Accumulated reserves hold back age-related neural compensation in speech-in-noise perception

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Abstract

Recruitment of neural activity or functional connectivity is commonly observed in older adults but poorly understood. We measured brain activity with fMRI during speech-in-noise tasks and assessed whether accumulated reserve accrued through musical training bolsters or holds back age-related neural compensation. Older musicians exhibited less upregulation of task-induced functional connectivity than older non-musicians in dorsal regions, which predicted better behavioral performance in older musicians. The findings suggest that accumulated reserve may hold back neural recruitment. Besides functional connectivity strength, we also found that older musicians showed more youth-like fine spatial patterns of functional connectivity than older non-musicians. However, benefits from visual lip movements were not specific to either hypothesis. Aligning with enhanced benefits in behavioral performance, older musicians showed more extensive functional connectivity enhancement, specifically in the right hemisphere, than older non-musicians. Our findings enlightened the intricate interplay between accumulated reserve and age-related neural compensation during speech in noise perception.

Introduction

Normal aging is associated with sensory and cognitive decline. Current theories posit that older adults may automatically or voluntarily (e.g., spending more effort) engage in strategies to mitigate an age-related decline in perception and cognition[1–5]. The recruitment of neural activity and strengthening of functional connectivity is thought to index older adults' compensatory strategy aiming to maintain optimal cognitive performance[6,7].

The degree to which compensatory strategies are engaged varies substantially among older adults and could be related to cognitive and brain reserve[6–8]. Positive lifestyle choices, like musical training, longer years of education, bilingualism, etc., contribute to cognitive and brain reserve, which describes the accumulation of cognitive and neural resources before aging affects the brain[4,6]. How the cumulative reserves, through positive lifestyle choices, mitigate the engagement of cognitive strategies when older adults perform cognitive tasks has yet to be characterized.

In this study, we used functional magnetic resonance imaging (fMRI) to examine how brain reserve accrued through long-term musical training interacts with brain compensation during speech-in-noise (SIN) perception. We focused on the complex activity of musical training because it requires sensory-motor integration and provides an ideal model for investigating experience-related plasticity[9–12]. Moreover, musicians show cognitive and brain reserve for auditory[13–21] and audiovisual perception[22–24]. Prior research revealed enhanced sensorimotor integration, better speech signal encoding and more robust functional connectivity in the auditory dorsal brain region during speech processing[25–29]. Older adults over-recruit dorsal stream brain regions to compensate for deficits in SIN perception[30,31]. Musicians showed greater activity and functional connectivity in dorsal stream brain regions when they perceive music and SIN[13,15,32], which indicates that musical training promotes neural reserve in the dorsal stream for SIN perception.

The auditory dorsal stream comprises auditory, inferior parietal, dorsal frontal motor, and frontal motor areas and supports sound-to-action mapping during speech processing[31,32]. In adverse listening situations, the processing of speech stimuli with visual lip movements (audiovisual speech) is associated with enhanced speech signal encoding and functional connectivity[25–29]. This may reflect an improved sensorimotor mapping of the visually congruent lip movements into articulatory representations, thereby easing SIN perception[25–29]. Such visual enhancement has been observed in young and older adults[29,33,34]. Studies have found that older adults either benefit as much as, or less than, young adults from visual cues in SIN perception[33–37]. In the present study, we examined how accumulated reserve provided by musical training modulates the recruitment of dorsal brain regions during SIN perception and visual enhancement by analyzing task-induced brain activation and functional connectivity.

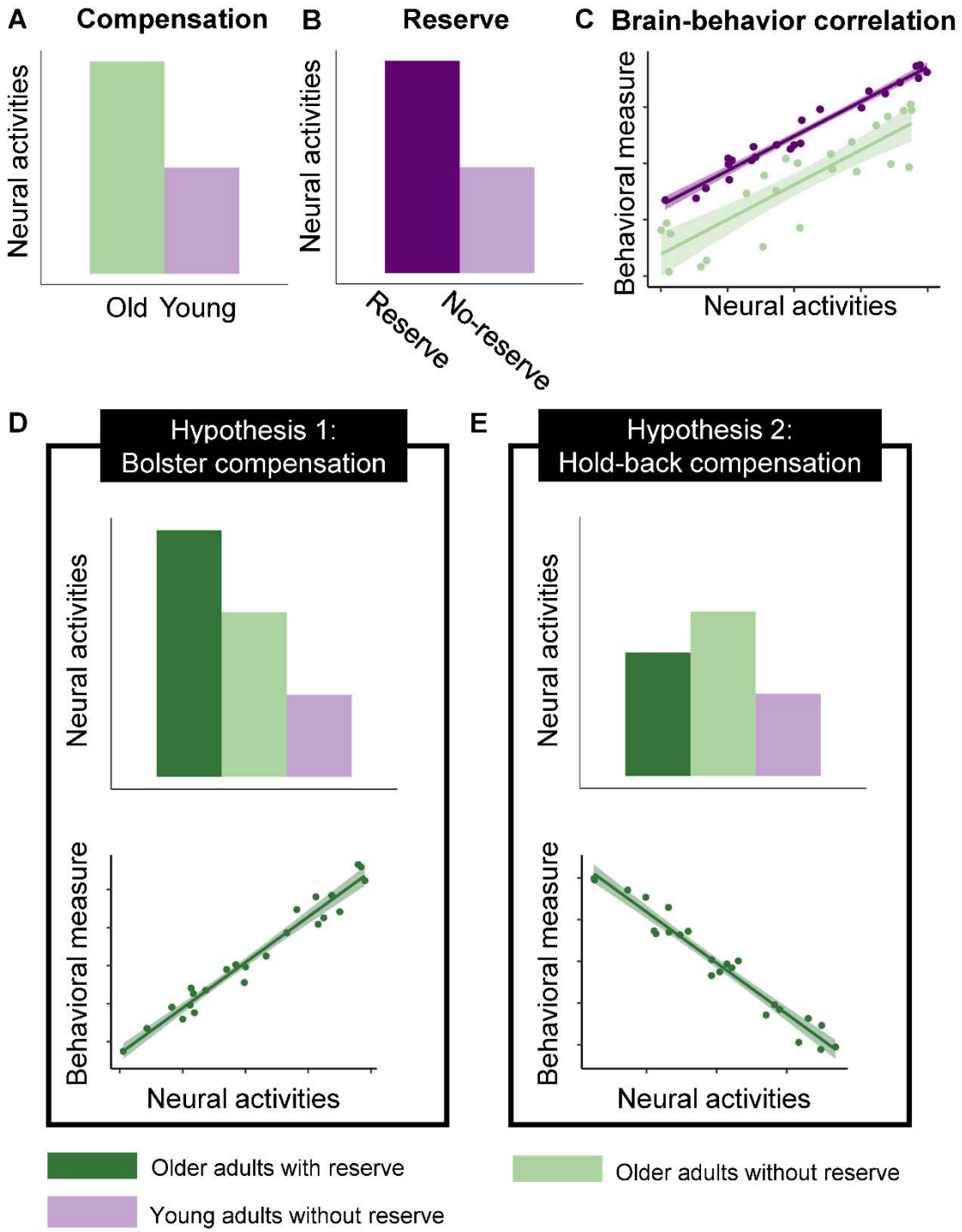

Fig. 1: **Illustration of "Bolster compensation" and "Hold-back compensation" hypotheses**. A-C, neural activity and brain-behavior correlation pattern that support age-related neural compensation and neural reserve. D-E, Hypothesized change in neural activities and brain-behavior correlation pattern due to the interplay between neural reserve and neural compensation.

Previous research has shown that older adults activate frontoparietal brain regions during cognitive tasks more than young adults, suggesting the adoption of compensatory strategies[4,6,30,31] (Fig. 1A, C). Similarly, younger musicians show enhanced brain activity in frontoparietal regions, potentially contributing to cognitive and brain reserve accumulation during adulthood[4,6,15] (Fig. 1B, C). We proposed two hypotheses regarding how brain reserve interacts with neural compensation in the dorsal stream when older adults perform SIN perception tasks. The “Bolster compensation hypothesis” (Fig. 1D) posits that brain reserve, representing the cumulative enhancement of neural resources, reinforces the compensatory upregulation of neural activity in older adults during cognitive tasks, as both mechanisms boost the neural activity to support cognitive performance[6]. Conversely, the “Hold-back compensation hypothesis” (Fig. 1E) proposes that older adults with greater brain reserve show neural activity levels more akin to those of younger adults, as brain reserve provides extra neural resources that could offset age-related neural decline[4,5]. The closer these activity levels resemble those of younger adults, the better the cognitive performance.

