The Compensatory Mechanism of the Prefrontal Cortex in Preserving Speech-in-Noise Comprehension Among Older Adults

Short title: Prefrontal Supports Elderly Speech-in-Noise Ability

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Abstract

Maintaining the ability to understand speech in real-life noisy environments is crucial for elderly adults, yet the underlying neural mechanisms remain elusive. To address this issue, we adopted an inter-brain neuroscience approach by modeling old listeners' neural activities to those of speakers in noisy conditions. Our findings reveal significant speaker-listener neural coupling from the old listener's prefrontal cortex and classical language regions. Notably, compared to young listeners, the old listeners exhibited a more robust and widespread neural coupling in the prefrontal cortex, with a stable integration with the language regions across varying noise levels. Furthermore, the neural responses in the prefrontal cortex were found to correlate with the old listeners' comprehension performance, particularly when noise level escalated. Collectively, this study underscores a compensatory mechanism of the prefrontal cortex in preserving the ability of older adults to comprehend speech amidst noise in naturalistic settings, providing insights into the neurocognitive basis of successful aging.

Introduction

As people age, their ability to understand speech in noisy environments, which is often encountered in daily life, becomes increasingly challenging. This difficulty is attributed to the progressive decline in both the structural and functional aspects of the auditory system (*1*) and the classical perisylvian language regions (*2*). These declines affect the early sensory processing of speech acoustics and the subsequent mapping of acoustics to meaningful content, making it difficult for older adults to adapt to noisy environments. Meanwhile, in response to these age-related neural deteriorations, additional brain regions, notably the frontal lobe, are recruited as compensatory mechanisms to mitigate the decline in cognitive performance and to maintain cognitive function in the elderly (*3, 4*). Numerous studies have documented significant activation in the prefrontal cortex among older adults, particularly in those who preserve a relatively high level of speech comprehension ability (*2, 5, 6*). However, the underlying neural mechanisms that support the older adult's speech comprehension in naturalistic noisy conditions are still largely unknown.

The functional role of the prefrontal cortex in natural speech-in-noise processing is a significant yet unresolved issue. Despite numerous reports of its activation in the older adults, it is unclear how the prefrontal cortex was involved to offset declines in the language-specific areas (*7*). One approach to resolve this question is by modeling the neural responses to the speech features (from acoustics to semantics) in natural speech, which could be quantitatively estimated by recently advanced natural language processing algorithms (*8-12*). Yet, the inherence complexity of speech dynamics and the interdependency of multi-level speech features make it challenging to directly model such a brain-to-stimuli correspondence (*13, 14*), calling for new computational methods to explore how the noisy speech is processed in the prefrontal cortex. Another question concerns how much the speech-in-noise processing is preserved in the classical language regions, especially under noisy conditions. Research has shown that younger people can adapt to difficult listening environments by selectively filtering out the background noise and (or) recovering a clear speech

representation within the language regions (*15-17*). In contrast, as age-related decline was widely observed in the fronto-temporo-parietal cortex (*2*), the natural speech-in-noise processing within these regions should be less efficient than that of younger individuals. Nonetheless, this hypothesis requires direct empirical examination. Besides, it remains to be fully investigated how the prefrontal cortex was functionally connected with the language network to support the speech-in-noise processing within the aging brain. Previous literature has widely reported that the prefrontal cortex and the perisylvian language regions were structurally and functionally connected in both young (*18, 19*) and older adults (*20, 21*). Given the potential compensatory function of the prefrontal cortex in mitigating age-related declines in the speech processing, we hypothesized that the prefrontal cortex was increasingly integrated to the language network when people grow older. In all, this study aims to address the above questions and further elucidate how older adults understand others' speech in real-life noisy environments.

We adopted an inter-brain neuroscience approach (*22-24*) by computing the coupling or synchrony between the neural activities from old listeners and speakers during naturalistic speech comprehension. With regarding the speaker's brain as a reference, this speaker-listener neural coupling can indicate the extent to which the speaker's speech is processed within the listener's brain (*25, 26*). Prior research has shown that speaker-listener neural coupling occurred across a wide range of brain regions, including both the classical language regions and the prefrontal cortex (*27-30*). Importantly, the strength of the speaker-listener neural coupling was associated with the listener's comprehension of the speech (*30-32*), suggesting the speaker-listener neural coupling as the inter-brain neural mechanisms of natural speech comprehension and communication (*22, 33*). In this way, the analysis of speaker-listener neural coupling circumvents the challenges of directly modeling the relationship between neural responses and natural speech (*26, 34*), and holds promise for unravelling the neural foundation of natural speech-in-noise comprehension from an inter-brain perspective (*26*). Our prior work demonstrated that in young listeners, neural activities of the broad language regions were coupled with the speakers, even

in noisy conditions. In particular, the neural coupling from the left inferior frontal gyrus was predictive of the listener's speech comprehension performance (*32*), highlighting its key role for young adults to adapt to the background noise. However, no inter-brain study has focused on the older adults and examined the neural mechanisms supporting their natural speech processing.

To address this research gap, the present study recruited a group of older adults (age 59-71 years old) to listen to narratives spoken by young speakers. The neural activities from old listeners and speakers were recorded by functional near-infrared spectroscopy (fNIRS), chosen for its motion insensitivity and minimal operational noise than functional magnetic resonance imaging. To fully explore the engagement and function of various brain regions, the speaker's narrative audio was added with meaningless white noise and processed into four graded noise levels from no noise to +2 dB, -6 dB and -9 dB. A significant speaker-listener neural coupling was hypothesized to reflect the functional involvement of the particular brain regions under noisy conditions. Results showed that these old listeners' neural activities from the prefrontal cortex, ventral language regions (superior and middle temporal gyrus, inferior parietal lobe, etc.) and dorsal language regions (inferior frontal gyrus, precentral and postcentral gyrus, etc.) were significantly coupled to the speaker, even in noisy conditions. When compared to a group of young listeners who listened to the same narratives (*32*), the neural coupling of the old listeners was stronger and more distributed over the brain, especially involving the prefrontal cortex. Interestingly, for the old listeners, the neural coupling from the prefrontal cortex was robustly correlated with that from the language regions in various noise levels, indicating its possible integration to the classical language network to compensate for the functional decline within the language networks. Furthermore, the neural response from the prefrontal cortex was positively correlated with the old listener's comprehension to the speech when the background noise became strong. In conclusion, the present study revealed how the older adult's brain processed naturalistic noisy speech, particularly highlighting the compensatory mechanism of the prefrontal cortex in preserving older adults' speech-in-noise comprehension ability. It enhances our

understanding of the neural basis for the cognitive preservation in older adults, shedding lights into the pathways towards the successful aging in later years of the human lifespan.

