazade, S., and Joni Shah, N. (1999). Attention modulates activity in the primary and the secondary auditory cortex: A functional magnetic resonance imaging study in human subjects. *Neuroscience Letters*, 266:125–128. [https://doi.org/10.1016/S0304-3940\(99\)00288-8](https://doi.org/10.1016/S0304-3940(99)00288-8)
- Jenkins, J., III, Idsardi, W. J., and Poeppel, D. (2010). The analysis of simple and complex auditory signals in human auditory cortex: Magnetoencephalographic evidence from M100 modulation. *Ear & Hearing*, 31(4):515–526. <https://doi.org/10.1097/AUD.0b013e3181d99a75>
- Jensen, O., Spaak, E., and Zumer, J. M. (2014). Human brain oscillations: From physiological mechanisms to analysis and cognition. In S. Supek and C. J. Aine (Eds.), *Magnetoencephalography: From Signals to Dynamic Cortical Networks* (pp. 359–403). Springer Berlin Heidelberg (1st ed.). https://doi.org/10.1007/978-3-642-33045-2_17
- Jenstad, L. and Moon, J. (2011). Systematic review of barriers and facilitators to hearing aid uptake in older adults. *Audiology Research*, 1:e25. <https://doi.org/10.4081/audiores.2011.e25>
- Jimura, K. and Braver, T. S. (2010). Age-related shifts in brain activity dynamics during task switching. *Cerebral Cortex*, 20(6):1420–1431. <https://doi.org/10.1093/cercor/bhp206>
- Joos, K., Gilles, A., Van de Heyning, P., De Ridder, D., and Vanneste, S. (2014). From sensation to percept: The neural signature of auditory event-related potentials. *Neuroscience & Biobehavioral Reviews*, 42:148–156. <https://doi.org/10.1016/j.neubiorev.2014.02.009>
- Kang, W., Wang, J., and Malvaso, A. (2022). Inhibitory control in aging: The compensation-related utilization of neural circuits hypothesis. *Frontiers in Aging Neuroscience*, 13:771885. <https://doi.org/10.3389/fnagi.2021.771885>

- Karawani, H., Bitan, T., Attias, J., and Banai, K. (2016). Auditory perceptual learning in adults with and without age-related hearing loss. *Frontiers in Psychology*, 6. <https://doi.org/10.3389/fpsyg.2015.02066>
- Kasten, F. H., Busson, Q., and Zoefel, B. (2024). Opposing neural processing modes alternate rhythmically during sustained auditory attention. *Communications Biology*, 7:1125. <https://doi.org/10.1038/s42003-024-06834-x>
- Katsuki, F. and Constantinidis, C. (2014). Bottom-up and top-down attention: Different processes and overlapping neural systems. *The Neuroscientist*, 20(5):509–521. <https://doi.org/10.1177/1073858413514136>
- Kattner, F., Cochrane, A., Cox, C. R., Gorman, T. E., and Green, C. S. (2017). Perceptual learning generalization from sequential perceptual training as a change in learning rate. *Current Biology*, 27:840–846. <https://doi.org/10.1016/j.cub.2017.01.046>
- Keay, D. G. and Murray, J. A. M. (1988). Hearing loss in the elderly: A 17-year longitudinal study. *Clinical Otolaryngology*, 13:31–35. <https://doi.org/10.1111/j.1365-2273.1988.tb00278.x>
- Keller, A. S., Payne, L., and Sekuler, R. (2017). Characterizing the roles of alpha and theta oscillations in multisensory attention. *Neuropsychologia*, 99:48–63. <https://doi.org/10.1016/j.neuropsychologia.2017.02.021>
- Key, A. P. F., Dove, G. O., and Maguire, M. J. (2005). Linking brainwaves to the brain: An ERP primer. *Developmental Neuropsychology*, 27(2):183–215. https://doi.org/10.1207/s15326942dn2702_1
- Khalil, M. (2018). *Primary and secondary auditory cortex* (Living reference work. Accessed: March, 2025). In T. K. Shackelford and V. A. Weekes-Shackelford (Eds.), *Encyclopedia of Evolutionary Psychological Science*. Springer International Publishing. https://doi.org/10.1007/978-3-319-16999-6_996-1
- Kim, H. (2014). Involvement of the dorsal and ventral attention networks in oddball stimulus processing: A meta-analysis. *Human Brain Mapping*, 35:2265–2284. <https://doi.org/10.1002/hbm.22326>
- Kishon-Rabin, L., Avivi-Reich, M., and Ari-Even Roth, D. (2013). Improved gap detection thresholds following auditory training: Evidence of auditory plasticity in older adults. *American Journal of Audiology*, 22:343–346. [https://doi.org/10.1044/1059-0889\(2013/12-0084\)](https://doi.org/10.1044/1059-0889(2013/12-0084))

- Klamer, S., Elshahabi, A., Lerche, H., Braun, C., Erb, M., Scheffler, K., and Focke, N. K. (2015). Differences between MEG and high-density EEG source localizations using a distributed source model in comparison to fMRI. *Brain Topography*, 28:87–94. <https://doi.org/10.1007/s10548-014-0405-3>
- Klein, D., Mok, K., Chen, J.-K., and Watkins, K. E. (2014). Age of language learning shapes brain structure: A cortical thickness study of bilingual and monolingual individuals. *Brain and Language*, 131:20–24. <https://doi.org/10.1016/j.bandl.2013.05.014>
- Klein, D., Zatorre, R. J., Milner, B., and Zhao, V. (2001). A cross-linguistic PET study of tone perception in Mandarin Chinese and English speakers. *NeuroImage*, 13(4):646–653. <https://doi.org/10.1006/nimg.2000.0738>
- Koen, J. D. and Rugg, M. D. (2019). Neural dedifferentiation in the aging brain. *Trends in Cognitive Sciences*, 23(7):547–559. <https://doi.org/10.1016/j.tics.2019.04.012>
- Kramer, A. F. and Madden, D. J. (2008). Attention. In F. I. M. Craik and T. A. Salthouse (Eds.), *The Handbook of Aging and Cognition* (Chapter 5, pp. 189–250). Psychology Press (3rd ed.). <https://doi.org/10.4324/9780203837665>
- Krauzlis, R. J., Wang, L., Yu, G., and Katz, L. N. (2023). What is attention? *WIREs Cognitive Science*, 14:e1570. <https://doi.org/10.1002/wcs.1570>
- Krumbholz, K., Nobis, E. A., Weatheritt, R. J., and Fink, G. R. (2009). Executive control of spatial attention shifts in the auditory compared to the visual modality. *Human Brain Mapping*, 30:1457–1469. <https://doi.org/10.1002/hbm.20615>
- Kubetschek, C. and Kayser, C. (2021). Delta/Theta band EEG activity shapes the rhythmic perceptual sampling of auditory scenes. *Scientific Reports*, 11:2370. <https://doi.org/10.1038/s41598-021-82008-7>
- Kuchibhotla, K. and Bathellier, B. (2018). Neural encoding of sensory and behavioral complexity in the auditory cortex. *Current Opinion in Neurobiology*, 52:65–71. <https://doi.org/10.1016/j.conb.2018.04.002>
- Kyu, H. H., Abate, D., Abate, K. H., Abay, S. M., Abbafati, C., Abbasi, N., Abbastabar, H., Abd-Allah, F., Abdela, J., Abdelalim, A., Abdollahpour, I., Abdulkader, R. S., Abebe, M., Abebe, Z., Abil, O. Z., Aboyans, V., Abrham, A. R., Abu-Raddad, L. J., Abu-Rmeileh, N. M. E., Accrombessi, M. M. K., ... Murray, C. J. L. (2018). Global, regional, and national disability-adjusted life-years (DALYs) for 359 diseases and injuries and

- healthy life expectancy (HALE) for 195 countries and territories, 1990–2017: A systematic analysis for the Global Burden of Disease Study 2017. *The Lancet*, 392(10159):1859–1922. [https://doi.org/10.1016/S0140-6736\(18\)32335-3](https://doi.org/10.1016/S0140-6736(18)32335-3)
- Ladouce, S., Donaldson, D. I., Dudchenko, P. A., and Ietswaart, M. (2017). Understanding minds in real-world environments: Toward a mobile cognition approach. *Frontiers in Human Neuroscience*, 10:694. <https://doi.org/10.3389/fnhum.2016.00694>
- Laufs, H., Holt, J. L., Elfont, R., Krams, M., Paul, J. S., Krakow, K., and Kleinschmidt, A. (2006). Where the BOLD signal goes when alpha EEG leaves. *NeuroImage*, 31:1408–1418. <https://doi.org/10.1016/j.neuroimage.2006.02.002>
- Learmonth, G., Benwell, C. S. Y., Thut, G., and Harvey, M. (2017). Age-related reduction of hemispheric lateralisation for spatial attention: An EEG study. *NeuroImage*, 153:139–151. <https://doi.org/10.1016/j.neuroimage.2017.03.050>
- Lentz, J. J., Humes, L. E., and Kidd, G. R. (2022). Differences in auditory perception between young and older adults when controlling for differences in hearing loss and cognition. *Trends in Hearing*, 26:1–17. <https://doi.org/10.1177/23312165211066180>
- Livingston, G., Huntley, J., Liu, K. Y., Costafreda, S. G., Selbæk, G., Alladi, S., Ames, D., Banerjee, S., Burns, A., Brayne, C., Fox, N. C., Ferri, C. P., Gitlin, L. N., Howard, R., Kales, H. C., Kivimäki, M., Larson, E. B., Nakasujja, N., Rockwood, K., Samus, Q., ... Mukadam, N. (2024). Dementia prevention, intervention, and care: 2024 report of the Lancet standing Commission. *The Lancet*, 404(10452):572–628. [https://doi.org/10.1016/S0140-6736\(24\)01296-0](https://doi.org/10.1016/S0140-6736(24)01296-0)
- Livingston, G., Huntley, J., Sommerlad, A., Ames, D., Ballard, C., Banerjee, S., Brayne, C., Burns, A., Cohen-Mansfield, J., Cooper, C., Costafreda, S. G., Dias, A., Fox, N., Gitlin, L. N., Howard, R., Kales, H. C., Kivimäki, M., Larson, E. B., Ogunniyi, A., Orgeta, V., ... Mukadam, N. (2020). Dementia prevention, intervention, and care: 2020 report of the Lancet Commission. *The Lancet*, 396(10248):413–446. [https://doi.org/10.1016/S0140-6736\(20\)30367-6](https://doi.org/10.1016/S0140-6736(20)30367-6)
- Livingston, G., Sommerlad, A., Orgeta, V., Costafreda, S. G., Huntley, J., Ames, D., Ballard, C., Banerjee, S., Burns, A., Cohen-Mansfield, J., Cooper, C., Fox, N., Gitlin, L. N., Howard, R., Kales, H. C., Larson, E. B., Ritchie, K., Rockwood, K., Sampson, E. L., Samus, Q., ... Mukadam, N. (2017). Dementia prevention, intervention, and care. *The Lancet*, 390(10113):2673–2734. [https://doi.org/10.1016/S0140-6736\(17\)31363-6](https://doi.org/10.1016/S0140-6736(17)31363-6)