To test the proposed hypotheses, we invited 25 older musicians (OM), 25 older non-musicians (ONM), and 24 young non-musicians (YNM) to identify syllables in noise (signal-to-noise ratio (SNR): -8, 0, +8 dB) with congruent visual lip movements (AV condition) or with a static lip picture (A condition). We conducted region of interest (ROI)-based generalized psychophysiological interaction (gPPI) analyses from bilateral auditory seeds (posterior superior frontal gyrus (pSTG)) to bilateral auditory dorsal stream regions (supramarginal gyrus (SMG), supplementary motor area (SMA), superior part of precentral gyrus (PrCGsup), speech motor areas (SM) including inferior part of precentral gyrus (PrCGinf) and opercular part of inferior frontal gyrus (IFGop). We also extracted blood-oxygen-level-dependent (BOLD) activation in these ROIs. These areas are crucial for audiovisual SIN perception[25–29] and may be relevant for the musicians’ advantage in music and SIN perception[13,15,32]. Additionally, we analyzed the resting-state functional connectivity (RSFC) of the three groups to investigate whether the hypotheses are supported solely by task-induced activity or intrinsic activity observed during the resting state.

Observing downregulated neural activities in OMs compared to ONMs supports the “Hold-back compensation hypothesis.” In this case, we expect the level of neural activities in OMs to range between ONMs and YNMs. We anticipate the effect size of the difference between OMs and YNMs to be lower than the difference between ONMs and YNMs. We also expect a negative correlation between neural activities in OMs and their behavioral performance. In contrast, we would interpret an extra upregulation of the neural activities in OMs as support for the “Bolster compensation hypothesis.” This would be reflected by a more significant effect size of the difference between OMs and YNMs than the difference between ONMs and YNMs and a positive correlation between neural activities in OMs and their behavioral performance.

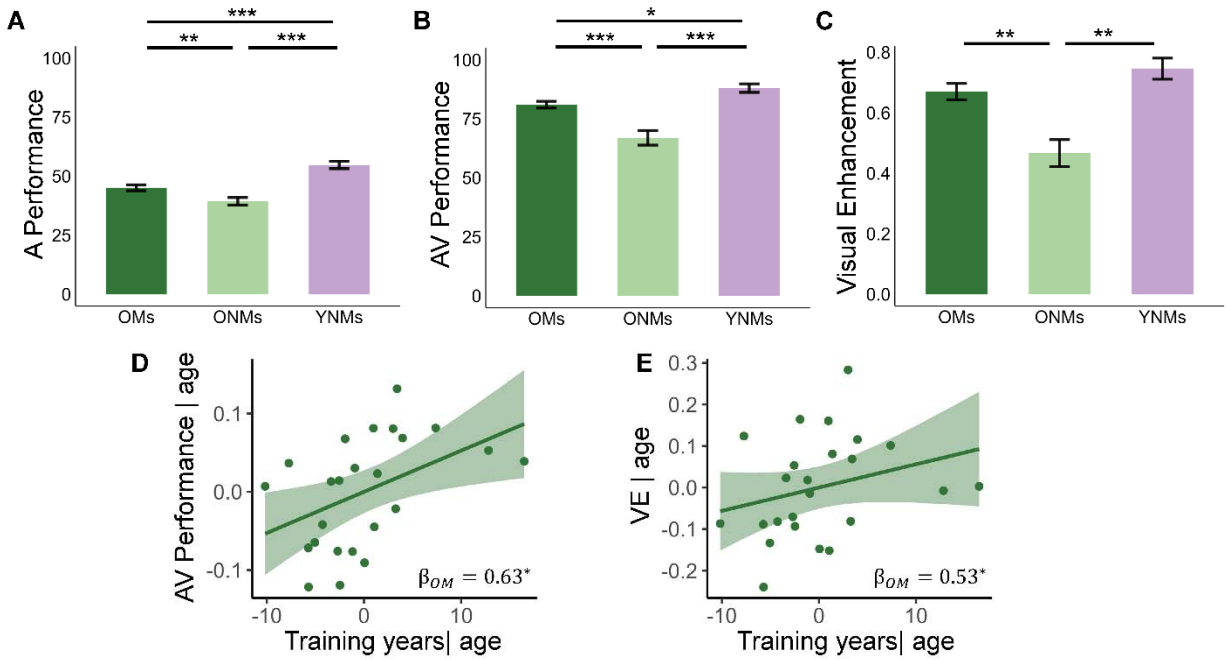

Fig. 2: **Behavioral performance of the three groups and the correlations between behavioral performance and musical training years in OMs**. A-C, Group means and standard error of behavioral performance. OMs performed worse than YNMs, but better than ONMs under both A and AV conditions. OMs showed comparable visual enhancement (VE) to YNMs, and both YNMs and OMs showed greater VE than ONMs. Bar plots show the group mean behavioral performance and visual enhancement. Error bars indicate the SEM. D-E, Years of musical training was correlated with behavioral performance under the AV condition and VE after controlling for age. ***P_{fdr} < 0.001, **P_{fdr} < 0.01, *P_{fdr} < 0.05, note that p value is not corrected in D-E. OMs, older musicians; ONMs, older non-musicians; YNMs, young non-musicians.

Results

Behaviors

Musical training mitigated age-related declines in SIN perception

First, we analyzed the accuracy of syllable identification to examine whether long-term musical training protects against age-related declines in SIN perception among older musicians. We performed two-way mixed-design analyses of variance (ANOVA) separately under the A and AV conditions.

Consistent with previous studies[13,38], OMs showed better behavioral performance than ONMs under both conditions, albeit worse than YNMs, and YNMs performed better than ONMs (Fig.2, A and B, Supplementary Table 1). Through robust linear regression analysis, we found that years of musical training positively correlated with better performance in the AV condition (β = 0.63, *P* = 0.016) after controlling for age in OMs (Fig. 2D).

Musical training mitigated age-related loss in visual enhancement

A two-way mixed-design ANOVA examining the effects of group on visual enhancement of SIN perception revealed a main effect of group ($F_{group}(2, 71) = 15.99$, p < 0.001) (Fig. 1C). Pairwise comparisons showed that visual enhancement was larger in OMs than in ONMs (*t*(71) = 4.01, P_{fdr} < 0.001) and larger in YNMs than in ONMs (*t*(71) = 5.45, P_{fdr} < 0.001). However, differences between OMs and YNMs were not significant (*t*(71) = 1.48, P_{fdr} = 0.492). Furthermore, robust linear regression analysis found that years of musical training positively correlated with visual enhancement on SIN perception (β = 0.53, p = 0.041) after controlling for age (Fig. 2E).