Results

Noise impacts old listener's perception and comprehension to speech

Figure 1A illustrates the experimental design of this study. A group of older adults with normal or close-to-normal hearing threshold (as shown in Figure 1D) were recruited to listen to narratives pre-recorded from a group of younger speakers (*32*). The listener's experiment was conducted separately after the speaker's experiment, for the convenience of controlling the speaking quality of speakers and incorporating noise into the speaker's narrative audios. The neural activities from the speakers and the listeners were measured by fNIRS from the same coverage of brain regions, including prefrontal cortex and classical language regions (Figure 1B, see Method for more details). The listeners' subjective ratings of the narratives' clarity and intelligibility and their comprehension scores were collected. Results are shown in Figure 1C. The repeated-measures analysis of variance (rmANOVA) revealed that noise level significantly affected the old listeners' perception and comprehension to the speech (clarity: $F(3, 84) = 76.17$, $p < .001$, partial $\eta^2 = .73$; intelligibility: $F(3, 84) = 51.15$, $p < .001$, partial $\eta^2 = .65$; comprehension: $F(3, 84) = 19.69$, $p < .001$, partial $\eta^2 = .41$). Post hoc analysis showed that, for the clarity and the intelligibility ratings, all pairwise comparisons between noise levels were significant (post hoc *t*-test, $p < .001$, corrected by false discovery rate (FDR), (*35*)), with a lower rating when noise increased. For the comprehension score, except for the comparison between NN and 2 dB (post hoc *t*-test, $p > .999$), the other pairwise comparisons were significant (post hoc *t*-test, $p < .05$, FDR corrected). Notably, the comprehension scores of all the listeners are substantially higher that the random level (25%) in all conditions. Even in the strongest noise level (-9 dB), the average score was 65.3±2.6% (mean±SE), suggesting a pretty good preservation of speech-in-noise comprehension ability for

the old listeners in this study.

To examine the relationship between the perceptual ratings and comprehension performance, the correlation coefficients were computed across these behavioral measures. Results showed that the average ratings of clarity and intelligibility was significantly correlated (Pearson r = .40, p = .03). In contrast, the correlation between these two ratings and the comprehension score was not significant (ps > .23), suggesting a dissociation between the older listener's perceptual feeling and actual comprehension of the speech. Besides, no significant correlation between these behavioral measures and the old listener's hearing thresholds or age was found (ps > .14).

Old listener's neural activities are coupled to the speaker

To examine how old listener's neural activities were coupled to the speaker, we conducted an rmANOVA on the speaker-listener neural coupling among all the four noise levels and the resting-state baseline. It could help to reveal significant neural coupling at any noise levels than the baseline and (or) the significant difference in the coupling strength across different noisy levels. A non-parametric cluster-based methodology (see Methods for more details) identified 57 clusters where speaker-listener neural coupling differed among the five conditions. These clusters covered the bilateral superior temporal gyrus (STG), middle temporal gyrus (MTG) (CH19/21/29/31) and right inferior frontal gyrus (IFG) (CH27) at the speaker's side, which were likely to be speech-production-related brain regions (*30, 36*). At the listener's side, the clusters covered an extensive range of brain regions, including the wide range of the prefrontal cortex (CH2, CH5-16) and the classical language regions. Based on the anatomical localization and functional organization within the language network (*31, 32, 37, 38*), these language regions were divided into ventral language regions, including right STG, MTG (CH29/31/35), bilateral inferior parietal lobe (IPL, CH23/24/26/33/34/36), and dorsal language regions, including bilateral IFG (CH17/27), bilateral pre- and post-central gyrus (pre-/postCG, CH18/20/22/28/30/31). The channel and localization of these channel combinations are shown in Figure 2A

and S1A. The strength of the neural coupling for each cluster is shown in Figure S2. For all these clusters, the frequency band was around 0.01-0.03 Hz, as shown in Figure S1B. It was in the same frequency band as discovered in our previous studies on young listeners (*31, 32*). The specific information of all the clusters, including the channels of speaker and listener, frequency band, and cluster-level statistics, are listed in Table S1.

Based on the brain region at the listener's side, these inter-brain clusters were grouped into three patterns, i.e., O-Prefrontal (prefrontal cortex, O means the clusters from the old listeners), O-Ventral (ventral language regions) and O-Dorsal (dorsal language regions). The neural coupling for these three inter-brain patterns was derived by averaging the coupling values across clusters within the same group. These results at the pattern level are illustrated in Figure 2C. Post hoc analysis showed that for all of these three patterns, the neural coupling at the four noise levels were significantly higher than the resting-state condition (post hoc *t*-test, $p < .05$, FDR corrected), indicating that the neural activities of old listeners were significantly coupled to the speaker in both quiet and noisy conditions. Besides, the neural coupling of the O-Prefrontal pattern at NN is higher than -9 dB (post hoc *t*-test, $p = .016$, FDR corrected), and marginally higher than that at 2 dB and -6 dB (post hoc *t*-test, *p*s = .052, .052, FDR corrected), suggesting its sensitivity to the appearance of background noise. However, no significant difference was observed between the neural coupling of the O-Prefrontal pattern and that from the O-Ventral or O-Dorsal patterns, even in the noisy conditions (*p*s > .10, FDR corrected).

Distinct inter-brain neural patterns between old listeners and young listeners

To explore how age influenced the neural mechanisms of speech-in-noise processing, we compared the speaker-listener neural coupling of the old listeners to a group of young listeners who listened to the same narratives (*32*). As illustrated in Figure 2A/B, the inter-brain neural patterns of the young listeners differed from that of the old listeners. As compared to the old listeners, the inter-brain neural patterns of the young listeners did not engage the prefrontal cortex, and only covered a few brain regions in

the ventral language regions (CH33/35/36, right MTG/IPL) and the dorsal language regions (CH17, left IFG). In contrast, they covered extensive brain regions at the speaker's side, involving the prefrontal cortex and a broad coverage of ventral and dorsal language regions. These clusters were also grouped into two patterns and named as Y-Ventral and Y-Dorsal respectively (Y means the clusters from young listeners, to distinguish them from the patterns of the old listeners), based on their anatomical location at the listener's side. The information of the young listeners' clusters is listed in Table S2.