- Loewy, R., Fisher, M., Ma, S., Carter, C., Ragland, J. D., Niendam, T. A., Stuart, B., Schlosser, D., Amirfathi, F., Yohannes, S., and Vinogradov, S. (2022). Durable cognitive gains and symptom improvement are observed in individuals with recent-onset schizophrenia 6 months after a randomized trial of auditory training completed remotely. *Schizophrenia Bulletin*, 48(1):262–272. <https://doi.org/10.1093/schbul/sbab102>
- Lopes da Silva, F. (2013). EEG and MEG: Relevance to neuroscience. *Neuron*, 80:1112–1128. <https://doi.org/10.1016/j.neuron.2013.10.017>
- López-Caballero, F., Coffman, B. A., Curtis, M., Sklar, A. L., Yi, S., and Salisbury, D. F. (2025). Auditory sensory processing measures using EEG and MEG predict symptom recovery in first-episode psychosis with a single-tone paradigm. *NeuroImage: Clinical*, 45:103730. <https://doi.org/10.1016/j.nicl.2024.103730>
- López-Madrona, V. J., Trébuchon, A., Bénar, C. G., Schön, D., and Morillon, B. (2024). Different sustained and induced alpha oscillations emerge in the human auditory cortex during sound processing. *Communications Biology*, 7:1570. <https://doi.org/10.1038/s42003-024-07297-w>
- Lüdecke, D., Ben-Shachar, M. S., Patil, I., Wiernik, B. M., Bacher, E., Thériault, R., and Makowski, D. (2022). *easystats: Framework for easy statistical modeling, visualization, and reporting* [R package version 0.7.0]. The Comprehensive R Archive Network. <https://easystats.github.io/easystats/>
- Luo, D., Ganesh, S., and Koolaard, J. (2022). *predictmeans: Predicted means for linear and semi parametric models* [R package version 1.0.8]. The Comprehensive R Archive Network. <https://cran.r-project.org/package=predictmeans>
- Lustig, C., Shah, P., Seidler, R., and Reuter-Lorenz, P. A. (2009). Aging, training, and the brain: A review and future directions. *Neuropsychology Review*, 19(4):504–522. <https://doi.org/10.1007/s11065-009-9119-9>
- Maffei, C., Soria, G., Prats-Galino, A., and Catani, M. (2015). Imaging white-matter pathways of the auditory system with diffusion imaging tractography. In G. G. Celesia and G. Hickok (Eds.), *The human auditory system: Fundamental organization and clinical disorders*, Vol. 129(S.III) of *Handbook of Clinical Neurology* (Chapter 16, pp. 277–288). Elsevier. <https://doi.org/10.1016/B978-0-444-62630-1.00016-0>

- Maharani, A., Dawes, P., Nazroo, J., Tampubolon, G., and Pendleton, N. (2018). Longitudinal relationship between hearing aid use and cognitive function in older Americans. *Journal of the American Geriatrics Society*, 66(6):1130–1136. <https://doi.org/10.1111/jgs.15363>
- Mahncke, H. W., Connor, B. B., Appelman, J., Ahsanuddin, O. N., Hardy, J. L., Wood, R. A., Joyce, N. M., Boniske, T., Atkins, S. M., and Merzenich, M. M. (2006). Memory enhancement in healthy older adults using a brain plasticity-based training program: A randomized, controlled study. *Proceedings of the National Academy of Sciences*, 103(33):12523–12528. <https://doi.org/10.1073/pnas.0605194103>
- Mai, G., Minett, J. W., and Wang, W. S. Y. (2016). Delta, theta, beta, and gamma brain oscillations index levels of auditory sentence processing. *NeuroImage*, 133:516–528. <https://doi.org/10.1016/j.neuroimage.2016.02.064>
- Majdan, A., Sziklas, V., and Jones-Gotman, M. (1996). Performance of healthy subjects and patients with resection from the anterior temporal lobe on matched tests of verbal and visuo-perceptual learning. *Journal of Clinical and Experimental Neuropsychology*, 18(3):416–430. <https://doi.org/10.1080/01688639608408998>
- Malekpour, S., Gubner, J. A., and Sethares, W. A. (2018). Measures of generalized magnitude-squared coherence: Differences and similarities. *Journal of the Franklin Institute*, 355(5):2932–2950. <https://doi.org/10.1016/j.jfranklin.2018.01.014>
- Mamashli, F., Huang, S., Khan, S., Hämäläinen, M. S., Ahlfors, S. P., and Ahveninen, J. (2020). Distinct regional oscillatory connectivity patterns during auditory target and novelty processing. *Brain Topography*, 33:477–488. <https://doi.org/10.1007/s10548-020-00776-3>
- Manrique-Huarte, R., Calavia, D., Huarte Irujo, A., Girón, L., and Manrique-Rodríguez, M. (2016). Treatment for hearing loss among the elderly: Auditory outcomes and impact on quality of life. *Audiology and Neurotology*, 21(Suppl. 1):29–35. <https://doi.org/10.1159/000448352>
- Martin, J. S. and Jerger, J. F. (2005). Some effects of aging on central auditory processing. *The Journal of Rehabilitation Research and Development*, 42(4 Suppl. 2):25–44. <https://doi.org/10.1682/jrrd.2004.12.0164>
- Martins, R., Joannette, Y., and Monchi, O. (2015). The implications of age-related neurofunctional compensatory mechanisms in executive function and language

- processing including the new Temporal Hypothesis for Compensation. *Frontiers in Human Neuroscience*, 9:221. <https://doi.org/10.3389/fnhum.2015.00221>
- Martins, R., Simard, F., Provost, J.-S., and Monchi, O. (2012). Changes in regional and temporal patterns of activity associated with aging during the performance of a lexical set-shifting task. *Cerebral Cortex*, 22(6):1395–1406. <https://doi.org/10.1093/cercor/bhr222>
- Maruta, M., Tabira, T., Sagari, A., Miyata, H., Yoshimitsu, K., Han, G., Yoshiura, K., Matsuo, T., and Kawagoe, M. (2020). Impact of sensory impairments on dementia incidence and symptoms among Japanese older adults. *Psychogeriatrics*, 20:262–270. <https://doi.org/10.1111/psyg.12494>
- Matsubara, T., Peled, N., Ahlfors, S. P., Sundaram, P., Okada, Y., Hämäläinen, M., and Stufflebeam, S. M. (2022). *Distance between scalp and SQUID sensors in clinical practice* (AES 2022 conference submission 2204588. Abstract no. 2.029). American Epilepsy Society. <https://aesnet.org/abstractslisting/distance-between-scalp-and-squid-sensors-in-clinical-practice>
- Matsushita, R., Puschmann, S., Baillet, S., and Zatorre, R. J. (2021). Inhibitory effect of tDCS on auditory evoked response: Simultaneous MEG-tDCS reveals causal role of right auditory cortex in pitch learning. *NeuroImage*, 233:117915. <https://doi.org/10.1016/j.neuroimage.2021.117915>
- McCarthy, P., Benuskova, L., and Franz, E. A. (2014). The age-related posterior–anterior shift as revealed by voxelwise analysis of functional brain networks. *Frontiers in Aging Neuroscience*, 6:301. <https://doi.org/10.3389/fnagi.2014.00301>
- McKee, M. M., Choi, H., Wilson, S., DeJonckheere, M. J., Zazove, P., and Levy, H. (2019). Determinants of hearing aid use among older americans with hearing loss. *The Gerontologist*, 59(6):1171–1181. <https://doi.org/10.1093/geront/gny051>
- McNair, S. W., Kayser, S. J., and Kayser, C. (2019). Consistent pre-stimulus influences on auditory perception across the lifespan. *NeuroImage*, 186:22–32. <https://doi.org/10.1016/j.neuroimage.2018.10.085>
- Mellor, S., Tierney, T. M., Seymour, R. A., Timms, R. C., O'Neill, G. C., Alexander, N., Spedden, M. E., Payne, H., and Barnes, G. R. (2023). Real-time, model-based magnetic field correction for moving, wearable MEG. *NeuroImage*, 278:120252. <https://doi.org/10.1016/j.neuroimage.2023.120252>