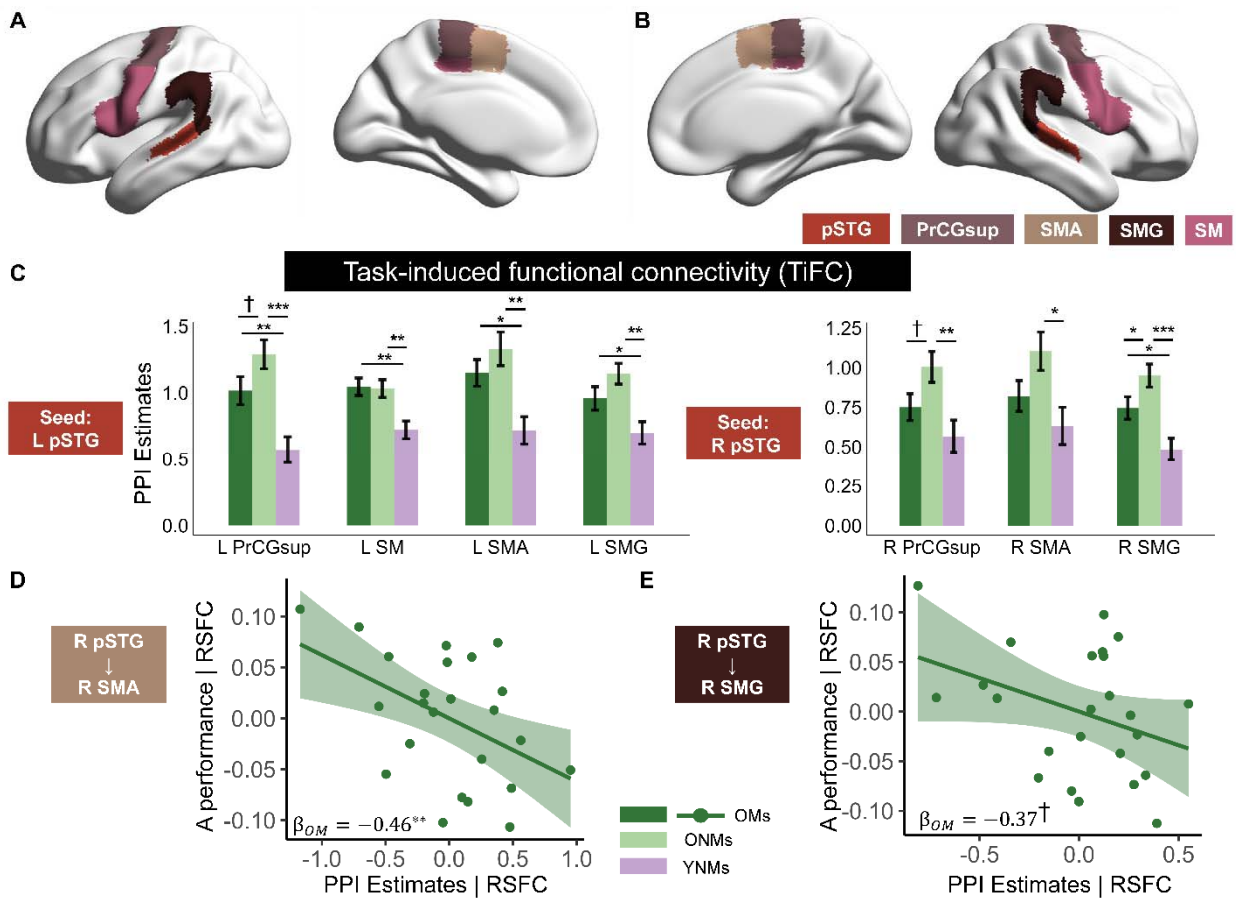

Fig. 3: **TiFC of the three groups under audio condition, and brain-behavior correlations.** A-B, left (A) and right (B) ROIs used in PPI analysis. Bilateral posterior superior temporal gyrus (pSTG) were set as seed. Bilateral auditory dorsal stream regions including supramarginal gyrus (SMG), supplementary motor area (SMA), superior part of precentral gyrus (PrCGsup), and speech motor areas (SM) were set as target regions. C, ONMs showed upregulated task-induced functional connectivity (TiFC) in bilateral dorsal streams compared to YNMs, while OMs exhibited TiFC resembling YNMs. Bar plots show the group mean TiFC in specific target regions. Error bars indicate the SEM. D-E, The closer TiFC strength of OMs resemble that of YNMs, the better the behavioral performance after controlling for resting-state functional connectivity (RSFC). ***P_{fdr} < 0.001, **P_{fdr} < 0.01, *P_{fdr} < 0.05, †P_{fdr} < 0.1; OMs, older musicians; ONMs, older non-musicians; YNMs, young non-musicians; L, left; R, right.

Task-induced functional connectivity (TiFC)

ONMs showed compensatory upregulated TiFC during SIN perception

We performed gPPI analysis to investigate how aging and musical training modulated the TiFC within the bilateral auditory dorsal streams during SIN perception under the A condition. According to the dual model of auditory processing[39,40] and previous results of speech perception studies[15,29,39,41], we used bilateral posterior STG as seeds in the auditory dorsal streams. Target regions of interest (ROIs) included bilateral SMG, SMA, PrCGsup, and speech motor areas composed of PrCGinf and IFGop. Two-way mixed-design ANOVAs (group * SNR) were performed to investigate the group effect on TiFC in the bilateral auditory dorsal streams.

We found a main effect of group on TiFC within the bilateral auditory dorsal streams (LpSTG-LSMA, LSMG, LPrCGsup, LSM; RpSTG-RSMA, RSMG, RPrCGsup, Fig. 3C, for statistics, see Supplementary Table 2). For connectivity that showed significant group effect after FDR correction, pairwise comparison revealed stronger TiFC in ONMs than young adults (LpSTG-LSMA, LSMG, LPrCGsup, LSM; RpSTG-RSMA, RSMG, RPrCGsup, Fig. 3C, Supplementary Table 2)

Additionally, we employed robust linear mixed-effects analysis to investigate the effect of group on the left and right hemisphere TiFC after controlling for participants and brain regions. We found stronger overall TiFC in ONMs than YNMs (left: β_{group} = 0.56, P < 0.001; Right: β_{group} = 0.45, P < 0.001).

To investigate the visual modulation of TiFC, we also calculated TiFC along bilateral dorsal stream under AV condition, which will be introduced in later part. We found a significant positive correlation between TiFC and behavioral performance (β_{ONMs} = 0.57, P = 0.002, Fig. S1A). And like under the A condition, ONMs showed upregulated TiFC compared to YNMs (LpSTG- LSMG: t(46) = 2.21, p = 0.032, Fig. S1B). With robust linear mixed-effects analysis, we found a positive correlation between TiFC upregulation from LpSTG to LSMG and behavioral SIN performance after controlling for participants and visual conditions (β_{ONMs} = 0.57, P = 0.011). This suggests a compensatory role of TiFC upregulation in ONMs.

Connectivity strength in OM was more akin to YNM than ONM

Both OMs and ONMs showed stronger connectivity than YNMs in the left hemisphere (LpSTG-LSMA, LPrCGsup, LSM Fig. 3C, for statistics, see Supplementary Table 2). However, the mean effect size of the difference between OMs and YNMs across left ROIs was smaller than that between ONMs and YNMs (0.38 vs. 0.53).

ONMs showed stronger connectivity in the right hemisphere than OMs (RpSTG-RSMA) and YNMs (RpSTG-LSMA, RPrCGsup, RSMG), but differences between OMs and YNMs were not evident. The mean effect size of the difference between OMs and YNMs across left ROIs was smaller than that between ONMs and YNMs (0.23 vs. 0.49). Additionally, with a linear mixed model, regardless of brain regions, we found stronger TiFC in ONMs than OMs (β_{group} = 0.21 P = 0.023) in the right brain. OMs also showed stronger TiFC than YNMs (β_{group} = 0.23 P = 0.021).

Moreover, we observed a negative correlation between TiFC strength and behavioral

performance in OMs in the right SMA (β_{OMs} = -0.46, *P* = 0.008, Fig. 3D) and a marginally negative correlation in right SMG (β_{OMs} = -0.37, *P* = 0.078, Fig. 3D). In right PrCGsup, the TiFC-behavior correlation is also negative but not significant (β_{OMs} = -0.32, *P* = 0.163). That is, the connectivity strengths of OMs who showed better behavioral performance were more akin to those of young adults. Thus, long-term musical training provides the neural reserve to mitigate age-related declines in SIN perception. The TiFC strength supports the "Hold-back compensation" hypothesis.

OMs showed higher spatial alignment of TiFC to YNMs than ONMs

We performed inter-subject spatial correlation (ISPC) to further explore whether OMs also showed more youth-like TiFC in fine spatial patterns in the regions exhibiting significant or marginally significant lower TiFC strength than ONMs. ISPC measures the spatial neural alignment of multivoxel TiFC spatial patterns of the older brain to that observed in younger brains (Fig. 4A). We found that OMs showed higher ISPC to YNMs than ONMs in left PrCGsup (t(46) = 2.74, P_{fdr} = 0.026, Fig. 4B), which provided the evidence that OMs showed both more youth-like TiFC strength and spatial TiFC pattern than ONMs. More importantly, higher ISPC of OMs to YNMs negatively correlated to the TiFC strength (β_{OMs} = -0.37, *P* = 0.029, Fig. 4C). This suggests that the more youth-like spatial pattern is related to greater "Hold-back compensation."

Next, we explored how the TiFC spatial pattern in left PrCGsup was shifted in ONMs. By extracting the mean coordinate of the top 10 percent voxels, we could examine whether the positions of the voxels were different between the two older adult groups and YNMs (Fig. 4D). We found a significant difference between ONMs and YNMs in the Z-axis direction (t(46) = 2.73, P_{fdr} = 0.027, Fig. 4E). Since Z-axis increases from inferior to superior, this meant the position of the top voxels in ONMs are more superior to that in YNMs. As expected, we found no difference between OMs and YNMs (t(46) = 1.60, P_{fdr} = 0.175, Fig. 4E).

We also calculated ISPC within groups. A higher within-group ISPC denotes that the TiFC spatial patterns are more similar within this group. We found that ONMs exhibited a higher ISPC than YNMs in left PrCGsup (t(46) = 3.71, P_{fdr} = 0.002, Fig. 4F). However, no difference was found between OMs and YNMs (t(46) = 0.37, p = 0.715, Fig. 4F). In summary, ONMs' TiFC spatial pattern consistently deviated more from YNMs than OMs.