We examined whether the neural coupling from the Y-Ventral and Y-Dorsal patterns was significant in the old listeners. Results showed that for the Y-Ventral pattern, the neural coupling at NN and +2 dB was higher than that of the resting-state (Paired samples *t*-test, *t*s = 2.25, 3.48; *p*s = .032, .005, FDR corrected; Cohen's *d*s = 0.42, 0.65), -6 dB and -9 dB was marginally higher than the resting-state (Paired samples *t*-test, *t*s = 1.77, 1.57; *p*s = .054, .063, FDR corrected; Cohen's *d*s = 0.33, 0.29). For the Y-Dorsal pattern, the neural coupling at NN and -9 dB was higher than that of the resting-state (Paired samples *t*-test, *t*s = 3.16, 3.17; *p*s = .005, .005, FDR corrected; Cohen's *d*s = 0.59, 0.59), +2 dB and -6 dB were marginally higher than resting-state (Paired samples *t*-test, *t*s = 1.83, 1.73; *p*s = .054, .054, FDR corrected; Cohen's *d*s = 0.34, 0.32). For the young listeners, the significance of neural coupling at O-Prefrontal, O-Ventral and O-Dorsal patterns was also examined. As shown in Figure S3, their neural coupling in all the four noise levels was significantly higher than that of the resting-state baseline (Paired samples *t*-test, *t*s > 3.00; *p*s < .05, FDR corrected; Cohen's *d*s > 0.91).

To examine the specificity of these neural patterns for particular listener groups, we compared the strength of these inter-brain neural coupling between the old listener and the young listener. The coherence of the resting-state baseline was first subtracted from that of the four noise levels, and then devoted to a two-way mixed-design ANOVA (between-participant factor: listener group/age; within-participant factor: SNR) to analyze how age impacted the neural coupling. Results showed that, for all the five patterns, the main effects of listener group were significant (*F*s > 4.11, *p*s

< .05, FDR corrected). For the O-Prefrontal, O-Ventral and O-Dorsal patterns, the neural coupling of the old listener was significantly higher than that of young listener. In contrast, for the Y-Ventral and Y-Dorsal patterns, the neural coupling of the young listener was significantly higher than that of the old listener. These results are shown in Figure 2D. The main effect of SNR and the interaction effect between the listener group and SNR were not significant (Fs < 1.84, ps > .14). The group comparisons of the neural coupling in four noise levels are shown in Figure S4.

Furthermore, we compared the inter-brain neural coupling between two types of inter-brain neural patterns (O-Prefrontal/Ventral/Dorsal vs. Y-Ventral/Dorsal). A two-way rmANOVA (within-participant factors: inter-brain pattern, SNR) was conducted for each listener group. Results showed that the main effect of the inter-brain pattern was significant for both listener groups (old listener: $F(4, 112) = 16.46$, $p < .001$; young listener: $F(4, 56) = 4.51$, $p = .003$). Post hoc analysis further showed that, for the old listeners, the neural coupling from the O-Prefrontal, O-Ventral and O-Dorsal patterns was significantly higher than that from both the Y-Ventral and Y-Dorsal patterns (post hoc t-test, ps < .05, FDR corrected). In contrast, for the young listeners, the neural coupling from the O-Prefrontal, O-Ventral and O-Dorsal patterns was significantly lower than that from the Y-Dorsal pattern (post hoc t-test, ps = .040, .003, .007, FDR corrected), but not the Y-Ventral pattern (post hoc t-test, ps > .05, FDR corrected). The main effect of SNR and interaction effect between inter-brain pattern and SNR were not significant (Fs < 1.56, uncorrected ps > .10). These findings suggested distinct inter-brain neural patterns for speech(-in-noise) processing in the old versus young listeners.

Inter-brain neural coupling from prefrontal cortex correlates with old listener's comprehension under noisy conditions

To examine the behavioral relevance of the speaker-listener neural coupling, a correlation analysis was performed between the old listeners' speech comprehension scores and their neural coupling. The analysis was conducted both at the cluster level (Figure 3A/C) and at the pattern level (Figure 3B/D). At the cluster level, these r-

values were computed for each cluster, and then Fisher- *z* transformed. These *r*-values were then devoted to a one-sample *t*-test to examine their significance in each noise level, and further compared between different noise levels to examine the effects of noise. At the pattern level, the correlation between the average neural coupling of all clusters for one particular inter-brain neural pattern and comprehension score was computed.

For the O-Prefrontal pattern, significant correlation was observed in the moderate or strong noise level. At the cluster level, the *r*-values were significant at -6 dB and -9 dB (One sample *t*-test, *t*s = 5.84, 4.14; *p*s < .001, FDR corrected; Cohen's *d*s = 1.12, 0.80), but not at NN and +2 dB (*p*s > .26). The pairwise *t*-test further showed that the *r*-values at NN were lower than those at the other three conditions (Paired samples *t*-test, *t*s < -3.21; *p*s < .05, FDR corrected; Cohen's *d*s > 0.61), and the *r*-values at +2 dB were lower than those at -6 dB and -9 dB (Paired samples *t*-test, *t*s = -2.60, -2.06; *p*s = .023, .059, FDR corrected; Cohen's *d*s = 0.50, 0.40). At the pattern level, the correlation between the neural coupling of the O-Prefrontal pattern and the comprehension score was significant at -6 dB and -9 dB (Pearson *r*s = .39, .37; *p*s = .035, .047, uncorrected), but not at NN and +2 dB (*p*s > .39).

For the O-Ventral pattern, significant correlation results were mainly observed in the moderate noise level. At the cluster level, the *r*-values were significant at -6 dB and -9 dB (One sample *t*-test, *t*s = 3.92, 3.89; *p*s = .001, .001, FDR corrected; Cohen's *d*s = 0.92, 0.91), but not at NN and +2 dB (*p*s > .13). However, no significant results were found when comparing the results between any noise levels (*p*s > .07, FDR corrected). At the pattern level, the correlational relationship between the average neural coupling of the O-Ventral pattern and comprehension was only significant at -6 dB (Pearson *r* = .49, *p* = .007, uncorrected), but not in the other three conditions (*p*s > .12).