- Mengotti, P., Käsbauer, A.-S., Fink, G. R., and Vossel, S. (2020). Lateralization, functional specialization, and dysfunction of attentional networks. *Cortex*, 132:206–222. <https://doi.org/10.1016/j.cortex.2020.08.022>
- Menning, H., Roberts, L. E., and Pantev, C. (2000). Plastic changes in the auditory cortex induced by intensive frequency discrimination training. *NeuroReport*, 11(4):817–822. <https://doi.org/10.1097/00001756-200003200-00032>
- Mercier, M. R., Dubarry, A.-S., Tadel, F., Avanzini, P., Axmacher, N., Cellier, D., Vecchio, M. D., Hamilton, L. S., Hermes, D., Kahana, M. J., Knight, R. T., Llorens, A., Megevand, P., Melloni, L., Miller, K. J., Piai, V., Puce, A., Ramsey, N. F., Schwiedrzik, C. M., Smith, S. E., ... Oostenveld, R. (2022). Advances in human intracranial electroencephalography research, guidelines and good practices. *NeuroImage*, 260:119438. <https://doi.org/10.1016/j.neuroimage.2022.119438>
- Meyer, M., Lamers, D., Kayhan, E., Hunnius, S., and Oostenveld, R. (2021). Enhancing reproducibility in developmental EEG research: BIDS, cluster-based permutation tests, and effect sizes. *Developmental Cognitive Neuroscience*, 52:101036. <https://doi.org/10.1016/j.dcn.2021.101036>
- Mick, P. T., Hämmäläinen, A., Kolisang, L., Pichora-Fuller, M. K., Phillips, N., Guthrie, D., and Wittich, W. (2021). The prevalence of hearing, vision, and dual sensory loss in older Canadians: An analysis of data from the Canadian Longitudinal Study on Aging. *Canadian Journal on Aging / La Revue canadienne du vieillissement*, 40(1):1–22. <https://doi.org/10.1017/S0714980820000070>
- Minati, L. (2006). Neuroimaging techniques: A conceptual overview of physical principles, contribution and history. In D. M. Dubois (Ed.), *AIP Conference Proceedings*, Vol. 839, pp. 503–519. <https://doi.org/10.1063/1.2216661>
- Mishra, J., de Villers-Sidani, E., Merzenich, M., and Gazzaley, A. (2014). Adaptive training diminishes distractibility in aging across species. *Neuron*, 84(5):1091–1103. <https://doi.org/10.1016/j.neuron.2014.12.005>
- Mishra, J. and Gazzaley, A. (2013). Preserved discrimination performance and neural processing during crossmodal attention in aging. *PLoS ONE*, 8(11):e81894. <https://doi.org/10.1371/journal.pone.0081894>
- Mishra, J., Rolle, C., and Gazzaley, A. (2015). Neural plasticity underlying visual perceptual learning in aging. *Brain Research*, 1612:140–151. <https://doi.org/10.1016/J.BRAINRES.2014.09.009>

- Moezzi, B., Pratti, L. M., Hordacre, B., Graetz, L., Berryman, C., Lavrencic, L. M., Ridding, M. C., Keage, H. A. D., McDonnell, M. D., and Goldsworthy, M. R. (2019). Characterization of young and old adult brains: An EEG functional connectivity analysis. *Neuroscience*, 422:230–239. <https://doi.org/10.1016/j.neuroscience.2019.08.038>
- Moore, B. C. J., Mariathasan, S., and Søk, A. P. (2019). Effects of age and hearing loss on the discrimination of amplitude and frequency modulation for 2- and 10-Hz rates. *Trends in Hearing*, 23:1–12. <https://doi.org/10.1177/2331216519853963>
- Moore, B. C. J. and Peters, R. W. (1992). Pitch discrimination and phase sensitivity in young and elderly subjects and its relationship to frequency selectivity. *The Journal of the Acoustical Society of America*, 91(5):2881–2893. <https://doi.org/10.1121/1.402925>
- Moradi, E., Hallikainen, I., Hänninen, T., Tohka, J., and Alzheimer's Disease Neuroimaging Initiative (2017). Rey's Auditory Verbal Learning Test scores can be predicted from whole brain MRI in Alzheimer's disease. *NeuroImage: Clinical*, 13:415–427. <https://doi.org/10.1016/j.nicl.2016.12.011>
- Morcom, A. M. and Henson, R. N. A. (2018). Increased prefrontal activity with aging reflects nonspecific neural responses rather than compensation. *The Journal of Neuroscience*, 38(33):7303–7313. <https://doi.org/10.1523/JNEUROSCI.1701-17.2018>
- Motlagh Zadeh, L., Jalilvand Karimi, L., and Silbert, N. H. (2018). Bilingualism leads to greater auditory capacity. *International Journal of Audiology*, 57(11):831–837. <https://doi.org/10.1080/14992027.2018.1516896>
- Müller, N. and Weisz, N. (2012). Lateralized auditory cortical alpha band activity and interregional connectivity pattern reflect anticipation of target sounds. *Cerebral Cortex*, 22(7):1604–1613. <https://doi.org/10.1093/cercor/bhr232>
- Müller, V., Gruber, W., Klimesch, W., and Lindenberger, U. (2009). Lifespan differences in cortical dynamics of auditory perception. *Developmental Science*, 12(6):839–853. <https://doi.org/10.1111/j.1467-7687.2009.00834.x>
- Murakami, S. and Okada, Y. (2006). Contributions of principal neocortical neurons to magnetoencephalography and electroencephalography signals. *The Journal of Physiology*, 575(3):925–936. <https://doi.org/10.1113/jphysiol.2006.105379>

- Murman, D. (2015). The impact of age on cognition. *Seminars in Hearing*, 36(3):111–121. <https://doi.org/10.1055/s-0035-1555115>
- Myrum, C. (2019). Is PASA passé?: Rethinking compensatory mechanisms in cognitive aging. *The Journal of Neuroscience*, 39(5):786–787. <https://doi.org/10.1523/JNEUROSCI.2348-18.2018>
- Nagel, S. and Spüler, M. (2019). Asynchronous non-invasive high-speed BCI speller with robust non-control state detection. *Scientific Reports*, 9:8269. <https://doi.org/10.1038/s41598-019-44645-x>
- Nahum, M., Nelken, I., and Ahissar, M. (2008). Low-level information and high-level perception: The case of speech in noise. *PLoS Biology*, 6(5):e126. <https://doi.org/10.1371/journal.pbio.0060126>
- Nguyen, L. T., Marini, F., Shende, S. A., Llano, D. A., and Mudar, R. A. (2020). Investigating EEG theta and alpha oscillations as measures of value-directed strategic processing in cognitively normal younger and older adults. *Behavioural Brain Research*, 391:112702. <https://doi.org/10.1016/j.bbr.2020.112702>
- NIDCD (2023). *Age-related hearing loss (presbycusis)* (NIDCD Fact sheet no. 23-DC-4235). National Institute on Deafness and Other Communication Disorders, National Institutes of Health. <https://www.nidcd.nih.gov/health/age-related-hearing-loss>
- Nkyekyer, J., Meyer, D., Pipingas, A., and Reed, N. (2019). The cognitive and psychosocial effects of auditory training and hearing aids in adults with hearing loss. *Clinical Interventions in Aging*, 14:123–135. <https://doi.org/10.2147/CIA.S183905>
- Obleser, J., Wöstmann, M., Hellbernd, N., Wilsch, A., and Maess, B. (2012). Adverse listening conditions and memory load drive a common alpha oscillatory network. *The Journal of Neuroscience*, 32(36):12376–12383. <https://doi.org/10.1523/JNEUROSCI.4908-11.2012>
- O'Brien, J. L., Lister, J. J., Fausto, B. A., Clifton, G. K., and Edwards, J. D. (2017). Cognitive training enhances auditory attention efficiency in older adults. *Frontiers in Aging Neuroscience*, 9:322. <https://doi.org/10.3389/fnagi.2017.00322>
- Olusanya, B. O., Davis, A. C., and Hoffman, H. J. (2019). Hearing loss grades and the International classification of functioning, disability and health. *Bulletin of the World Health Organization*, 97(10):725–728. <https://doi.org/10.2471/BLT.19.230367>