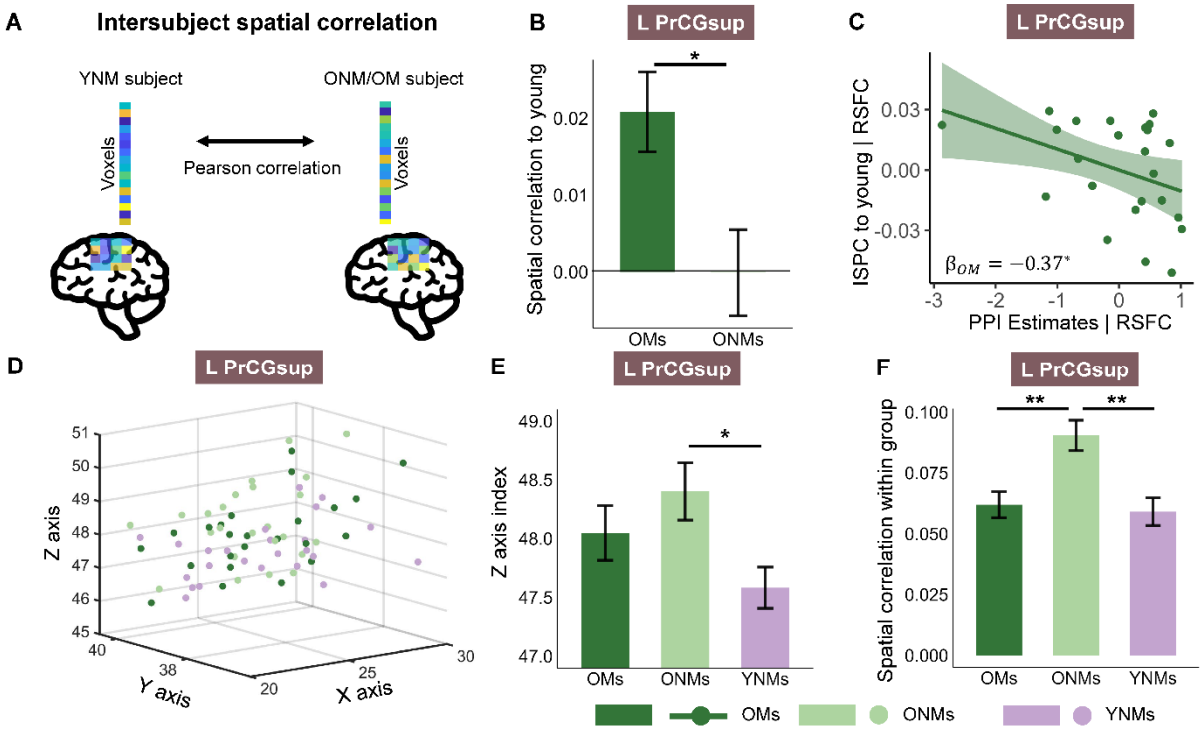

Fig. 4: **Spatial alignment of TiFC to YNMs and within group**. A, Illustration of calculation of intersubject spatial correlation, see Methods for details. B-C, OMs showed greater spatial alignment to YNMs than ONMs in left PrCGsup (B), and greater spatial alignment to YNMs predicted lower TiFC strength, which is closer to YNMs, in OMs. D-E, Mean 3D coordinates of the voxels that showed top 10% TiFC were plotted in D. Voxels of ONMs exhibited significant position in Z axis compared to YNMs, while no difference was found between OMs and YNMs (E). F, ONMs showed greater spatial correlation within group than OMs and YNMs. Bar plots show the group mean of specific index in L PrCGsup. Error bars indicate the SEM. $^{*}P_{fdr} < 0.05$, $^{**}P_{fdr} < 0.01$; OMs, older musicians; ONMs, older non-musicians; YNMs, young non-musicians; L PrCGsup, left superior part of precentral gyrus.

VE of TiFC for OMs was more pronounced in the right and for YNMs in the left hemisphere

The analysis of behavioral data revealed greater visual enhancement in OMs and YNMs than ONMs. Here, we investigated whether OMs and YNMs also showed greater visual enhancement in TiFC, which is defined by the difference between TiFC under the A and AV conditions (see supplementary text for TiFC under AV condition). The main effect of group was significant in bilateral auditory dorsal streams (LpSTG-LSMA, LSM; RpSTG-RSMA, RSMG, RprCGsup, RSM, Fig. 5A and 5B, for statistics, see Supplementary Table 2). Interestingly, YNMs showed a greater advantage of visual enhancement on functional connectivity in the left auditory dorsal stream compared to ONMs or OMs (LpSTG-LSMA, LSM, for statistics, Supplementary Table 2), while OMs demonstrated an advantage over ONMs in the right hemisphere (RpSTG-RSMA, SMG, RprCGsup, RSM, for statistics, Supplementary Table 2). Therefore, regarding the visual enhancement of SIN perception, we did not find evidence of age-related compensation in TiFC. At the same time, long-term musical training appeared to promote neural reserve in the right dorsal stream.

In OMs, the right brain TiFC during visual enhancement was positively correlated with musical training hours in the past three years (R SMA: $\beta_{OMs} = 0.40$, $P = 0.002$; R SMG, $\beta_{OMs} = 0.29$, $P = 0.056$, Fig. 5D-E). Although OMs did not exhibit greater visual enhancement in the left brain than ONMs, we also found a positive correlation between musical training hours in the past three years and visual enhancement of TiFC (L PrCGsup: $\beta_{OMs} = 0.31$, $P = 0.038$; L SMG, $\beta_{OMs} = 0.29$, $P = 0.064$). In addition, we found a positive correlation between visual enhancement of TiFC and behavioral performance after controlling for RSFC and baseline TiFC under A condition in non-musicians (Fig. 5C, RpSTG- RSMG: $\beta_{ONMs} = 0.38$, $P = 0.027$; $\beta_{YNMs} = 0.42$, $P = 0.073$). The disparity in TiFC strength within the left and right hemisphere suggests that interactions between neural reserve and age-related neural compensation vary depending on the context of SIN perception.

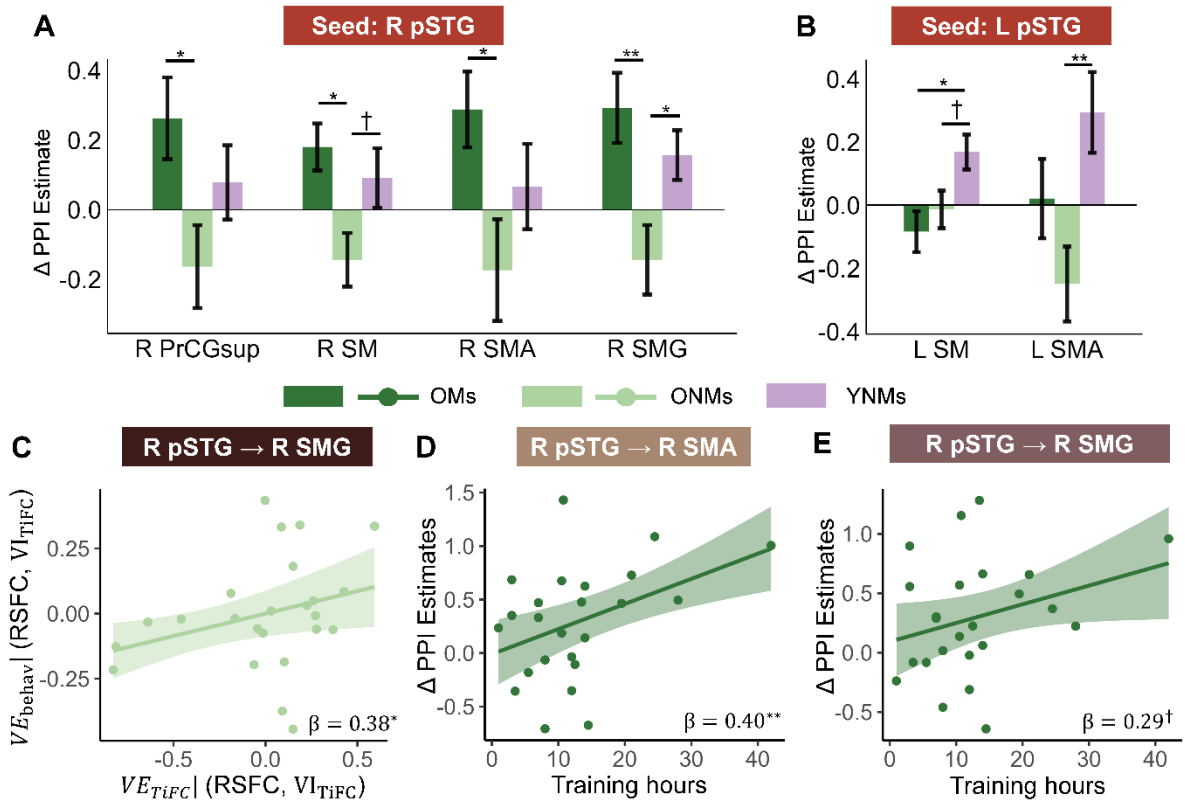

Fig.5: **Visual enhancement (VE) in the TiFC, and brain-behavior correlations.** A-B, OMs showed greater visual enhancement of TiFC in right dorsal stream compared to ONMs (A), while YNMs exhibited greater visual enhancement of TiFC in left dorsal stream compared to ONMs (B). Bar plots show the group mean of TiFC visual enhancement in specific target regions. Error bars indicate the SEM. C, Higher visual enhancement of TiFC predicted greater visual enhancement of behavioral performance in ONMs after controlling RSFC and baseline connectivity strength under A condition. D-E, Greater visual enhancement of TiFc in OMs was correlated to higher averaged training hours per week in recent three year. $^{**}P_{fdr} < 0.01$, $^{*}P_{fdr} < 0.05$, $^{\dagger}P_{fdr} < 0.1$, note that p value is not corrected in C-D; OMs, older musicians; ONMs, older non-musicians; YNMs, young non-musicians; RSFC, resting-state functional connectivity; TiFC, task-induced functional connectivity; pSTG, posterior part of superior temporal gyrus; SMG, supramarginal gyrus; SMA, supplementary areas; L, left; R, right.