For the O-Dorsal and Y-Ventral patterns, no significant results were found at the cluster level (*p*s > .10, FDR corrected) or at the pattern level (*p*s > .10). For the Y-Dorsal pattern, at the cluster level, the *r*-values at NN and -6 dB were higher than those at +2 dB and -9 dB (Paired samples *t*-test, *t*s > 2.48; *p*s < .05, FDR corrected; Cohen's *d*s > 0.64). However, these *r*-values were neither significant at the cluster

level (*p*s > .07, FDR corrected) or at the pattern level (*p*s > .10).

Neural coupling from prefrontal cortex integrates with language regions in old listener

To figure out how the prefrontal cortex was functionally connected with the language regions within the aging brain, the Spearman correlation between the neural coupling from these regions was computed under various noise levels and for both the old versus young listeners. For the old listeners, the inter-brain neural patterns of the O-Prefrontal, O-Ventral and O-Dorsal patterns were interconnected. At all the four noise levels, the neural coupling from the O-Prefrontal pattern was positively correlated with that from the O-Ventral pattern (Pearson *r*s = 45, .48, .38, .58; *p*s = .014, .008, .043, .001, FDR corrected), and the O-Dorsal pattern (Pearson *r*s = 50, .51, .43, .38; *p*s = .006, .006, .022, .042, FDR corrected). The coupling strength from the O-Ventral pattern was also positively correlated with the that from the O-Dorsal pattern in all the four noise levels (Pearson *r*s = 76, .69, .46, .43; *p*s < .001, < .001, .013, .021, FDR corrected). These results suggested a close within-network connectivity of the language regions and the possible integration of the prefrontal cortex into the language network in older adults (Figure 4A/C).

For the young listeners, the neural coupling from the O-Ventral and the O-Dorsal patterns was also correlated at all the four noise levels (Pearson *r*s = .69, .72, .87, .61; *p*s = .006, .004, < .001, .018, FDR corrected). However, the neural coupling from the O-Prefrontal pattern was only correlated with that from the O-Ventral and O-Dorsal patterns at -6 dB (Pearson *r*s = .65, .87; *p*s = .005, .010, FDR corrected), but not at the other noise levels (*p*s > .05, FDR corrected). These results indicated the prefrontal cortex might be less connected to the classical language regions for the young listeners. Interestingly, for both the old listeners or the young listeners, the correlation between the neural coupling from the Y-Ventral and the Y-Dorsal patterns were not significant at any noise levels (*p*s > .05, FDR corrected).

Besides, we also observed some correlation across two types of inter-brain neural patterns. For the old listeners, the neural coupling from the Y-Ventral pattern was

positively correlated with that from the O-Prefrontal pattern at +2 dB (Pearson r = .44, p = .048, FDR corrected), and the O-Ventral pattern at NN and +2 dB (Pearson rs = .37, .44; ps = .017, .017, FDR corrected). The neural coupling from the O-Dorsal was negatively correlated with that from the Y-Dorsal pattern (Pearson r = -.51, p = .006, FDR corrected). For the young listeners, the neural coupling from the Y-Ventral pattern was correlated with that from the O-Ventral pattern at NN and -9 dB (Pearson rs = .53, .54; ps = .045, .042, FDR corrected), and the O-Dorsal pattern at -6 dB (Pearson r = .60, p = .021, FDR corrected). The neural coupling from the Y-Dorsal pattern was correlated with that from both the O-Prefrontal and O-Ventral patterns at NN (Pearson rs = .57, .54; ps = .030, .042, FDR corrected). These results might reflect a complex relationship between the two types of the inter-brain neural patterns.

Single-brain activation from prefrontal cortex correlates with old listener's speech-in-noise comprehension

To better understand the mechanism and function of the prefrontal cortex and language-related regions within the aging brain, a single-brain neural activation analysis was performed. As shown in Figure 5A, significant activation was observed in both quiet and noisy conditions. The prefrontal cortex was significantly activated at NN, +2 dB and -9 dB (ps < .001, < .001, = .001, FDR corrected), and marginally significant at -6 dB (p = .073, FDR corrected). The ventral and dorsal language regions were all significantly activated in all the four noise levels (ps < .05, FDR corrected). No difference was found when comparing the neural activations in difference noise levels (ps > .18). The neural activation of the old listeners was further compared to that of the young listeners (Figure S5). No significant result was observed in any brain regions and in any noise level (ps > .18, FDR corrected).

A correlation analysis was conducted to explore the relationship between the old listener's brain activation and speech comprehension performance. As shown in Figure 5B, the activation of prefrontal cortex and ventral language regions were positively correlated with comprehension score at -9 dB (Pearson rs = .38, .38; ps = .041, .045, uncorrected). The correlations in the other noise levels and in the dorsal

language regions were not significant (*p*s > .15). Given that both the inter-brain neural coupling and single-brain activation of prefrontal cortex correlated with the comprehension performance when noise became strong (-9 dB), we analyzed their correlational relationship to further examine whether a high coupling of the old listeners related to a high activation within the corresponding brain region. This correlation result was not significant (Pearson r = .03, p = .86). The correlation in various noise levels and from other brain regions are further shown in Figure S6.

Discussion

This study employed an inter-brain neuroscience approach to investigate the neural mechanisms within the aging brain that support natural speech-in-noise comprehension. The speaker-listener neural coupling analysis revealed that the old listener's neural activities in the prefrontal cortex, ventral and dorsal language regions were coupled to the speakers, even under the noisy conditions. Compared to the young listeners, the old listener's neural coupling was stronger and involved more extensive brain regions, particularly the prefrontal cortex. Notably, the neural coupling in the prefrontal cortex was closely associated with that from the language regions, suggesting its integration into the classical language network for speech(-in-noise) processing. Moreover, when noise became strong, the strength of speaker-listener neural coupling and the activation from the prefrontal cortex were positively correlated with the old listener's comprehension performance. These results highlighted the compensatory and functional role of prefrontal cortex in maintaining the speech-in-noise comprehension ability for the older adults. In conclusion, the present study revealed the neural mechanisms of naturalistic noisy speech processing within the aging brain, shedding lights on how the prefrontal cortex contributed to the cognitive preservation in the older adults.