- Onoda, K., Ishihara, M., and Yamaguchi, S. (2012). Decreased functional connectivity by aging is associated with cognitive decline. *Journal of Cognitive Neuroscience*, 24(11):2186–2198. https://doi.org/10.1162/jocn_a_00269
- Oostenveld, R., Fries, P., Maris, E., and Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 2011(1):1–9. <https://doi.org/10.1155/2011/156869>
- OpenAI (2025). *ChatGPT* [Large language model]. <https://chat.openai.com/chat>
- Ostrowski, J. and Rose, M. (2024). Increases in pre-stimulus theta and alpha oscillations precede successful encoding of crossmodal associations. *Scientific Reports*, 14:7895. <https://doi.org/10.1038/s41598-024-58227-z>
- Ouda, L., Profant, O., and Syka, J. (2015). Age-related changes in the central auditory system. *Cell and Tissue Research*, 361(1):337–358. <https://doi.org/10.1007/s00441-014-2107-2>
- Paraskevoudi, N., Balci, F., and Vatakis, A. (2018). “Walking” through the sensory, cognitive, and temporal degradations of healthy aging. *Annals of the New York Academy of Sciences*, 1426:72–92. <https://doi.org/10.1111/nyas.13734>
- Park, D. C. and Reuter-Lorenz, P. (2009). The adaptive brain: Aging and neurocognitive scaffolding. *Annual Review of Psychology*, 60:173–196. <https://doi.org/10.1146/annurev.psych.59.103006.093656>
- Parker, A., Slack, C., and Skoe, E. (2020). Comparisons of auditory brainstem responses between a laboratory and simulated home environment. *Journal of Speech, Language, and Hearing Research*, 63(11):3877–3892. https://doi.org/10.1044/2020_JSLHR-20-00383
- Parviainen, T. and Kujala, J. (2023). Event-related potentials (ERPs) and event-related fields (ERFs). In M. Grimaldi, E. Brattico, and Y. Shtyrov (Eds.), *Language Electrified: Principles, Methods, and Future Perspectives of Investigation*, Vol. 202 of *Neuromethods* (Chapter 7, pp. 195–239). Humana Press. https://doi.org/10.1007/978-1-0716-3263-5_7
- Paulus, P. B. (1983). Group influence on individual task performance. In P. B. Paulus (Ed.), *Basic Group Processes* (Chapter 5, pp. 97–120). Springer New York (1st ed.). https://doi.org/10.1007/978-1-4612-5578-9_5

- Paxton, J. L., Barch, D. M., Racine, C. A., and Braver, T. S. (2008). Cognitive control, goal maintenance, and prefrontal function in healthy aging. *Cerebral Cortex*, 18(5):1010–1028. <https://doi.org/10.1093/cercor/bhm135>
- Pearlman, R. C. (1982). Presbycusis: The need for a clinical definition. *The American journal of otology*, 3(3):183–186. https://journals.lww.com/otology-neurotology/abstract/1982/01000/presbycusis_the_need_for_a_clinical_definition.2.aspxhttps://pubmed.ncbi.nlm.nih.gov/7055232/
- Peelle, J. E. (2019). The neural basis for auditory and audiovisual speech perception. In W. F. Katz and P. F. Assmann (Eds.), *The Routledge Handbook of Phonetics* (Chapter 8, pp. 193–216). Routledge (1st ed.). <https://doi.org/10.4324/9780429056253-9>
- Peelle, J. E., Troiani, V., Grossman, M., and Wingfield, A. (2011). Hearing loss in older adults affects neural systems supporting speech comprehension. *The Journal of Neuroscience*, 31(35):12638–12643. <https://doi.org/10.1523/JNEUROSCI.2559-11.2011>
- Peelle, J. E. and Wingfield, A. (2016). The neural consequences of age-related hearing loss. *Trends in Neurosciences*, 39(7):486–497. <https://doi.org/10.1016/j.tins.2016.05.001>
- Peers, P. V., Ludwig, C. J. H., Rorden, C., Cusack, R., Bonfiglioli, C., Bundesen, C., Driver, J., Antoun, N., and Duncan, J. (2005). Attentional functions of parietal and frontal cortex. *Cerebral Cortex*, 15:1469–1484. <https://doi.org/10.1093/cercor/bhi029>
- Pellico, J., Gawne, P. J., and T. M. de Rosales, R. (2021). Radiolabelling of nanomaterials for medical imaging and therapy. *Chemical Society Reviews*, 50(5):3355–3423. <https://doi.org/10.1039/D0CS00384K>
- Petersen, E. B., Wöstmann, M., Obleser, J., Stenfelt, S., and Lunner, T. (2015). Hearing loss impacts neural alpha oscillations under adverse listening conditions. *Frontiers in Psychology*, 6:177. <https://doi.org/10.3389/fpsyg.2015.00177>
- PHAC (2017). *Dementia in Canada, including Alzheimer's disease: Highlights from the Canadian Chronic Disease Surveillance System* (Fact sheet no. 170098). Public Health Agency of Canada. <https://www.canada.ca/en/public-health/services/publications/diseases-conditions/dementia-highlights-canadian-chronic-disease-surveillance.html>
- Pichora-Fuller, M. K., Kramer, S. E., Eckert, M. A., Edwards, B., Hornsby, B. W. Y., Humes, L. E., Lemke, U., Lunner, T., Matthen, M., Mackersie, C. L., Naylor, G.,

- Phillips, N. A., Richter, M., Rudner, M., Sommers, M. S., Tremblay, K. L., and Wingfield, A. (2016). Hearing impairment and cognitive energy: The Framework for Understanding Effortful Listening (FUEL). *Ear & Hearing*, 37(Suppl. 1):5S–27S. <https://doi.org/10.1097/AUD.0000000000000312>
- Polomac, N., Leicht, G., Nolte, G., Andreou, C., Schneider, T. R., Steinmann, S., Engel, A. K., and Mulert, C. (2015). Generators and connectivity of the early auditory evoked gamma band response. *Brain Topography*, 28:865–878. <https://doi.org/10.1007/s10548-015-0434-6>
- Pratt, H. (2011). Sensory ERP components. In E. S. Kappenman and S. J. Luck (Eds.), *The Oxford Handbook of Event-Related Potential Components* (Chapter 4, pp. 90–114). Oxford University Press (1st ed.). <https://doi.org/10.1093/oxfordhb/9780195374148.013.0050>
- Prettyman, A. (2019). Perceptual learning. *Wiley Interdisciplinary Reviews: Cognitive Science*, 10:e1489. <https://doi.org/10.1002/WCS.1489>
- Price, C. N. and Moncrieff, D. (2021). Defining the role of attention in hierarchical auditory processing. *Audiology Research*, 11:112–128. <https://doi.org/10.3390/audiolres11010012>
- Profant, O., Škoch, A., Balogová, Z., Tintěra, J., Hlinka, J., and Syka, J. (2014). Diffusion tensor imaging and MR morphometry of the central auditory pathway and auditory cortex in aging. *Neuroscience*, 260:87–97. <https://doi.org/10.1016/j.neuroscience.2013.12.010>
- Qiu, C. and Fratiglioni, L. (2018). Aging without dementia is achievable: Current evidence from epidemiological research. *Journal of Alzheimer's Disease*, 62(3):933–942. <https://doi.org/10.3233/JAD-171037>
- R Core Team (2023). *R: A language and environment for statistical computing* [Software version 4.3.1]. R Foundation for Statistical Computing. <https://www.r-project.org/>
- Rajah, M. N. and D'Esposito, M. (2005). Region-specific changes in prefrontal function with age: A review of PET and fMRI studies on working and episodic memory. *Brain*, 128(9):1964–1983. <https://doi.org/10.1093/brain/awh608>
- Ramage-Morin, P. L., Banks, R., Pineault, D., and Atrach, M. (2019). *Unperceived hearing loss among Canadians aged 40 to 79* (Catalogue no. 82-003-X). In *Health*

- Reports*, Vol. 30(8), pp. 11–20. Statistics Canada. <https://doi.org/10.25318/82-003-x201900800002-eng>
- Ramsay, I. S., Fryer, S., Roach, B. J., Boos, A., Fisher, M., Loewy, R., Ford, J. M., Vinogradov, S., and Mathalon, D. H. (2021). Response to targeted cognitive training may be neuroprotective in patients with early schizophrenia. *Psychiatry Research: Neuroimaging*, 312:111285. <https://doi.org/10.1016/j.pscychresns.2021.111285>
- Rao, R. P. N. and Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, 2(1):79–87. <https://doi.org/10.1038/4580>
- Rawson, H. and Miner, M. (Eds.) (2008). *Mary Anne Rademacher*. The Oxford Dictionary of American Quotations. Oxford University Press. <https://doi.org/10.1093/acref/9780195168235.001.0001>
- Reed, N. S., Garcia-Morales, E. E., Myers, C., Huang, A. R., Ehrlich, J. R., Killeen, O. J., Hoover-Fong, J. E., Lin, F. R., Arnold, M. L., Oh, E. S., Schrack, J. A., and Deal, J. A. (2023). Prevalence of hearing loss and hearing aid use among US Medicare beneficiaries aged 71 years and older. *JAMA Network Open*, 6(7):e2326320. <https://doi.org/10.1001/jamanetworkopen.2023.26320>
- Reetzke, R., Xie, Z., Llanos, F., and Chandrasekaran, B. (2018). Tracing the trajectory of sensory plasticity across different stages of speech learning in adulthood. *Current Biology*, 28(9):1419–1427.e4. <https://doi.org/10.1016/j.cub.2018.03.026>
- Reinke, K. S., He, Y., Wang, C., and Alain, C. (2003). Perceptual learning modulates sensory evoked response during vowel segregation. *Cognitive Brain Research*, 17(3):781–791. [https://doi.org/10.1016/S0926-6410\(03\)00202-7](https://doi.org/10.1016/S0926-6410(03)00202-7)
- Ren, Y., Chen, P., Li, Y., Zhou, Z., Dong, Y., Li, S., Qian, R., Yang, J., Wu, J., and Yang, W. (2024). Perceptual training improves audiovisual integration by enhancing alpha-band oscillations and functional connectivity in older adults. *Cerebral Cortex*, 34(8):bhae216. <https://doi.org/10.1093/cercor/bhae216>
- Ressel, V., Pallier, C., Ventura-Campos, N., Díaz, B., Roessler, A., Ávila, C., and Sebastián-Gallés, N. (2012). An effect of bilingualism on the auditory cortex. *The Journal of Neuroscience*, 32(47):16597–16601. <https://doi.org/10.1523/JNEUROSCI.1996-12.2012>