BOLD activation and RSFC

No group difference in BOLD activation was found

We extracted BOLD activation in auditory dorsal stream regions to assess the two hypotheses regarding regional activation levels. However, we did not observe any main effect of BOLD activation difference between the three groups (for statistics, see Supplementary Table 3).

Older adults showed stronger intrinsic Resting-State Functional Connectivity (RSFC) in the auditory dorsal stream than young adults

We examined whether the two hypotheses were supported by intrinsic functional connectivity by extracting RSFC in auditory dorsal stream regions seeded from bilateral posterior STG. As illustrated in Fig. 6, OMs demonstrated stronger RSFC than YNMs (LpSTG-LSMA, LSMG, LprCGsup; RpSTG-RSMA, RSMG, RPrCGsup, RSM, for statistics, see Supplementary Table 4), with no significant difference observed between OMs and ONMs. ONMs also showed stronger RSFC than YNMs (LpSTG-LSMG; RpSTG-RSMA, for statistics, see Supplementary Table 4).

However, we did not find any significant RSFC-behavior correlation in both OMs and ONMs groups. Therefore, it cannot be concluded that the stronger intrinsic functional connectivity observed in older adults serves as a compensatory mechanism.

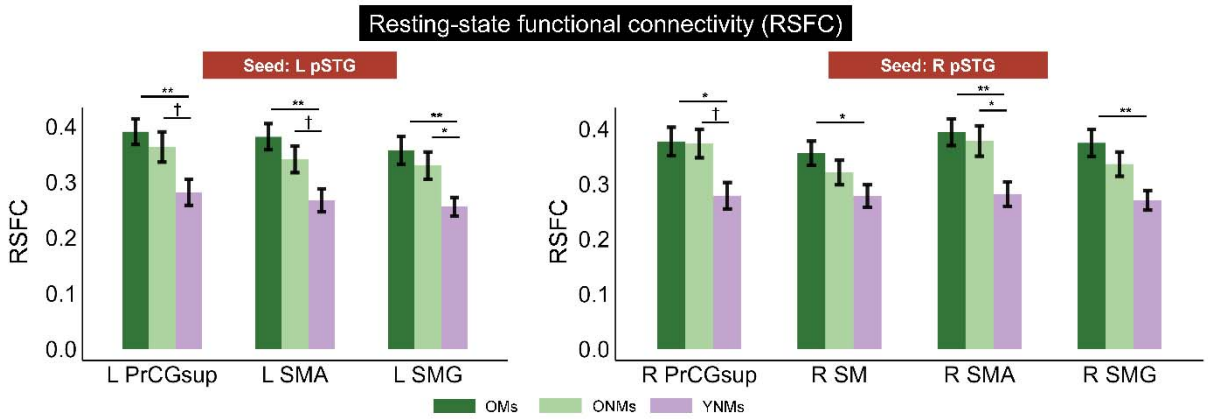

Fig. 6: **Bilateral RSFC of the three groups.** ONMs and OMs showed upregulated resting-state functional connectivity (RSFC) in bilateral dorsal streams compared to YNMs. Bar plots show the group mean RSFC in specific target regions. Error bars indicate the SEM. **P_{fdr} < 0.01, *P_{fdr} < 0.05, †P_{fdr} < 0.1, OMs, older musicians; ONMs, older non-musicians; YNMs, young non-musicians; pSTG, posterior part of superior temporal gyrus; SMG, supramarginal gyrus; SMA, supplementary areas; SM, speech motor areas; PrCGsup, superior part of precentral gyrus; L, left; R, right.

Discussion

This study examined how accumulated brain reserve through long-term musical training interacts with age-related neural compensation during SIN perception. We found reduced age-related declines in SIN perception and preserved visual benefits from lip reading in older adults with extensive musical training. As expected, ONMs showed the typical age-related compensatory upregulation of TiFC in bilateral auditory dorsal stream. Notably, OMs exhibited a connectivity pattern in the bilateral auditory dorsal stream resembling YNMs, with weaker connectivity correlating with better SIN performance. These findings support our “Hold-back compensation” hypothesis, where neural reserve from musical training promotes a more youthful functional connectivity pattern, leading to superior behavioral outcomes. By further investigating fine spatial pattern of TiFC, we found OMs exhibited more youth-like spatial TiFC patterns, and ONMs showed a more consistently deviating TiFC spatial pattern to YNMs compared to OMs. OMs also demonstrated greater visual enhancement in TiFC than ONMs in the right hemisphere, correlating with better performance and years of musical training. In comparison, YNMs showed greater visual enhancement in the left hemisphere. Lastly, an increase in intrinsic functional connectivity (RSFC) was found in older adults, while no brain-behavior correlation was found in RSFC. Overall, our findings shed light on the intricate interplay between age-related neural compensation and accumulated reserve. Reserve accrued from long-term musical training hold back the age-related compensation of neural activities in both strength level and fine spatial pattern such that OMs present youth-like listening skills.

We found a decline in SIN perception associated with aging, which is evident in both A and AV conditions. Previous studies using audiovisual illusion paradigms, like the sound-induced flash illusion and the McGurk illusion, have suggested that older adults tend to rely more on multisensory information (for reviews, see[36,42]) potentially as a compensatory strategy for age-related hearing loss. Previous studies have highlighted ONMs upregulating frontal BOLD activity as a compensatory mechanism during SIN perception[30,31]. However, conflicting findings have been reported in other studies[43–46]. In the current study, ONMs did not show increased regional BOLD activation. However, they exhibited heightened TiFC strength within bilateral auditory dorsal streams, indicative of enhanced sensorimotor integration during SIN perception. The positive relationship between higher connectivity strength and better behavioral performance suggests that ONMs may employ the compensatory upregulation of sensorimotor integration to improve SIN perception.

By investigating the neural responses of OMs, we showed how accumulated brain reserve supported by long-term musical training interacts with age-related brain compensation mechanisms. Previous studies in young adults have found that musicians show greater TiFC from auditory to motor areas during SIN perception, supporting their superior SIN perception performance[15]. Additionally, musicians displayed enhanced sensorimotor integration due to intensive sensory-motor interaction during musical training[9,11,19,47]. In contrast to ONMs, we found that OMs showed comparable TiFC strength to YNMs in the right dorsal stream under the A condition. In the left brain, from the plot of the mean TiFC strength and the effect size of the group difference, we also observed that OMs showed a connectivity profile more akin to YNMs than ONMs under

both conditions. In addition, lower connectivity strength predicts better behavioral performance in OMs, opposite to the positive brain-behavior correlation in ONMs. These results support the “Hold-back compensation” hypothesis, suggesting that the brain reserve provided by long-term musical training preserves a youth-like brain activity strength, leading to better behavioral performance. This is consistent with our previous findings using the same dataset in this study, which shows that OMs preserve SIN perception performance by keeping youth-like representations in sensorimotor regions[13]. The present study significantly extends prior research by showing TiFC strength during audiovisual speech processing. Brain reserve provided by long-term musical training helps OMs mitigate age-related decline in SIN perception by keeping the youth-like TiFC in task-related neural networks.

Although older adults exhibit visual benefits in SIN perception comparable to those of young adults[33,35], our study identified a significant age-related decline in the visual benefit of SIN. This could be influenced by using a relative benefit index and not considering visual degradation in this study. OMs exhibited a more pronounced visual enhancement in SIN perception than ONMs, and a comparable benefit to YNMs. This advantage in audiovisual speech integration is consistent with previous findings in young adults[22–24], indicating the retention of sensory-motor integration advantages in aging musicians. Moreover, the examination of BOLD activation and TiFC revealed that OMs exhibited greater BOLD activation than ONMs and greater functional connectivity strength than YNMs in the right dorsal brain regions with congruent lip movements. OMs also showed greater visual enhancement of functional connectivity than ONMs. These findings suggest that greater sensorimotor integration in the right dorsal pathway may mediate musicians' advantage in the visual enhancement of SIN perception.

The contribution of the dorsal pathway tends to be left-lateralized when processing speech without visual cues[39]. However, a meta-analysis of neuroimaging studies has indicated that bilateral auditory dorsal stream regions are involved in audiovisual speech perception[25,48–53]. With congruent visual lip movements, listeners could employ extra visual articulatory information, which promotes sensorimotor integration in the dorsal stream[25–29], to aid SIN perception. The lack of visual enhancement of TiFC in the left dorsal stream in older adults suggests that older adults failed to boost the sensorimotor integration in the brain network directly related to speech processing with valid visual cues. However, older adults with long-term musical training showed an extra boost in the right dorsal stream, which correlated with the intensity of musical training. Previous studies have found that young musicians exhibit both functional and structural advantages of the right dorsal stream compared to young non-musicians[15,54–56]. Therefore, long-term musical training might enable OMs to adopt a different strategy for right-hemispheric involvement in audiovisual SIN perception. The superior visual enhancement in the right dorsal stream is consistent with neural reserve accrued through long-term musical training.