This study advanced our understanding about the compensatory mechanisms of the prefrontal cortex in older adults. Although prior studies have widely reported its activation during speech processing in older adults (*2, 5, 6, 20*), it remains much

elusive how the prefrontal cortex was involved to facilitate the speech processing within the aging brain. By regarding the speaker's brain as a reference, we found that the neural activities from the old listener's prefrontal cortex was coupled to the speaker's speech-related neural activities. This speaker-listener neural coupling was notably significant in both quiet and noisy conditions, suggesting that the prefrontal cortex was broadly involved in the speech processing in various listening environments. As compared to the young listeners, the old listener's neural coupling from the prefrontal cortex was stronger. Considering the age-related neural deteriorations took place almost over the whole brain, this age-enhanced response could be interpreted as a compensatory mechanism for preventing a sharp decrease of the cognitive function in the older adults (*3, 39*). Moreover, we found that for the old listeners, the neural coupling from the prefrontal cortex was stably associated with that from the language regions in various noisy levels. In contrast, this phenomenon was not observed in young listeners. These results suggest that the prefrontal cortex might be integrated into the classical language network to compensate for the age-related declines of the speech processing within the language network. These results coincide with existing discoveries of an increasing global connectivity within the aging brain (*20, 40, 41*), which have suggested a substantial neural reorganization serving to offset the widespread neural deterioration (*41-43*). Taken together, this study highlighted the compensatory engagement of the prefrontal cortex in the language-specific processing for facilitating the speech-in-noise processing in older adults.

Furthermore, this study for the first time highlighted the functional role of the prefrontal cortex in older adult's speech-in-noise comprehension in naturalistic noisy environments. We found that both the neural coupling and the activation of the prefrontal cortex was positively correlated with the old listener's comprehension to the speaker's speech, especially when the environmental noise became strong. Considering the pretty good speech-in-noise comprehension performance exhibited by the old listeners in this study, our findings suggest the critical role of the prefrontal cortex for the cognitive preservation of the old adult's speech-in-noise ability.

Moreover, this study largely extends previous studies that mainly relied on simplified language materials, such as syllables or words (*2, 5, 6, 20, 44*), which could not fully cover the complex neurocognitive components as involved in the understanding of naturalistic speech, e.g., narratives, in real-life scenarios (*13, 14*). By employing the speaker's unrehearsed narratives as the stimuli, this study therefore offers a more ecologically valid insight into how the prefrontal cortex facilitates the older adults' comprehension to others in everyday noisy settings. Notably, while the speaker-listener neural coupling and the natural activation both correlated with the older adult's speech-in-noise performance, their correlation was not significant. It suggests that the speech processing within a brain region does not necessarily correlate with the intensity of neural activities. Thus, the analysis of speaker-listener neural coupling might offer complementary insights beyond the single-brain neural activation analysis (*45*), calling for more attention in future research.

This study also examined the processing of natural speech within the classical language regions of the aging brain. We found that older listeners' neural activities across a wide range of brain areas in both hemispheres were coupled to the speaker. It contrasts with the more localized neural coupling observed in young listeners (*31, 32*). Our results indicated that older adults not only recruited brain regions outside their typical functional networks, like the prefrontal cortex discussed above, but also utilized extensive regions within the language networks and engaged homologous regions on bilateral hemispheres for maintaining their speech ability (*5, 46, 47*). Interestingly, this study identified a link between the old listeners' speech comprehension and neural responses from the ventral language regions, especially under moderate to strong noise levels, whereas the dorsal language regions did not show a significant correlation. One possible explanation for this discrepancy could contribute to the distinct adaptive mechanisms for adapting to background noise within these brain regions. The ventral regions may selectively process target speech to filter out background noise (*15, 17*) and (or) resolve noise-induced ambiguities through contextual integration (*48*). Behavioral evidence has shown that the contextual cues can improve the old listener's speech comprehension in noisy

environments (*49*). In the same line, the old listener's speech-in-noise comprehension was inherently associated with the neural responses from the ventral language regions. In contrast, the dorsal language regions could facilitate the speech processing by generating an internal representation of speech (*50, 51*), e.g., enabling the clear phonological structures of the noise-masked speech by referring to pre-acquired phonological knowledge (*52*). While this could be crucial for accurately perceiving the speech morphology, e.g., identifying the phoneme and syllable units (*53, 54*), in noise, it may be less critical for understanding speech content in real-life situations, explaining the lack of association between speech comprehension and neural responses from the dorsal regions. This explanation, however, necessitates further empirical investigation in future studies.

Furthermore, the inter-brain neural patterns at the speaker's side could offer evidence of the decreased computational efficiency in the aging brain (*55, 56*). While the old listeners recruit a wide array of brain regions for speech processing, the neural coupling at the speaker's brain is limited to fewer regions. In contrast, the younger listeners exhibit neural coupling with a more extensive network of regions in the speaker's brain, including the bilateral prefrontal cortex, which is crucial for higher-level speech processing tasks. The neural coupling between speakers and listeners from specific brain regions associates with the processing of different speech aspects (*27, 33*). For example, coupling from the primary auditory cortex is linked to early acoustic processing (*30*), whereas coupling from higher-level regions like the posterior temporal lobe and frontal cortex is associated with more complex processes such as semantic and contextual interpretation (*27*). For older adults, the limited coverage of inter-brain neural patterns at the speaker's side, particularly the absence of coverage in the speaker's prefrontal cortex, suggests a diminished capability for higher-level speech processing compared to younger adults. This is further evidenced by our findings that old listeners showed significantly weaker neural coupling from the speakers' prefrontal cortex than younger listeners. These substantial differences in the inter-brain neural patterns, which are respectively specific to either young or older adults, imply that older and young adults could engage distinct inter-brain

mechanisms to achieve their natural speech-in-noise comprehension. Yet, this hypothesis still requires more exploration in future research.