- Reuter, M., Schmansky, N. J., Rosas, H. D., and Fischl, B. (2012). Within-subject template estimation for unbiased longitudinal image analysis. *NeuroImage*, 61(4):1402–1418. <https://doi.org/10.1016/j.neuroimage.2012.02.084>
- Reuter-Lorenz, P. A. (2002). New visions of the aging mind and brain. *Trends in Cognitive Sciences*, 6(9):394–400. [https://doi.org/10.1016/S1364-6613\(02\)01957-5](https://doi.org/10.1016/S1364-6613(02)01957-5)
- Reuter-Lorenz, P. A. and Cappell, K. A. (2008). Neurocognitive aging and the compensation hypothesis. *Current Directions in Psychological Science*, 17(3):177–182. <https://doi.org/10.1111/j.1467-8721.2008.00570.x>
- Reuter-Lorenz, P. A. and Lustig, C. (2005). Brain aging: Reorganizing discoveries about the aging mind. *Current Opinion in Neurobiology*, 15(2):245–251. <https://doi.org/10.1016/j.conb.2005.03.016>
- Reuter-Lorenz, P. A. and Mikels, J. A. (2006). The aging mind and brain: implications of enduring plasticity for behavioral and cultural change. In P. B. Baltes, P. A. Reuter-Lorenz, and F. Rösler (Eds.), *Lifespan development and the brain: The perspective of biocultural co-constructivism* (Chapter 12, pp. 255–276). Cambridge University Press. <https://doi.org/10.1017/CBO9780511499722.014>
- Reuter-Lorenz, P. A. and Park, D. C. (2014). How does it STAC up? Revisiting the Scaffolding Theory of Aging and Cognition. *Neuropsychology Review*, 24:355–370. <https://doi.org/10.1007/s11065-014-9270-9>
- Rey, A. (1964). *L'examen clinique en psychologie* (2nd ed.). Presses universitaires de France.
- Ricci, M., Graef, S., Blundo, C., and Miller, L. A. (2012). Using the Rey Auditory Verbal Learning Test (RAVLT) to differentiate Alzheimer's dementia and behavioural variant fronto-temporal dementia. *The Clinical Neuropsychologist*, 26(6):926–941. <https://doi.org/10.1080/13854046.2012.704073>
- Rieck, B. and Born, J. (2023). *latex-credits* [GitHub repository version 709a62b]. GitHub. <https://github.com/Pseudomanifold/latex-credits>
- Rigters, S. C., Bos, D., Metselaar, M., Roshchupkin, G. V., Baatenburg de Jong, R. J., Ikram, M. A., Vernooij, M. W., and Goedegebure, A. (2017). Hearing impairment is associated with smaller brain volume in aging. *Frontiers in Aging Neuroscience*, 9:2. <https://doi.org/10.3389/fnagi.2017.00002>

- Roalf, D. R. and Gur, R. C. (2017). Functional brain imaging in neuropsychology over the past 25 years. *Neuropsychology*, 31(8):954–971. <https://doi.org/10.1037/neu0000426>
- Roberts, K. L. and Allen, H. A. (2016). Perception and cognition in the ageing brain: A brief review of the short- and long-term links between perceptual and cognitive decline. *Frontiers in Aging Neuroscience*, 8:39. <https://doi.org/10.3389/fnagi.2016.00039>
- Robertson, B. D., Al Jaja, A. S., MacDonald, A. A., Hiebert, N. M., Tamjeedi, R., Seergobin, K. N., Schwarz, U. I., Kim, R. B., and MacDonald, P. A. (2018). SLC6A3 polymorphism predisposes to dopamine overdose in Parkinson's disease. *Frontiers in Neurology*, 9:693. <https://doi.org/10.3389/fneur.2018.00693>
- Rossi, S., Huang, S., Furtak, S. C., Belliveau, J. W., and Ahveninen, J. (2014). Functional connectivity of dorsal and ventral frontoparietal seed regions during auditory orienting. *Brain Research*, 1583:159–168. <https://doi.org/10.1016/j.brainres.2014.08.002>
- Ruhnau, P., Herrmann, B., Maess, B., and Schröger, E. (2011). Maturation of obligatory auditory responses and their neural sources: Evidence from EEG and MEG. *NeuroImage*, 58:630–639. <https://doi.org/10.1016/j.neuroimage.2011.06.050>
- Russo, N. M., Nicol, T. G., Zecker, S. G., Hayes, E. A., and Kraus, N. (2005). Auditory training improves neural timing in the human brainstem. *Behavioural Brain Research*, 156:95–103. <https://doi.org/10.1016/j.bbr.2004.05.012>
- Sala-Llonch, R., Bartrés-Faz, D., and Junqué, C. (2015). Reorganization of brain networks in aging: a review of functional connectivity studies. *Frontiers in Psychology*, 6:663. <https://doi.org/10.3389/fpsyg.2015.00663>
- Salmi, J., Rinne, T., Koistinen, S., Salonen, O., and Alho, K. (2009). Brain networks of bottom-up triggered and top-down controlled shifting of auditory attention. *Brain Research*, 1286:155–164. <https://doi.org/10.1016/j.brainres.2009.06.083>
- Sarant, J., Harris, D., Busby, P., Maruff, P., Schembri, A., Lemke, U., and Launer, S. (2020). The effect of hearing aid use on cognition in older adults: Can we delay decline or even improve cognitive function? *Journal of Clinical Medicine*, 9(254). <https://doi.org/10.3390/jcm9010254>
- Savage, R. M. and Gouvier, W. D. (1992). Rey Auditory-Verbal Learning Test: The effects of age and gender, and norms for delayed recall and story recognition

- trials. *Archives of Clinical Neuropsychology*, 7(5):407–414. [https://doi.org/10.1016/0887-6177\(92\)90153-E](https://doi.org/10.1016/0887-6177(92)90153-E)
- Savoy, R. L. (2001). History and future directions of human brain mapping and functional neuroimaging. *Acta Psychologica*, 107:9–42. [https://doi.org/10.1016/S0001-6918\(01\)00018-X](https://doi.org/10.1016/S0001-6918(01)00018-X)
- Scarpina, F. and Tagini, S. (2017). The Stroop Color and Word Test. *Frontiers in Psychology*, 8:557. <https://doi.org/10.3389/fpsyg.2017.00557>
- Schaefer, A., Kong, R., Gordon, E. M., Laumann, T. O., Zuo, X.-N., Holmes, A. J., Eickhoff, S. B., and Yeo, B. T. T. (2018). Local-global parcellation of the human cerebral cortex from intrinsic functional connectivity MRI. *Cerebral Cortex*, 28(9):3095–3114. <https://doi.org/10.1093/cercor/bhx179>
- Scharenborg, O. and Janse, E. (2013). Comparing lexically guided perceptual learning in younger and older listeners. *Attention, Perception, & Psychophysics*, 75(3):525–536. <https://doi.org/10.3758/s13414-013-0422-4>
- Scheeringa, R., Petersson, K. M., Oostenveld, R., Norris, D. G., Hagoort, P., and Bastiaansen, M. C. M. (2009). Trial-by-trial coupling between EEG and BOLD identifies networks related to alpha and theta EEG power increases during working memory maintenance. *NeuroImage*, 44(3):1224–1238. <https://doi.org/10.1016/j.neuroimage.2008.08.041>
- Schneider-Garces, N. J., Gordon, B. A., Brumback-Peltz, C. R., Shin, E., Lee, Y., Sutton, B. P., Maclin, E. L., Gratton, G., and Fabiani, M. (2010). Span, CRUNCH, and Beyond: Working memory capacity and the aging brain. *Journal of Cognitive Neuroscience*, 22(4):655–669. <https://doi.org/10.1162/jocn.2009.21230>
- Schneiders, J. A., Opitz, B., Tang, H., Deng, Y., Xie, C., Li, H., and Mecklinger, A. (2012). The impact of auditory working memory training on the fronto-parietal working memory network. *Frontiers in Human Neuroscience*, 6:173. <https://doi.org/10.3389/fnhum.2012.00173>
- Schönwiesner, M., Novitski, N., Pakarinen, S., Carlson, S., Tervaniemi, M., and Näätänen, R. (2007). Heschl's gyrus, posterior superior temporal gyrus, and mid-ventrolateral prefrontal cortex have different roles in the detection of acoustic changes. *Journal of Neurophysiology*, 97(3):2075–2082. <https://doi.org/10.1152/jn.01083.2006>