RSFC is an excellent approach to examining the intrinsic connectivity of participants independent of a specific task. Previous studies have found that musicians showed more robust RSFC than non-musicians in the speech-related brain network[57–59]. Therefore, we also extracted the intrinsic functional connectivity for three groups to investigate the group effect and took intrinsic connectivity as a covariate when performing

brain-behavior correlation analysis. We found that both ONMs and OMs showed superior intrinsic connectivity compared to YNMs. Previous studies have found decreased within-network connectivity but increased between-network connectivity in older adults compared to young adults (for reviews, see[60]). This is consistent with our findings that older adults' connectivity between auditory and frontal motor areas increased. However, whether RSFC is necessarily correlated with behavioral performance remains unclear[58,61]. In this study, since we did not find any significant RSFC-behavior correlation in both groups, it cannot be concluded that the stronger intrinsic functional connectivity observed in older adults serves as a compensatory mechanism. Further studies are need to explore the relationship between RSFC and speech perception in older adults.

In conclusion, this fMRI study offers new insights into the intricate interplay between neural reserve and neural compensation in SIN perception among older adults. Specifically, it examines the newly proposed hypotheses of "Hold-back compensation" and "Bolster compensation" within this context. Our findings suggest that long-term musical training mitigates age-related decline in SIN perception by enhancing accumulated neural reserve, which interacts with compensatory upregulation of tasked-induced functional connectivity, fitting with the "Hold-back compensation" hypothesis. Moreover, regarding visual enhancement, ONMs do not show compensation in the bilateral dorsal stream. OMs exhibit an advantage in the right hemisphere, while YNMs show a left hemispheric advantage. Our results underscore the importance of considering both neural reserve and age-related neural compensation in understanding cognitive performance like SIN perception in older adults. These findings may inform interventions to preserve cognitive function and improve communication outcomes in aging populations.

Methods

Participants

Twenty-five OMs, 25 ONMs, and 24 YNMs participated in this study. One OM was excluded from the fMRI analysis because of excessive head movements, and another ONM because of left-handedness. All remaining participants were healthy, right-handed, native Mandarin speakers with no history of neurological disorder and normal hearing (average pure tone threshold < 20 dB hearing level between 250 Hz and 4000 Hz) in both ears. All older adults passed the Beijing version of the Montreal Cognitive Assessment (MoCA, ≥26 scores)[62]. All OMs started musical training before the age of 23 years (10.90 ± 4.56 years old) and had at least 32 years of musical training (50.88 ± 8.75 years). Also, all OMs practiced regularly in the last three years (12.70 ± 8.99 hours per week). All non-musicians reported less than two years of musical expertise experience. The demographic information of the three groups is summarized in Supplementary Table 5. OMs and ONMs were not different in age, pure tone average (PTA), and MoCA score. However, self-reported education years differed between groups (OM > ONM, $t = 4.15$, $P < 0.001$). We conducted supplementary analyses to control for the effect of years of education on our results (see Supplementary Text of the Supplementary Materials). All participants provided written consent before taking part in the study, which was approved by the ethics committee of the Institute of Psychology, Chinese Academy of Science.

Stimuli and procedure

The stimuli comprised four naturally pronounced consonant-vowel syllables (/ba/, /da/, /pa/, /ta/) uttered by a 23 years old Chinese female. The utterances were recorded in a soundproof room. Each syllable was captured in a video that lasted for one second and was digitized at a rate of 30 frames per second with a resolution of 1024-by-768 pixels. The pictures of the videos retained the mouth and the neck. The audio syllable stimuli were about 400 ms in duration, aligned in time by lip movement onset, low-pass filtered (4 kHz), and matched for average root-mean-square sound pressure level (for more details, see[13,29]). The masker was a speech spectrum-shaped noise (4-kHz low-pass, 10-ms rise-decay envelope) representative of 113 sentences by 50 young Chinese female speakers (age range 20 to 26 years). The audio stimuli were delivered at a level of 90 dB sound pressure level (SPL). The SPL of the masking sounds was modified to create three signal-to-noise ratios (SNRs) of -8, 0, and 8 dB. The audio stimuli were transmitted using MRI-compatible insert earphones (S14, Sensimetrics Corporation), which attenuated the scanner noise by up to 40 dB.

The experiment was a 3 (SNRs) × 2 (sensory modality: audiovisual (AV) with congruent lip movements and auditory (A) with static lip pictures) factorial design. Matching lip movement videos and still lip pictures were presented with speech signals in the AV and A conditions, respectively. In the fMRI scanner, participants listened to the speech signals, watched the mouth on the screen, and identified the syllables by pressing the corresponding button using their right-hand fingers (index to little fingers in response to ba, da, pa, and ta in half of the participants or pa, ta, ba and da in the other half of the participants sequentially). Each participant completed four blocks. Each block contained 60 stimuli (20 trials × 3 SNRs), pseudo-randomly presented with an average

inter-stimuli-interval of 5 s (4–6 s, 0.5 s step).

Behavior data analysis

Mixed-design ANOVAs were performed to investigate the main effect of group on behavioral performance under A and AV conditions, as well as the visual enhancement (VE) of behavioral performance, which was calculated according to the following equation[34]:

$$VE = \frac{AV - A}{1 - A}$$

The relative benefit index adjusts the “room for gain” and corrects for possible floor effects[34,37,63,64]. Greenhouse–Geisser correction was applied if the sphericity assumption was violated. FDR correction accounted for multiple comparisons in post hoc analysis. Statistical analyses were performed with the package bruceR[65] in R.

Imaging data acquisition and preprocessing

Functional imaging data was collected by a 3T MRI system (Siemens Magnetom Trio), and T1 weighted images were acquired using the MPRAGE sequence (TR = 2200 ms, TE = 3.49 ms, FOV = 256 mm, voxel size = 1×1×1 mm). Blood oxygen level-dependent (BOLD) images were acquired using the multiband-accelerated EPI sequence (acceleration factor = 4, TR = 640 ms, TE = 30 ms, slices = 40, FOV = 192, voxel sizes = 3×3×3 mm).

Task-state functional imaging data were preprocessed using AFNI software[66]. The first eight volumes were removed. The following preprocessing steps included slice timing, motion correction, aligning functional images with anatomy, spatial normalization (MNI152 space), spatial smoothing with 6-mm FWHM isotropic Gaussian kernel, and scaling each voxel time series to have a mean of 100.

Univariate general linear model (GLM) analysis

Single-subject multiple-regression modeling was performed using the AFNI program 3dDeconvolve. Six conditions of four syllables and six regressors corresponding to motion parameters were entered into the analysis. TRs would be censored if the motion derivatives exceeded 0.3. For each SNR and visual validity, the four syllables were grouped and contrasted against the baseline.

Task-induced functional connectivity

gPPI analysis was performed to investigate the TiFC between auditory seeds and other regions in the auditory dorsal stream[67]. Auditory seeds were defined as bilateral posterior division of superior temporal gyrus labels from the Harvard-Oxford atlas. Target regions were auditory dorsal stream regions, including bilateral SMG, SMA, PrCGsup, and SM area, which comprises preCGinf and IFGop[29,39,41]. Subject-level gPPI GLM analyses were conducted separately for left and right auditory seeds using the AFNI program 3dDeconvolve. PPI regressors, the seed time series and the regressors of the original GLM model were included in the model.

Resting-state functional connectivity

We also investigated intrinsic functional connectivity by analyzing resting-state functional

data. Resting-state data were preprocessed using the GRETNA toolbox[68]. After removing the first ten volumes, the remaining 740 volumes entered the following preprocessing steps: slice timing, realignment, spatial normalization, and detrending. Lastly, the normalized images were temporally filtered between 0.02 and 0.1 Hz, and covariates, including cerebrospinal fluid signal, white matter region signal, and head motion parameters, were regressed out.

Pearson correlation coefficients were calculated between voxel-wise time series in auditory dorsal stream regions, the same target ROIs used in gPPI analysis and the mean time series in bilateral auditory seeds to obtain the intrinsic functional connectivity in the auditory dorsal stream.

ROI-based group analysis

To specifically investigate how aging and musical training modulate neural activities in the auditory dorsal stream during audiovisual speech perception, we performed the ROI analysis in BOLD activation, TiFC and RSFC. According to previous studies and reviews, bilateral posterior division of superior temporal gyrus from Harvard-Oxford atlas STG were set as auditory seeds. Bilateral SMG, SMA, PrCGsup, and SM areas, including PrCGinf and IFGop, were set as target ROIs. Note that since inter-hemispheric connectivity was not of interest in this study, only intra-hemispheric functional connectivity was discussed in this study (right seed to right target; left seed to right target). Voxel-wise TiFC, RSFC, and BOLD activation were extracted for each ROI. Then, voxels with the top 40% activation or connectivity levels across conditions were selected and averaged for the following statistical analysis[69]. Mixed-design ANOVAs (group*SNRs) were performed for A and visual enhancement. FDR correction was applied for multiple comparisons across ROIs and post hoc analyses.