In conclusion, the present study revealed how natural speech was processed within the aging brain and particularly highlighted the compensatory role of prefrontal cortex in the cognitive preservation of the older adults' speech-in-noise ability. Future studies could build upon these findings in the following aspects. Firstly, this study focused exclusively on healthy aging adults with normal hearing thresholds and pretty good cognitive abilities. However, the old adult population exhibits significant heterogeneity across a broader age range (*57, 58*), diverse hearing loss or impairments (*59, 60*), varying language experience (*61*), education backgrounds (*62*) and etc. These variables can profoundly influence the structure, function, and (re)organization of the aging brain. To obtain a more comprehensive understanding of how the aging brain processes speech in noise, future studies could recruit different groups of older adults and further compare their neural responses during speech-in-noise comprehension. Secondly, this study identified and organized the speaker-listener neural coupling patterns based on the anatomical structure at the listener's side. The recent development of advanced mathematical methodologies, e.g., dynamic inter-brain synchrony state analysis (*63*), offered a data-driven approach to define the inter-brain neural patterns. Future studies could adopt these techniques for a hypothesis-free exploration of inter-brain neural patterns (*64*). It could also help to better understand the functional organization of these brain regions. Thirdly, future studies could model speaker-listener neural coupling with multi-level features of speaker's speech, e.g., acoustics and semantics, to further identify the computational processes underlying these compensatory inter-brain neural mechanisms. These speech features could be either modelled to the speaker's or listener's neural responses (*36*) or directly modelled to the temporal dynamics of speaker-listener neural coupling (*65*). This approach would provide further insights into the specific computational processing behind those age-related compensatory neural coupling.

Methods

Participants

Thirty older adults (15 males, 15 females; age 59 to 71 years old) participated in the study. The sample size was determined by a prior power analysis using G*Power (*66*), with the repeated measures F-test was employed (number of measurements = 4). The effect size was designed at the medium level of 0.25. The significance level (alpha) was set as 0.05, and the power was set as 0.9. All participants were native Chinese speakers, right-handed, and had an educational level equivalent to or higher than high school, ensuring basic reading proficiency. All participant passed the Mini-Mental State Examination (MMSE) of Chinese version (>26 scores). Based on the definition of hearing loss (World Report on Hearing by WHO, https://www.who.int/publications/i/item/9789240020481), one female participant was excluded due to a mild to moderate hearing loss as assessed by pure-tone audiometry (34 dB hearing level, average pure tone threshold between 500 and 4000Hz). For the remaining twenty-nine participants, twenty-seven of them have a normal hearing threshold (≤20 dB), the rest two of them have a close-to-normal hearing threshold (22, 23 dB). Figure 1D shows the group average and standard deviation of their hearing levels.

The study was conducted in accordance with the Declaration of Helsinki and was approved by the local Ethics Committee of Tsinghua University and the Institutional Review Board of the Beijing Institute of Otolaryngology and Beijing Tongren Hospital. All participants provided written informed consent prior to the experiment.

Experimental Design

The experimental design is illustrated in Figure 1A. The old listeners were instructed to listen to pre-recorded narrative audios under various noise conditions. These narratives were spoken by a group of young speakers, which were from our previous study (*32*). Both the neural activities of the old listeners and the young speakers were measured by fNIRS.

Stimuli

Each participant listened to sixteen narratives, with each lasting for 85 to 90 seconds. These narratives were about daily topics that were adapted from the National Mandarin Proficiency Test, such as favorite movies or travelling experiences. The narratives were spoken by four young adults (2 males, 2 females; 21 to 25 years old), all of whom were native Chinese speakers with professional training in broadcasting and hosting. Two of them (one male, one female) contributed five stories each, and two speakers (one male, one female) contributed three stories each. All narratives were about the speaker's personal experiences, which were unfamiliar to the listeners. These audios were recorded by a regular microphone at a sampling rate of 44,100 Hz in a sound-attenuated room, and were then resampled to the 48,000 Hz to align with the speaker’s output frequency for this study.

Narrative audios were added with meaningless broadband white noise. For each listener, they were processed into one of four noise levels: no noise (NN) level and three noisy levels with the signal-to-noise ratio (SNR) of +2 dB, -6 dB, and -9 dB. Each noise level included four narratives. All processed audios were normalized for the average root mean square sound pressure level (SPL). For each narrative, four four-choice questions regarding narrative content were prepared to evaluate the listener’s comprehension performance. For example, one question was, “What is the relationship between the speaker and her friend? (说话人和朋友是什么关系)” and the four choices were 1) teacher-student, 2) cousins, 3) neighbors, and 4) roommates (1.师生关系, 2.姐妹关系, 3.邻居关系, and 4.室友关系).

Experimental Procedure

The listener’s experiment was carried out in a sound-attenuated room. Sixteen narratives are structured into sixteen trials, with one narrative in each trial. During each trial, participants listened to one narrative under one of the four noise levels. After listening, they rated the clarity and intelligibility of the audio using a 7-point

Likert scale, and completed a comprehension test based on the four choice questions. The comprehension score was calculated as the accuracy of these questions. Then, they could arrange a rest for a minimum of 10 seconds before proceeding to the next trial. One practice trial was conducted using an additional speech audio stimulus at -2 dB SNR level.

Before the task session, there is a 3-min resting-state session. Participants were instructed to get relaxed with their eyes closed. This resting-state session serves as the baseline for task session.

Neural measurement

The listeners' neural activities were recorded from 36 channels using an fNIRS system (NirScan Inc., HuiChuang, Beijing). The fNIRS signals were collected at a sampling rate of 11 Hz, utilizing near-infrared light of two different wavelengths (730 and 850 nm). The concentration change of oxy-hemoglobin (HbO) and deoxy-hemoglobin (HbR) for each channel was then obtained based on the modified Beer–Lambert law.

Three sets of optode probes were positioned to cover the prefrontal cortex and bilateral inferior frontal, pre- and post-central, inferior parietal, middle and superior temporal gyrus, etc. As shown in Figure 1C, the positions of CH21 and CH31 were aligned with T3 and T4, respectively, as per the international 10–20 system. The central point of the prefrontal probe set was placed at the FPz position. To obtain a probabilistic reference to specific cortical region for each fNIRS channel, the topographic data was mapped onto a standardized MNI-space (Montreal Neurological Institute) (*67, 68*) by using NIRS_SPM (*69*). The MNI coordinates and anatomical labels for each channel are listed in Table S3.

Neural data of speaker and young listeners

The neural data of the speakers and a group of young listeners were from our previous study (*32*). The speakers' neural activities were recorded from the same coverage of brain regions, but by another fNIRS system (NirScan Inc., HuiChuang, Beijing) with

a sampling rate of 12 Hz and using near-infrared light at three different wavelengths (785, 808, and 850 nm). These data were downsampled to 11 Hz to match the sampling rate of the old listener in this study.