- Schröger, E., Marzecová, A., and SanMiguel, I. (2015). Attention and prediction in human audition: A lesson from cognitive psychophysiology. *European Journal of Neuroscience*, 41:641–664. <https://doi.org/10.1111/ejn.12816>
- Schubert, C. R., Fischer, M. E., Pinto, A. A., Klein, B. E. K., Klein, R., Tweed, T. S., and Cruickshanks, K. J. (2017). Sensory impairments and risk of mortality in older adults. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, 72(5):710–715. <https://doi.org/10.1093/gerona/glw036>
- Schult, J., Stadler, M., Becker, N., Greiff, S., and Sparfeldt, J. R. (2017). Home alone: Complex problem solving performance benefits from individual online assessment. *Computers in Human Behavior*, 68:513–519. <https://doi.org/10.1016/j.chb.2016.11.054>
- Seghier, M. L. (2008). Laterality index in functional MRI: Methodological issues. *Magnetic Resonance Imaging*, 26(5):594–601. <https://doi.org/10.1016/j.mri.2007.10.010>
- Shahin, A. J., Roberts, L. E., Miller, L. M., McDonald, K. L., and Alain, C. (2007). Sensitivity of EEG and MEG to the N1 and P2 auditory evoked responses modulated by spectral complexity of sounds. *Brain Topography*, 20(2):55–61. <https://doi.org/10.1007/s10548-007-0031-4>
- Shamma, S. A. and Micheyl, C. (2010). Behind the scenes of auditory perception. *Current Opinion in Neurobiology*, 20:361–366. <https://doi.org/10.1016/j.conb.2010.03.009>
- Singh, S. P. (2014). Magnetoencephalography: Basic principles. *Annals of Indian Academy of Neurology*, 17:S107–S112. <https://doi.org/10.4103/0972-2327.128676>
- Slade, K., Plack, C. J., and Nuttall, H. E. (2020). The effects of age-related hearing loss on the brain and cognitive function. *Trends in Neurosciences*, 43(10):810–821. <https://doi.org/10.1016/j.tins.2020.07.005>
- Smiley, J. F. (2009). Auditory cortex anatomy and asymmetry in schizophrenia. In A. Lajtha, D. C. Javitt, and J. T. Kantrowitz (Eds.), *Handbook of Neurochemistry and Molecular Neurobiology: Schizophrenia* (Chapter 3.3, pp. 353–381). Springer US (3rd ed.). https://doi.org/10.1007/978-0-387-30410-6_11
- Srinivasan, R., Winter, W. R., and Nunez, P. L. (2006). Source analysis of EEG oscillations using high-resolution EEG and MEG. In C. Neuper and W. Klimesch (Eds.), *Event-Related Dynamics of Brain Oscillations*, Vol. 159 of *Progress in Brain Research* (Chapter 3, pp. 29–42). Elsevier. [https://doi.org/10.1016/S0079-6123\(06\)59003-X](https://doi.org/10.1016/S0079-6123(06)59003-X)

- Stanley, J. A. and Raz, N. (2018). Functional magnetic resonance spectroscopy: The “new” MRS for cognitive neuroscience and psychiatry research. *Frontiers in Psychiatry*, 9:76. <https://doi.org/10.3389/fpsyt.2018.00076>
- Statistics Canada (2024). *Population estimates on July 1, by age and gender* (Statistics Canada table no. 17-10-0005-01). <https://doi.org/10.25318/1710000501-eng>
- Statistics Canada (2025). *Population projections for Canada (2024 to 2074), provinces and territories (2024 to 2049)* (Statistics Canada catalogue no. 91-520-X). <https://www150.statcan.gc.ca/n1/pub/91-520-x/91-520-x2025001-eng.htm>
- Stern, Y. (2009). Cognitive reserve. *Neuropsychologia*, 47(10):2015–2028. <https://doi.org/10.1016/j.neuropsychologia.2009.03.004>
- Stern, Y. (2012). Cognitive reserve in ageing and Alzheimer’s disease. *The Lancet Neurology*, 11:1006–1012. [https://doi.org/10.1016/S1474-4422\(12\)70191-6](https://doi.org/10.1016/S1474-4422(12)70191-6)
- Stothart, G. and Kazanina, N. (2016). Auditory perception in the aging brain: The role of inhibition and facilitation in early processing. *Neurobiology of Aging*, 47:23–34. <https://doi.org/10.1016/j.neurobiolaging.2016.06.022>
- Strauß, A., Wöstmann, M., and Obleser, J. (2014). Cortical alpha oscillations as a tool for auditory selective inhibition. *Frontiers in Human Neuroscience*, 8:350. <https://doi.org/10.3389/fnhum.2014.00350>
- Strenziok, M., Parasuraman, R., Clarke, E., Cisler, D. S., Thompson, J. C., and Greenwood, P. M. (2014). Neurocognitive enhancement in older adults: Comparison of three cognitive training tasks to test a hypothesis of training transfer in brain connectivity. *NeuroImage*, 85:1027–1039. <https://doi.org/10.1016/j.neuroimage.2013.07.069>
- Stropahl, M., Besser, J., and Launer, S. (2020). Auditory training supports auditory rehabilitation: A state-of-the-art review. *Ear & Hearing*, 41(4):697–704. <https://doi.org/10.1097/AUD.0000000000000806>
- Strunk, J. and Duarte, A. (2019). Prestimulus and poststimulus oscillatory activity predicts successful episodic encoding for both young and older adults. *Neurobiology of Aging*, 77:1–12. <https://doi.org/10.1016/j.neurobiolaging.2019.01.005>
- Strzelczyk, D. and Langer, N. (2024). Pre-stimulus activity mediates event-related theta synchronization and alpha desynchronization during memory formation in healthy aging. *Imaging Neuroscience*, 2:1–22. https://doi.org/10.1162/imag_a_00398

- Studenova, A., Forster, C., Engemann, D. A., Hensch, T., Sanders, C., Mauche, N., Hegerl, U., Loffler, M., Villringer, A., and Nikulin, V. (2023). Event-related modulation of alpha rhythm explains the auditory P300-evoked response in EEG. *eLife*, 12:RP88367. <https://doi.org/10.7554/eLife.88367>
- Szczepanski, S. M., Konen, C. S., and Kastner, S. (2010). Mechanisms of spatial attention control in frontal and parietal cortex. *The Journal of Neuroscience*, 30(1):148–160. <https://doi.org/10.1523/JNEUROSCI.3862-09.2010>
- Sziklas, V. and Jones-Gotman, M. (2008). RAVLT and nonverbal analog: French forms and clinical findings. *Canadian Journal of Neurological Sciences / Journal Canadien des Sciences Neurologiques*, 35(3):323–330. <https://doi.org/10.1017/S0317167100008908>
- Tadel, F., Baillet, S., Mosher, J. C., Pantazis, D., and Leahy, R. M. (2011). Brainstorm: A user-friendly application for MEG/EEG analysis. *Computational Intelligence and Neuroscience*, 2011:1–13. <https://doi.org/10.1155/2011/879716>
- Tadel, F., Bock, E., and Baillet, S. (Accessed: September 23, 2022). *Tutorial 4: Channel file / MEG-MRI coregistration*. Brainstorm. https://neuroimage.usc.edu/brainstorm/Tutorials/ChannelFile#Manual_registration
- Tadel, F., Bock, E., and Baillet, S. (Accessed: August 2, 2022). *Tutorial 12: Artifact detection*. Brainstorm. https://neuroimage.usc.edu/brainstorm/Tutorials/ArtifactsDetect#Other_detection_processes
- Tadel, F., Bock, E., Niso, G., Mosher, J. C., Cousineau, M., Pantazis, D., Leahy, R. M., and Baillet, S. (2019). MEG/EEG group analysis with Brainstorm. *Frontiers in Neuroscience*, 13:76. <https://doi.org/10.3389/fnins.2019.00076>
- Tanaka, N., Ahlfors, S. P., and Stufflebeam, S. M. (2025). Sensor–head distance and signal strength in whole-head magnetoencephalography: Report of 996 patients with epilepsy. *Journal of Clinical Neurophysiology*, 42(3):208–214. <https://doi.org/10.1097/WNP.0000000000001114>
- Tavano, A., Rimmele, J. M., Michalareas, G., and Poeppel, D. (2023). Neural oscillations in EEG and MEG. In M. Grimaldi, E. Brattico, and Y. Shtyrov (Eds.), *Language Electrified: Principles, Methods, and Future Perspectives of Investigation*, Vol. 202 of *Neuromethods* (Chapter 8, pp. 241–284). Humana Press. https://doi.org/10.1007/978-1-0716-3263-5_8

- Teng, X., Tian, X., Rowland, J., and Poeppel, D. (2017). Concurrent temporal channels for auditory processing: Oscillatory neural entrainment reveals segregation of function at different scales. *PLOS Biology*, 15(11):e2000812. <https://doi.org/10.1371/journal.pbio.2000812>
- Tervaniemi, M. and Hugdahl, K. (2003). Lateralization of auditory-cortex functions. *Brain Research Reviews*, 43:231–246. <https://doi.org/10.1016/j.brainresrev.2003.08.004>
- Thieba, C., Long, X., Dewey, D., and Lebel, C. (2019). Young children in different linguistic environments: A multimodal neuroimaging study of the inferior frontal gyrus. *Brain and Cognition*, 134:71–79. <https://doi.org/10.1016/j.bandc.2018.05.009>
- Tierney, T. M., Mellor, S., O'Neill, G. C., Holmes, N., Boto, E., Roberts, G., Hill, R. M., Leggett, J., Bowtell, R., Brookes, M. J., and Barnes, G. R. (2020). Pragmatic spatial sampling for wearable MEG arrays. *Scientific Reports*, 10:21609. <https://doi.org/10.1038/s41598-020-77589-8>
- Tingley, D., Yamamoto, T., Hirose, K., Keele, L., and Imai, K. (2014). mediation: R package for causal mediation analysis. *Journal of Statistical Software*, 59(5):1–38. <https://doi.org/10.18637/jss.v059.i05>
- Tivadar, R. I. and Murray, M. M. (2019). A primer on electroencephalography and event-related potentials for organizational neuroscience. *Organizational Research Methods*, 22(1):69–94. <https://doi.org/10.1177/1094428118804657>
- Tolkien, J. R. R. (1937). The Last Stage. In *The hobbit, or, there and back again* (Chapter 19). George Allen & Unwin.
- Tong, Y., Melara, R. D., and Rao, A. (2009). P2 enhancement from auditory discrimination training is associated with improved reaction times. *Brain Research*, 1297:80–88. <https://doi.org/10.1016/j.brainres.2009.07.089>
- Trébuchon, A., Alario, F.-X., and Liégeois-Chauvel, C. (2021). Functional topography of auditory areas derived from the combination of electrophysiological recordings and cortical electrical stimulation. *Frontiers in Human Neuroscience*, 15:702773. <https://doi.org/10.3389/fnhum.2021.702773>
- Tremblay, K., Kraus, N., Carrell, T. D., and McGee, T. (1997). Central auditory system plasticity: Generalization to novel stimuli following listening training. *The Journal of the Acoustical Society of America*, 102:3762–3773. <https://doi.org/10.1121/1.420139>