A robust linear mixed model analysis was further performed to investigate the group effect (e.g., ONMs vs. YNMs) on neural indices regardless of brain regions, which showed significant group effects in each hemisphere. The formula was established as follows:

$$Neural\ index = group\ +\ (1|subject)\ + (1|brain\ regions)$$

The above analyses were performed using the packages “bruceR “ and “robustlmm” in R[65,70].

Inter-subject spatial correlation analysis (ISPC)

The TiFC of each voxel within the ROIs that showed significant or marginally significant group difference between OMs and ONMs under each condition was extracted for each participant. Then, we correlated the TiFC of each OM and ONM to that of each YNM for each ROI. The averaged correlation coefficients of each older adult to all YNMs represented the spatial alignment of the young. A higher spatial alignment measure denotes that the subject showed a higher TiFC spatial similarity as young adults. FDR correction was performed for multiple comparisons.

ISPC was also performed within the groups. That is, we correlated TiFC of each OM to that of other OMs for the ROI. The same procedure was also performed for the other two groups. The average correlation coefficients of each participant were calculated and compared to those of other participants within the group. Higher within-group ISPC

denotes that the neural activities of the subjects in that group are more homogeneous with each other, which probably suggests that subjects in that group employ similar processing strategies.

Activity spatial position analysis

Following ISPC, we performed the activity spatial position analysis within the specific ROI to examine whether older adults showed position differences of voxels that showed top TiFC. We extracted voxels that showed the top 10% TiFC of each participant within the ROI that showed significant ISPC group differences between OMs and ONMs for a more specific and targeted location analysis. Then, we averaged the x (left to right), y (posterior to anterior), and z (inferior to superior) axis coordinates of the voxels for each participant. T-tests were performed to compare the mean coordinates between groups. FDR correction was performed for multiple comparisons.

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Supplementary Materials

Accumulated reserves hold back age-related neural compensation in speech-in-noise perception

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Supplementary Text

Effect of years of education on the behavioral performance and neural responses in the audiovisual speech-in-noise perception task

We found that years of education including both formal and informal education were significantly different between ONM and OM. Due to historical reasons in China, all recruited older adults discontinued formal education at the same time (1960s-1970s). Therefore, the self-reported years of education cannot represent the education level of the older subjects reliably.

The years of education were highly correlated with the group variable between OM and ONM (point-biserial correlation r = 0.64), and were correlated with the group variable between older subjects and young subjects (ONM vs. YNM: r_{pb}= 1; OM vs. YNM: r_{pb}= 0.74). Therefore, it is not suitable to put the years of education variable into the analyses as a control variable because of the collinearity problem.

To exclude the effect of years of education on our results, we performed supplementary analysis to investigate the effect of years of education on the behavioral performance, BOLD activation, task-induced functional connectivity, and resting-state functional connectivity. We included the years of education in the mixed-designed ANOVA. We found years of education is not significant in all of the analysis (behavioral: all p > 0.522; BOLD activation: all P_{fdr} > 0.157; task-induced functional connectivity: all P_{fdr} > 0.098; resting-state functional connectivity: all P_{fdr} > 0.649). Therefore, years of education did not influence the behavioral performance and neural responses in this study.

Patterns of TiFC under AV condition showed hemisphere difference between groups

Under audiovisual condition, we also found a main effect of group on TiFC within the bilateral auditory dorsal streams (LpSTG-LPrCGsup; RpSTG-RSMA, RSMG, RPrCGsup, Fig. S2, for statistics, see Supplementary Table 2).

For connectivity that showed a significant group effect after FDR correction, the pairwise comparison revealed stronger TiFC in both OMs and ONMs than in young adults in left brain (LpSTG-LPrCGsup, Fig. S2 left, Supplementary Table 2). In right brain, OMs, rather than ONMs, demonstrated stronger functional connectivity than YNMs in the right hemisphere (RpSTG-RSMA, RSMG, RPrCGsup, Fig. S2 right, for statistics, see Supplementary Table 2). However, no brain-behavior correlation was found in OMs.

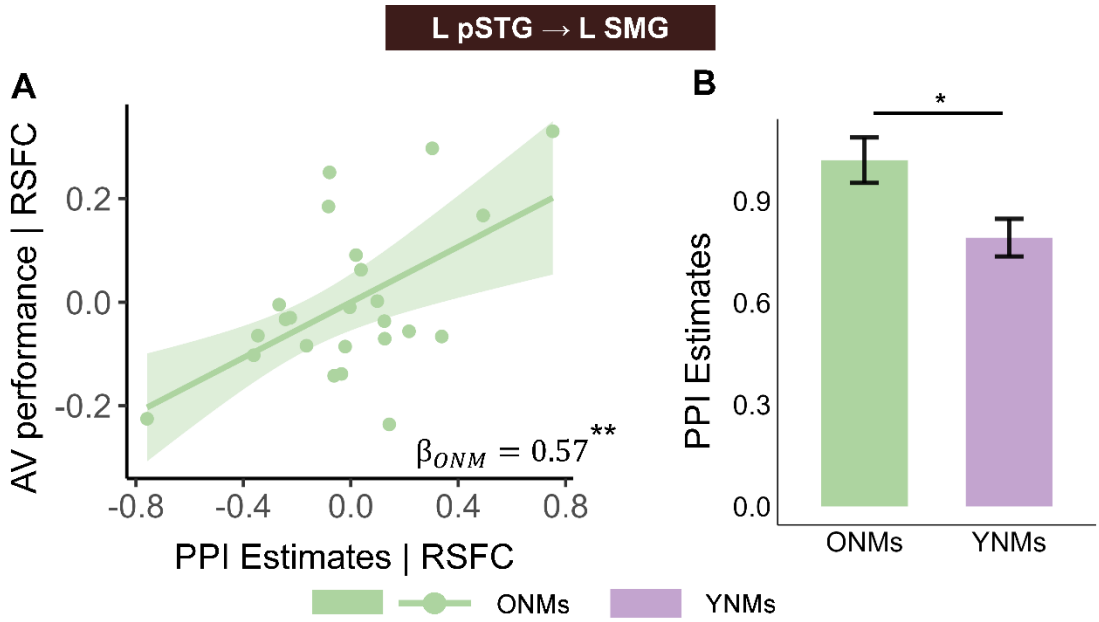

Fig. S1: **Brain-behavior correlation and TiFC in L SMG under AV condition.** A, Task-induced functional connectivity (TiFC) from left posterior superior temporal gyrus (L pSTG) to Left supramarginal gyrus (L SMG) predicted behavioral performance under audiovisual (AV) condition in ONMs. B, ONM showed greater TiFC than YNMs in L SMG under AV condition. Bar plots show the group mean TiFC in specific target regions. Error bars indicate the SEM. *P < 0.05, **P < 0.01; ONMs, older non-musicians; YNMs, young non-musicians.

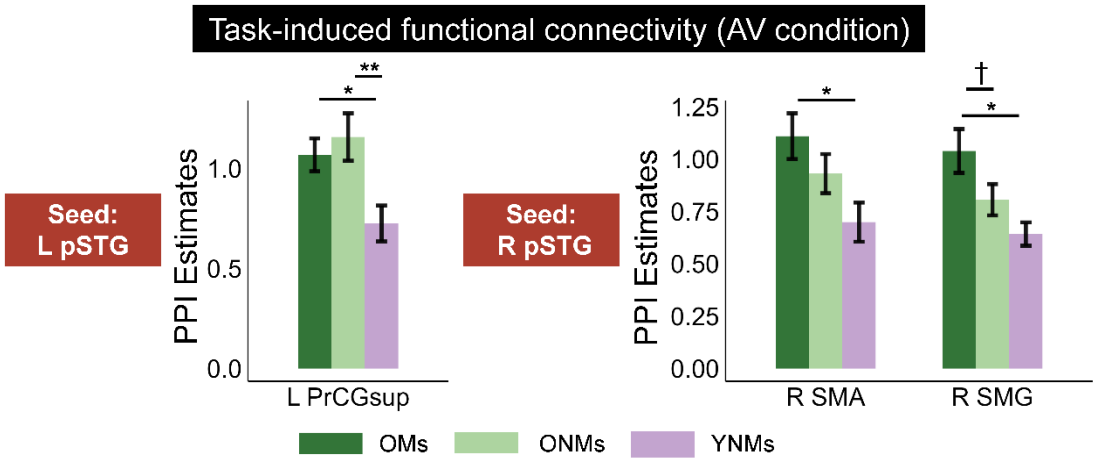

Fig. S2: **TiFC of the 3 groups under audiovisual (AV) condition** ONMs showed upregulated task-induced functional connectivity in left dorsal streams compared to YNMs, while older musicians OMs exhibited upregulated task-induced functional connectivity in bilateral functional connectivity compared YNMs. Bar plots show the group mean TiFC in specific target regions. Error bars indicate the SEM. **P_{fdr} < 0.01, *P_{fdr} < 0.05, †P_{fdr} < 0.1; OMs, older musicians; ONMs, older non-musicians; YNMs, young non-musicians; PrCGsup, left superior part of precentral gyrus, SMG, supramarginal gyrus, SMA, supplementary motor area, L, left; R, right.