The young listeners comprised fifteen young adults (7 males, 8 females; ages 18 to 24 years old). Their neural signals were obtained using the same fNIRS system, with the same brain coverage as the speakers. The experimental design for the young listeners were the same as that for old listeners in this study. However, they listened to a larger number of narratives (thirty-two narratives, with eight narratives in each noise level). Only neural data from the same sixteen narratives as used in this study were selected for the comparison between the young listeners versus the old listeners.

Data analysis

Preprocessing

A two-step preprocessing method based on HoMER2 software package (*70*) was employed to remove possible motion artifacts. The first step utilized an algorithm grounded in target principal component analysis (function: hmrMotionCorrectPCArecurse; input parameters: tMotion = 0.5, tMask = 1, STDthresh = 30, AMPthresh = 0.5, nSV = 0.97, maxIter = 5). This algorithm discerned artifact-associated principal components and then reconstructed the cleaned signals using the remaining components (*71*). Subsequently, the second step adopted a linear interpolation method (*72*), which identified the motion artifacts based on a predetermined threshold (function: hmrMotionArtifactByChannel; input parameters: tMotion = 0.5, tMask = 1, STDEVthresh = 30, AMPthresh = 0.5), and then corrected these artifacts through cubic spline interpolation (function hmrMotionCorrectSpline; input parameters: p = 0.99). The above algorithms and parameters were all in consistence with that for young listeners (*32*).

Inter-brain neural coupling analysis

The Wavelet Transform Coherence (WTC) was employed to analyze the relationship between the speaker's and listener's neural activity. WTC allows for the assessment of

cross-correlation between two physiological signal series across frequency and time dimensions (*73*). Each trial during the task sessions was initially segmented and further extended to a duration of 300 seconds, which included the 90-second trial and two additional 105-second periods both preceding and following the trial. This extension aimed to facilitate a reliable computation of inter-brain couplings across the desired frequency range. WTC was computed over the 300-second fNIRS signal segments from both the listener and the corresponding speaker, resulting in a coherence matrix organized across time and frequency domains. In the time domain, coherence values were averaged across the entire 90-second trial and subsequently converted to Fisher-*z* values. In the frequency domain, 75 frequency bins ranging from 0.01 to 0.7 Hz were selected for subsequent analysis. Frequencies outside this range were excluded to mitigate aliasing of higher-frequency physiological noise, like cardiac activity (~0.8–2.5 Hz), and very-low-frequency fluctuations (*74*). Next, coherence values from four trials under the same noise levels were averaged. The coherence value for the middle 90 s of the resting-state session were calculated in the same way. The above calculation was conducted for all speaker-listener channel combinations, creating a total of 1296 cross-channel combinations (36 channels from the speaker × 36 channels from the listener). Consequently, each listener had coherence value under five different conditions, i.e., four speech conditions vs. the resting-state condition, across 1296 channel combinations and 75 frequency bins (0.01-0.07 Hz).

At the group level, a repeated-measures analysis of variance (rmANOVA) was applied to examine the modulation of speech condition on the speaker-listener neural coupling for each channel combination and frequency bin. A nonparametric cluster-based permutation method was utilized to address the issue of multiple comparisons (*75*). This method grouped neighboring frequency bins with uncorrected p-values below 0.05 into clusters and summed the *F*-statistics of these bins as the cluster statistic. A null distribution was generated with the maximum cluster-level statistics from 1,000 permutations. In each permutation, the clusters were calculated with labels of different trials in five conditions shuffled within each participant. Corrected *p*-values for each

cluster were derived by comparing the cluster-level statistics to the null distribution. A cluster was significant if the *p*-value was lower than 0.05 level. For each cluster, the speaker-listener neural coupling within the corresponding frequency bins were averaged and further devoted to the subsequent analysis.

Comparison between old listeners and young listeners

A two-factor mixed-design ANOVA (within-subject factor: noise level; between-subject factor: listener group) was used to compare the speaker-listener neural coupling between the old listeners and young listeners. Post hoc analysis was further performed whether the main effect of listener group or the interaction effect between noise level and listener group was significant.

Except for the clusters obtained from the old listeners, the clusters showing significant speaker-listener neural coupling in the young listeners was also included into analysis. These clusters centered over the listener's left IFG (CH17), right MTG and IPL (CH35-36). They covered distributed brain areas at the speaker's side, including the bilateral prefrontal cortex (CH4-7/9/11-12/14-15), bilateral postCG (CH22/32) and bilateral IPL (CH23-24/26/30/32-34). The brain regions of these channel combinations are shown in Figure 2A. The channel combination and the frequency band of these clusters are listed in Table S2.

Behavioral relevance analysis

To assess the behavioral relevance of the speaker-listener neural coupling, the Spearman correlation was calculated between the coherence values and old listeners' speech comprehension performance at each noise level.

Single-brain activation analysis

To better explain the mechanism of those brain regions showing significant speaker-listener neural coupling, the neural activity of the brain regions was further analyzed. The preprocessed fNIRS signals were first filtered to 0.01-0.03Hz, which was determined by the above speaker-listener neural coupling analysis. Next, they were

normalized by the mean value and standard deviation from the middle 90 s of the resting-state session, and then averaged over the entire 90-s duration for each trial. Then, they were averaged among trials under the same noise level, and further averaged among multiple channels within the same region or network, i.e., prefrontal cortex, ventral language regions or dorsal language regions. Lastly, at the group level, the significance and the behavioral relevance of these neural activation were respectively examined by *t*-test and Spearman correlation analysis.

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Reference

1. J. E. Peelle, A. Wingfield, The Neural Consequences of Age-Related Hearing Loss. *Trends Neurosci* **39**, 486-497 (2016).
2. P. Tremblay, V. Brisson, I. Deschamps, Brain aging and speech perception: Effects of background noise and talker variability. *Neuroimage* **227**, (2021).
3. R. Cabeza, M. Albert, S. Belleville, F. I. M. Craik, A. Duarte, C. L. Grady, U. Lindenberger, L. Nyberg, D. C. Park, P. A. Reuter-Lorenz, M. D. Rugg, J. Steffener, M. N. Rajah, Maintenance,

reserve and compensation: the cognitive neuroscience of healthy ageing. *Nat Rev Neurosci* **19**, 701-710 (2018).