- Tremblay, K. L. (2007). Training-related changes in the brain: Evidence from human auditory-evoked potentials. *Seminars in Hearing*, 28(2):120–132. <https://doi.org/10.1055/s-2007-973438>
- Tremblay, K. L., Ross, B., Inoue, K., McClannahan, K., and Collet, G. (2014). Is the auditory evoked P2 response a biomarker of learning? *Frontiers in Systems Neuroscience*, 8:28. <https://doi.org/10.3389/fnsys.2014.00028>
- Tuokko, H., Griffith, L. E., Simard, M., and Taler, V. (2017). Cognitive measures in the Canadian Longitudinal Study on Aging. *The Clinical Neuropsychologist*, 31(1):233–250. <https://doi.org/10.1080/13854046.2016.1254279>
- Uchida, Y., Sugiura, S., Nishita, Y., Saji, N., Sone, M., and Ueda, H. (2019). Age-related hearing loss and cognitive decline—The potential mechanisms linking the two. *Auris Nasus Larynx*, 46:1–9. <https://doi.org/10.1016/j.anl.2018.08.010>
- UN (2022). *World population prospects 2022: Summary of results* (Publication no. UN DESA/POP/2021/TR/NO. 3). United Nations, Department of Economic and Social Affairs, Population Division. <https://doi.org/10.18356/9789210014380>
- UN (2024a). *File POP/01–2: Male population by single age, region, subregion and country, annually for 1950–2100 (thousands)* (Table no. POP/DB/WPP/Rev.2024/POP/F01-2). In *World Population Prospects 2024*. United Nations, Department of Economic and Social Affairs, Population Division. [https://population.un.org/wpp/assets/ExcelFiles/1_Indicator\(Standard\)/EXCEL_FILES/2_Population/WPP2024_POP_F01_2_POPULATION_SINGLE_AGE_MALE.xlsx](https://population.un.org/wpp/assets/ExcelFiles/1_Indicator(Standard)/EXCEL_FILES/2_Population/WPP2024_POP_F01_2_POPULATION_SINGLE_AGE_MALE.xlsx)
- UN (2024b). *File POP/01–3: Female population by single age, region, subregion and country, annually for 1950–2100 (thousands)* (Table no. POP/DB/WPP/Rev.2024/POP/F01-3). In *World Population Prospects 2024*. United Nations, Department of Economic and Social Affairs, Population Division. [https://population.un.org/wpp/assets/ExcelFiles/1_Indicator\(Standard\)/EXCEL_FILES/2_Population/WPP2024_POP_F01_3_POPULATION_SINGLE_AGE_FEMALE.xlsx](https://population.un.org/wpp/assets/ExcelFiles/1_Indicator(Standard)/EXCEL_FILES/2_Population/WPP2024_POP_F01_3_POPULATION_SINGLE_AGE_FEMALE.xlsx)
- Upadhyay, J., Silver, A., Knaus, T. A., Lindgren, K. A., Ducros, M., Kim, D.-S., and Tager-Flusberg, H. (2008). Effective and structural connectivity in the human auditory cortex. *The Journal of Neuroscience*, 28(13):3341–3349. <https://doi.org/10.1523/JNEUROSCI.4434-07.2008>

- Van Der Elst, W., Van Boxtel, M. P. J., Van Breukelen, G. J. P., and Jolles, J. (2005). Rey's Verbal Learning Test: Normative data for 1855 healthy participants aged 24–81 years and the influence of age, sex, education, and mode of presentation. *Journal of the International Neuropsychological Society*, 11(3):290–302. <https://doi.org/10.1017/S1355617705050344>
- van Ede, F., Szebényi, S., and Maris, E. (2014). Attentional modulations of somatosensory alpha, beta and gamma oscillations dissociate between anticipation and stimulus processing. *NeuroImage*, 97:134–141. <https://doi.org/10.1016/j.neuroimage.2014.04.047>
- van Maanen, L., Forstmann, B. U., Keuken, M. C., Wagenmakers, E.-J., and Heathcote, A. (2016). The impact of MRI scanner environment on perceptual decision-making. *Behavior Research Methods*, 48(1):184–200. <https://doi.org/10.3758/s13428-015-0563-6>
- Varao-Sousa, T. L., Smilek, D., and Kingstone, A. (2018). In the lab and in the wild: How distraction and mind wandering affect attention and memory. *Cognitive Research: Principles and Implications*, 3(42):1–9. <https://doi.org/10.1186/s41235-018-0137-0>
- Velanova, K., Lustig, C., Jacoby, L. L., and Buckner, R. L. (2007). Evidence for frontally mediated controlled processing differences in older adults. *Cerebral Cortex*, 17(5):1033–1046. <https://doi.org/10.1093/cercor/bhl013>
- Verhaeghen, P., Marcoen, A., and Goossens, L. (1992). Improving memory performance in the aged through mnemonic training: A meta-analytic study. *Psychology and Aging*, 7(2):242–251. <https://doi.org/10.1037/0882-7974.7.2.242>
- Vinogradov, S., Fisher, M., and de Villers-Sidani, E. (2012). Cognitive training for impaired neural systems in neuropsychiatric illness. *Neuropsychopharmacology*, 37:43–76. <https://doi.org/10.1038/npp.2011.251>
- Virtanen, J., Ahveninen, J., Ilmoniemi, R., Näätänen, R., and Pekkonen, E. (1998). Replicability of MEG and EEG measures of the auditory N1/N1m-response. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, 108(3):291–298. [https://doi.org/10.1016/S0168-5597\(98\)00006-9](https://doi.org/10.1016/S0168-5597(98)00006-9)
- Voss, P., Thomas, M., Chou, Y. C., Cisneros-Franco, J. M., Ouellet, L., and de Villers-Sidani, E. (2016). Pairing cholinergic enhancement with perceptual training promotes

- recovery of age-related changes in rat primary auditory cortex. *Neural Plasticity*, 2016:1801979. <https://doi.org/10.1155/2016/1801979>
- Voss, P., Thomas, M. E., Cisneros-Franco, J. M., and de Villers-Sidani, É. (2017). Dynamic brains and the changing rules of neuroplasticity: Implications for learning and recovery. *Frontiers in Psychology*, 8(OCT):1–11. <https://doi.org/10.3389/fpsyg.2017.01657>
- Vossel, S., Geng, J. J., and Fink, G. R. (2014). Dorsal and ventral attention systems: Distinct neural circuits but collaborative roles. *The Neuroscientist*, 20(2):150–159. <https://doi.org/10.1177/1073858413494269>
- Voytek, B., Kramer, M. A., Case, J., Lepage, K. Q., Tempesta, Z. R., Knight, R. T., and Gazzaley, A. (2015). Age-related changes in 1/f neural electrophysiological noise. *The Journal of Neuroscience*, 35(38):13257–13265. <https://doi.org/10.1523/JNEUROSCI.2332-14.2015>
- Wang, J. and Puel, J.-L. (2020). Presbycusis: An update on cochlear mechanisms and therapies. *Journal of Clinical Medicine*, 9:218. <https://doi.org/10.3390/jcm9010218>
- Wayne, R. V. and Johnsrude, I. S. (2015). A review of causal mechanisms underlying the link between age-related hearing loss and cognitive decline. *Ageing Research Reviews*, 23:154–166. <https://doi.org/10.1016/j.arr.2015.06.002>
- Wecker, N. S., Kramer, J. H., Wisniewski, A., Delis, D. C., and Kaplan, E. (2000). Age effects on executive ability. *Neuropsychology*, 14(3):409–414. <https://doi.org/10.1037/0894-4105.14.3.409>
- Weisz, N., Hartmann, T., Müller, N., Lorenz, I., and Obleser, J. (2011). Alpha rhythms in audition: Cognitive and clinical perspectives. *Frontiers in Psychology*, 2:73. <https://doi.org/10.3389/fpsyg.2011.00073>
- Weisz, N., Kraft, N. G., and Demarchi, G. (2020). Auditory cortical alpha/beta desynchronization prioritizes the representation of memory items during a retention period. *eLife*, 9:1–20. <https://doi.org/10.7554/eLife.55508>
- Weisz, N., Müller, N., Jatzew, S., and Bertrand, O. (2014). Oscillatory alpha modulations in right auditory regions reflect the validity of acoustic cues in an auditory spatial attention task. *Cerebral Cortex*, 24(10):2579–2590. <https://doi.org/10.1093/cercor/bht113>