Supplementary table 1. Mixed-design ANOVA and post hoc analysis of behavioral performance under audio conditions (A), audiovisual conditions (AV), as well as visual enhancement (VE). The F values and associated p values represent the main effect of the group from a Mixed-design ANOVA. The t values and p values are from post hoc pairwise comparisons with FDR correction.

	Group main effect $F_{2,71}$(p)	OMs vs. ONMs t_{71}(p)	OMs vs. YNMs t_{71}(p)	ONMs vs. YNMs t_{71}(p)
A	28.65(<0.001)	2.80(0.007)	-4.72(<0.001)	-7.50(<0.001)
AV	22.89(<0.001)	4.48(<0.001)	-2.19(0.032)	-6.62(<0.001)
VE	15.99(<0.001)	4.01(<0.001)	-1.48(0.143)	-5.45(<0.001)

Supplementary table 2. Mixed-design ANOVA and post hoc analysis of task-induced functional connectivity under audio conditions (A), audiovisual conditions (AV), as well as visual enhancement (VE). The F values and associated p values represent the main effect of the group from a Mixed-design ANOVA. The reported p values have been corrected for multiple comparisons across the ROIs using the FDR method. The t values and associated p values are from post hoc pairwise comparisons with FDR correction.

Seed: LSTG	Target regions	Group main effect $F_{2,69}(P_{fdr})$	OMs vs. ONMs $t_{69}(P_{fdr})$	OMs vs. YNMs $t_{69}(P_{fdr})$	ONMs vs. YNMs $t_{69}(P_{fdr})$
A	L SMA	8.14(0.001)	1.16(0.250)	-2.77(0.011)	-3.93(0.001)
	L SMG	7.18(0.001)	1.57(0.120)	-2.20(0.047)	-3.77(0.001)
	L PrCGsup	12.06(<0.001)	1.85(0.069)	-3.01(0.005)	-4.86(0.000)
	L SM	7.58(0.001)	-0.14(0.890)	-3.44(0.002)	-3.30(0.002)
AV	L SMA	0.66(0.522)	-0.65(0.622)	-1.14(0.622)	-0.50(0.622)
	L SMG	2.61(0.162)	0.58(0.567)	-1.63(0.163)	-2.20(0.093)
	L PrCGsup	5.38(0.027)	0.64(0.524)	-2.47(0.024)	-3.11(0.008)
	L SM	1.10(0.453)	0.66(0.512)	-0.82(0.512)	-1.48(0.431)
VE	L SMA	4.77(0.025)	-1.54(0.129)	1.55(0.129)	3.09(0.009)
	L SMG	1.57(0.215)	-1.03(0.462)	0.74(0.462)	1.77(0.246)
	L PrCGsup	1.89(0.211)	-1.23(0.332)	0.68(0.496)	1.92(0.177)
	L SM	4.69(0.025)	0.83(0.411)	2.97(0.012)	2.14(0.054)
Seed: RSTG	Target regions				
A	R SMA	4.47(0.020)	1.78(0.119)	-1.19(0.239)	-2.97(0.012)
	R SMG	10.69(<0.001)	2.03(0.047)	-2.59(0.018)	-4.61(0.000)
	R PrCGsup	5.40(0.013)	1.90(0.092)	-1.37(0.175)	-3.27(0.005)
	R SM	2.70(0.074)	1.59(0.174)	-0.67(0.506)	-2.26(0.081)
AV	R SMA	4.30(0.035)	-1.28(0.206)	-2.93(0.014)	-1.65(0.156)
	R SMG	6.06(0.015)	-2.03(0.070)	-3.46(0.003)	-1.44(0.156)
	R PrCGsup	3.34(0.055)	-1.21(0.231)	-2.58(0.036)	-1.37(0.231)
	R SM	1.70(0.191)	-1.61(0.179)	-1.58(0.179)	0.04(0.971)
VE	R SMA	3.31(0.042)	-2.57(0.037)	-1.23(0.222)	1.34(0.222)
	R SMG	5.95(0.017)	-3.37(0.004)	-1.05(0.299)	2.32(0.035)
	R PrCGsup	3.48(0.042)	-2.63(0.032)	-1.14(0.259)	1.49(0.211)
	R SM	4.75(0.023)	-2.98(0.012)	-0.81(0.418)	2.17(0.051)

Supplementary table 3. Mixed-design ANOVA and post hoc analysis of BOLD activation under audio conditions (A), as well as visual enhancement (VE). The F values and associated p values represent the main effect of the group from a Mixed-design ANOVA. The reported p values have been corrected for multiple comparisons across the ROIs using the FDR method. The t values and associated p values are from post hoc pairwise comparisons with FDR correction.

A	Group main effect $F_{2,69}(P_{fdr})$	OMs vs. ONMs $t_{69}(P_{fdr})$	OMs vs. YNMs $t_{69}(P_{fdr})$	ONMs vs. YNMs $t_{69}(P_{fdr})$
L SMA	2.29(0.241)	-2.05(0.132)	-0.51(0.613)	1.54(0.190)
L SMG	1.75(0.241)	-1.87(0.199)	-0.80(0.426)	1.07(0.426)
L PrCGsup	0.24(0.791)	-0.59(0.832)	-0.59(0.832)	-0.00(0.999)
L SM	2.57(0.241)	-2.27(0.080)	-1.12(0.265)	1.14(0.265)
R SMA	1.19(0.356)	-1.43(0.343)	-1.21(0.343)	0.22(0.830)
R SMG	1.93(0.241)	-1.96(0.163)	-1.10(0.395)	0.86(0.395)
R PrCGsup	2.29(0.241)	-0.98(0.332)	-2.14(0.108)	-1.16(0.332)
R SM	1.87(0.241)	-1.53(0.194)	-1.78(0.194)	-0.25(0.803)
VE				
L SMA	1.34(0.525)	-1.42(0.240)	-0.00(1.000)	1.42(0.240)
L SMG	0.52(0.598)	-0.69(0.736)	0.30(0.766)	0.99(0.736)
L PrCGsup	2.41(0.525)	-1.90(0.093)	0.01(0.996)	1.90(0.093)
L SM	1.05(0.525)	-1.04(0.456)	0.36(0.722)	1.39(0.456)
R SMA	1.50(0.525)	-1.41(0.245)	0.17(0.869)	1.57(0.245)
R SMG	0.86(0.525)	-0.29(0.775)	0.97(0.506)	1.25(0.506)
R PrCGsup	1.60(0.525)	-1.22(0.338)	0.52(0.603)	1.74(0.256)
R SM	0.79(0.525)	-1.00(0.482)	0.16(0.876)	1.16(0.482)

Supplementary table 4. One-way ANOVA and post hoc analysis of intrinsic functional connectivity. The F values and associated p values represent the main effect of the group from a Mixed-design ANOVA. The reported p values have been corrected for multiple comparisons across the ROIs using the FDR method. The t values and associated p values are from post hoc pairwise comparisons with FDR correction.

Seed: LSTG	Target regions	Group main effect $F_{2,69}(P_{fdr})$	OMs vs. ONMs $t_{69}(P_{fdr})$	OMs vs. YNMs $t_{69}(P_{fdr})$	ONMs vs. YNMs $t_{69}(P_{fdr})$
	L SMA	6.20(0.010)	-0.66(0.511)	-3.52(0.002)	-2.11(0.058)
	L SMG	5.68(0.010)	-0.17(0.869)	-3.36(0.004)	-2.38(0.031)
	L PrCGsup	4.37(0.022)	-0.43(0.668)	-2.96(0.013)	-1.87(0.099)
	L SM	2.80(0.068)	-0.55(0.585)	-2.35(0.064)	-1.33(0.281)
Seed: RSTG	Target regions				
	R SMA	5.23(0.015)	0.05(0.964)	-3.20(0.006)	-2.42(0.027)
	R SMG	5.27(0.015)	-0.81(0.420)	-3.22(0.006)	-1.78(0.120)
	R PrCGsup	3.31(0.050)	0.06(0.954)	-2.54(0.040)	-1.94(0.085)
	R SM	3.12(0.050)	-0.71(0.481)	-2.47(0.048)	-1.29(0.301)

Supplementary table 5. The Group Mean (Standard Deviation) Values and Statistics of Age, Education, Pure Tone Average (PTA) at 250–4000 Hz, MOCA Score, Age of Training Onset, and Years of Music Training in Each Group

Group	Age	Edu	PTA	MOCA	Age of onset	Years of training
Older musicians	65.12 (4.06)	13.02 (2.96)	12.38 (5.39)	27.92 (1.19)	10.90 (4.56)	50.88 (8.75)
Older non-musicains	66.64 (3.40)	9.50 (3.02)	12.58 (3.58)	27.52 (1.39)	NA	NA
t (p)	-1.43 (0.158)	4.15 (<0.001)	-0.15 (0.881)	1.09 (0.28)		
Young non-musicains	23.13 (2.38)	16.50 (1.67)	0.71 (3.32)	NA	NA	NA