- Wen, X., Yao, L., Liu, Y., and Ding, M. (2012). Causal interactions in attention networks predict behavioral performance. *The Journal of Neuroscience*, 32(4):1284–1292. <https://doi.org/10.1523/JNEUROSCI.2817-11.2012>
- Werner, P., Barthel, H., Drzezga, A., and Sabri, O. (2015). Current status and future role of brain PET/MRI in clinical and research settings. *European Journal of Nuclear Medicine and Molecular Imaging*, 42:512–526. <https://doi.org/10.1007/s00259-014-2970-9>
- White, E. J., Hutka, S. A., Williams, L. J., and Moreno, S. (2013). Learning, neural plasticity and sensitive periods: Implications for language acquisition, music training and transfer across the lifespan. *Frontiers in Systems Neuroscience*, 7:90. <https://doi.org/10.3389/fnsys.2013.00090>
- WHO (1991). *Report of the informal working group on Prevention of Deafness and Hearing Impairment Programme planning, Geneva, 18-21 June 1991* (Document no. WHO/PDH/91.1. Unpublished). World Health Organization, Programme for the Prevention of Deafness and Hearing Impairment, Informal Working Group Programme Planning (1991: Geneva, Switzerland). <https://iris.who.int/handle/10665/58839>
- WHO (2012). *Dementia: A public health priority* (WHO Publication no. viii). World Health Organization and Alzheimer's Disease International. <https://iris.who.int/handle/10665/75263>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis* (2nd ed.). Use R! Springer-Verlag New York. <https://doi.org/10.1007/978-3-319-24277-4>
- Wickham, H., François, R., Henry, L., Müller, K., and Vaughan, D. (2023). *dplyr: A grammar of data manipulation* [R package version 1.1.3]. The Comprehensive R Archive Network. <https://cran.r-project.org/package=dplyr>
- Wiesman, A. I., Murman, D. L., Losh, R. A., Schantell, M., Christopher-Hayes, N. J., Johnson, H. J., Willett, M. P., Wolfson, S. L., Losh, K. L., Johnson, C. M., May, P. E., and Wilson, T. W. (2022). Spatially resolved neural slowing predicts impairment and amyloid burden in Alzheimer's disease. *Brain*, 145(6):2177–2189. <https://doi.org/10.1093/brain/awab430>
- Wiesman, A. I. and Wilson, T. W. (2020). Attention modulates the gating of primary somatosensory oscillations. *NeuroImage*, 211:116610. <https://doi.org/10.1016/j.neuroimage.2020.116610>

- Wiley, T. L., Cruickshanks, K. J., Nondahl, D. M., Tweed, T. S., Klein, R., and Klein, B. E. K. (1998). Aging and high-frequency hearing sensitivity. *Journal of Speech, Language, and Hearing Research*, 41(5):1061–1072. <https://doi.org/10.1044/jslhr.4105.1061>
- Wilson, J. T. L., Wiedmann, K. D., Hadley, D. M., Condon, B., Teasdale, G., and Brooks, D. N. (1988). Early and late magnetic resonance imaging and neuropsychological outcome after head injury. *Journal of Neurology, Neurosurgery & Psychiatry*, 51(3):391–396. <https://doi.org/10.1136/jnnp.51.3.391>
- Wingfield, A. and Grossman, M. (2006). Language and the aging brain: Patterns of neural compensation revealed by functional brain imaging. *Journal of Neurophysiology*, 96:2830–2839. <https://doi.org/10.1152/jn.00628.2006>
- Winkler, I., Denham, S., and Escera, C. (2022). Auditory event-related potentials. In D. Jaeger and R. Jung (Eds.), *Encyclopedia of Computational Neuroscience* (pp. 238–262). Springer New York (2nd ed.). https://doi.org/10.1007/978-1-0716-1006-0_99
- Wong, P. C. M., Jin, J. X., Gunasekera, G. M., Abel, R., Lee, E. R., and Dhar, S. (2009). Aging and cortical mechanisms of speech perception in noise. *Neuropsychologia*, 47:693–703. <https://doi.org/10.1016/j.neuropsychologia.2008.11.032>
- Wöstmann, M., Alavash, M., and Obleser, J. (2019). Alpha oscillations in the human brain implement distractor suppression independent of target selection. *The Journal of Neuroscience*, 39(49):9797–9805. <https://doi.org/10.1523/JNEUROSCI.1954-19.2019>
- Wöstmann, M., Herrmann, B., Wilsch, A., and Obleser, J. (2015). Neural alpha dynamics in younger and older listeners reflect acoustic challenges and predictive benefits. *The Journal of Neuroscience*, 35(4):1458–1467. <https://doi.org/10.1523/JNEUROSCI.3250-14.2015>
- Wöstmann, M., Maess, B., and Obleser, J. (2021). Orienting auditory attention in time: Lateralized alpha power reflects spatio-temporal filtering. *NeuroImage*, 228:117711. <https://doi.org/10.1016/j.neuroimage.2020.117711>
- Wright, B. A. and Zhang, Y. (2009). A review of the generalization of auditory learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1515):301–311. <https://doi.org/10.1098/rstb.2008.0262>

- Yang, L. and Wang, Z. (2025). Applications and advances of combined fMRI-fNIRs techniques in brain functional research. *Frontiers in Neurology*, 16:1542075. <https://doi.org/10.3389/fneur.2025.1542075>
- Yang, W., Guo, A., Li, Y., Qiu, J., Li, S., Yin, S., Chen, J., and Ren, Y. (2018). Audio-visual spatiotemporal perceptual training enhances the P300 component in healthy older adults. *Frontiers in Psychology*, 9:2537. <https://doi.org/10.3389/fpsyg.2018.02537>
- Yee, J., DeLuca, V., and Pliatsikas, C. (2023). The effects of multilingualism on brain structure, language control and language processing. In J. Cabrelli, A. Chaouch-Orozco, J. González Alonso, S. M. Pereira Soares, E. Puig-Mayenco, and J. Rothman (Eds.), *The Cambridge Handbook of Third Language Acquisition*, Cambridge Handbooks in Language and Linguistics (Chapter 22, pp. 577–605). Cambridge University Press. <https://doi.org/10.1017/9781108957823.023>
- Yeo, B. T. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., Roffman, J. L., Smoller, J. W., Zöllei, L., Polimeni, J. R., Fischl, B., Liu, H., and Buckner, R. L. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, 106:1125–1165. <https://doi.org/10.1152/jn.00338.2011>
- Yordanova, J. Y., Kolev, V. N., and Başar, E. (1998). EEG theta and frontal alpha oscillations during auditory processing change with aging. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, 108(5):497–505. [https://doi.org/10.1016/S0168-5597\(98\)00028-8](https://doi.org/10.1016/S0168-5597(98)00028-8)
- Zahodne, L. B. and Reuter-Lorenz, P. A. (2019). Compensation and brain aging: A review and analysis of evidence. In G. R. Samanez-Larkin (Ed.), *The aging brain: Functional adaptation across adulthood* (Chapter 7, pp. 185–216). American Psychological Association. <https://doi.org/10.1037/0000143-008>
- Zaltz, Y., Kishon-Rabin, L., Karni, A., and Ari-Even Roth, D. (2020). Practice makes transfer imperfect: Evidence from auditory learning. *Ear & Hearing*, 41(6):1470–1482. <https://doi.org/10.1097/AUD.0000000000000860>
- Zamrini, E., Maestu, F., Pekkonen, E., Funke, M., Makela, J., Riley, M., Bajo, R., Sudre, G., Fernandez, A., Castellanos, N., del Pozo, F., Stam, C. J., van Dijk, B. W., Bagic, A., and Becker, J. T. (2011). Magnetoencephalography as a putative biomarker for Alzheimer's disease. *International Journal of Alzheimer's Disease*, 2011:280289. <https://doi.org/10.4061/2011/280289>

- Zanto, T. P. and Gazzaley, A. (2016). Selective attention and inhibitory control in the aging brain. In R. Cabeza, L. Nyberg, and D. C. Park (Eds.), *Cognitive Neuroscience of Aging: Linking Cognitive and Cerebral Aging* (Chapter 8, pp. 207–234). Oxford University Press (2nd ed.). <https://doi.org/10.1093/ACPROF:OSO/9780199372935.003.0009>
- Zatorre, R. J. and Belin, P. (2001). Spectral and temporal processing in human auditory cortex. *Cerebral Cortex*, 11(10):946–953. <https://doi.org/10.1093/cercor/11.10.946>
- Zatorre, R. J., Belin, P., and Penhune, V. B. (2002). Structure and function of auditory cortex: Music and speech. *Trends in Cognitive Sciences*, 6(1):37–46. [https://doi.org/10.1016/S1364-6613\(00\)01816-7](https://doi.org/10.1016/S1364-6613(00)01816-7)
- Zatorre, R. J., Fields, R. D., and Johansen-Berg, H. (2012). Plasticity in gray and white: Neuroimaging changes in brain structure during learning. *Nature Neuroscience*, 15(4):528–536. <https://doi.org/10.1038/nn.3045>
- Zhang, G., Garrett, D. R., and Luck, S. J. (2024). Optimal filters for ERP research I: A general approach for selecting filter settings. *Psychophysiology*, 61(6):e14531. <https://doi.org/10.1111/psyp.14531>
- Zhou, Y. J., Ramchandran, A., and Haegens, S. (2023). Alpha oscillations protect working memory against distracters in a modality-specific way. *NeuroImage*, 278:120290. <https://doi.org/10.1016/j.neuroimage.2023.120290>