4. W. Kang, J. Wang, A. Malvaso, Inhibitory Control in Aging: The Compensation-Related Utilization of Neural Circuits Hypothesis. *Front Aging Neurosci* **13**, 771885 (2021).
5. J. Ansado, Y. Marsolais, I. Methqal, F. Alary, Y. Joanette, The adaptive aging brain: evidence from the preservation of communication abilities with age. *Eur J Neurosci* **37**, 1887-1895 (2013).
6. P. Tremblay, A. S. Dick, S. L. Small, Functional and structural aging of the speech sensorimotor neural system: functional magnetic resonance imaging evidence. *Neurobiol Aging* **34**, 1935-1951 (2013).
7. P. C. Wong, J. X. Jin, G. M. Gunasekera, R. Abel, E. R. Lee, S. Dhar, Aging and cortical mechanisms of speech perception in noise. *Neuropsychologia* **47**, 693-703 (2009).
8. M. Heilbron, K. Armeni, J. M. Schoffelen, P. Hagoort, F. P. de Lange, A hierarchy of linguistic predictions during natural language comprehension. *Proc Natl Acad Sci U S A* **119**, e2201968119 (2022).
9. A. Goldstein, Z. Zada, E. Buchnik, M. Schain, A. Price, B. Aubrey, S. A. Nastase, A. Feder, D. Emanuel, A. Cohen, A. Jansen, H. Gazula, G. Choe, A. Rao, C. Kim, C. Casto, L. Fanda, W. Doyle, D. Friedman, P. Dugan, L. Melloni, R. Reichart, S. Devore, A. Flinker, L. Hasenfratz, O. Levy, A. Hassidim, M. Brenner, Y. Matias, K. A. Norman, O. Devinsky, U. Hasson, Shared computational principles for language processing in humans and deep language models. *Nat Neurosci* **25**, 369-380 (2022).
10. G. Tuckute, A. Sathe, S. Srikant, M. Taliaferro, M. Wang, M. Schrimpf, K. Kay, E. Fedorenko, Driving and suppressing the human language network using large language models. *Nat Hum Behav*, (2024).
11. X. Zhang, J. Li, Z. Li, B. Hong, T. Diao, X. Ma, G. Nolte, A. K. Engel, D. Zhang, Leading and following: Noise differently affects semantic and acoustic processing during naturalistic speech comprehension. *Neuroimage* **282**, 120404 (2023).
12. J. Li, B. Hong, G. Nolte, A. K. Engel, D. Zhang, Preparatory delta phase response is correlated with naturalistic speech comprehension performance. *Cogn Neurodyn* **16**, 337-352 (2022).
13. L. S. Hamilton, A. G. Huth, The revolution will not be controlled: natural stimuli in speech neuroscience. *Lang Cogn Neurosci* **35**, 573-582 (2020).
14. S. Sonkusare, M. Breakspear, C. Guo, Naturalistic Stimuli in Neuroscience: Critically Acclaimed. *Trends Cogn Sci* **23**, 699-714 (2019).
15. B. Khalighinejad, J. L. Herrero, A. D. Mehta, N. Mesgarani, Adaptation of the human auditory cortex to changing background noise. *Nat Commun* **10**, 2509 (2019).
16. Y. Du, B. R. Buchsbaum, C. L. Grady, C. Alain, Noise differentially impacts phoneme representations in the auditory and speech motor systems. *P Natl Acad Sci USA* **111**, 7126-7131 (2014).
17. J. Gao, H. Chen, M. Fang, N. Ding, Original speech and its echo are segregated and separately processed in the human brain. *PLoS Biol* **22**, e3002498 (2024).
18. E. M. Gordon, T. O. Laumann, S. Marek, R. V. Raut, C. Gratton, D. J. Newbold, D. J. Greene, R. S. Coalson, A. Z. Snyder, B. L. Schlaggar, S. E. Petersen, N. U. F. Dosenbach, S. M. Nelson, Default-mode network streams for coupling to language and control systems. *Proc Natl Acad Sci U S A* **117**, 17308-17319 (2020).

19. E. T. Rolls, G. Deco, C. C. Huang, J. Feng, The human language effective connectome. *Neuroimage* **258**, 119352 (2022).
20. A. Pistono, L. Guerrier, P. Peran, M. Rafiq, M. Gimeno, C. Bezy, J. Pariente, M. Jucla, Increased functional connectivity supports language performance in healthy aging despite gray matter loss. *Neurobiol Aging* **98**, 52-62 (2021).
21. L. Marstaller, M. Williams, A. Rich, G. Savage, H. Burianova, Aging and large-scale functional networks: white matter integrity, gray matter volume, and functional connectivity in the resting state. *Neuroscience* **290**, 369-378 (2015).
22. L. Kingsbury, W. Hong, A Multi-Brain Framework for Social Interaction. *Trends Neurosci* **43**, 651-666 (2020).
23. Y. Farahzadi, Z. Kekecs, Towards a multi-brain framework for hypnosis: a review of quantitative methods. *Am J Clin Hypn* **63**, 389-403 (2021).
24. E. Redcay, L. Schilbach, Using second-person neuroscience to elucidate the mechanisms of social interaction. *Nat Rev Neurosci* **20**, 495-505 (2019).
25. U. Hasson, C. D. Frith, Mirroring and beyond: coupled dynamics as a generalized framework for modelling social interactions. *Philos Trans R Soc Lond B Biol Sci* **371**, (2016).
26. Z. Li, D. J. C. N. Zhang, How does the human brain process noisy speech in real life? Insights from the second-person neuroscience perspective. 1-12 (2023).
27. L. Schoot, P. Hagoort, K. Segaert, What can we learn from a two-brain approach to verbal interaction? *Neurosci Biobehav Rev* **68**, 454-459 (2016).
28. B. A. Kelsen, A. Sumich, N. Kasabov, S. H. Y. Liang, G. Y. Wang, What has social neuroscience learned from hyperscanning studies of spoken communication? A systematic review. *Neurosci Biobehav Rev* **132**, 1249-1262 (2022).
29. J. Jiang, L. Zheng, C. Lu, A hierarchical model for interpersonal verbal communication. *Soc Cogn Affect Neurosci* **16**, 246-255 (2021).
30. G. J. Stephens, L. J. Silbert, U. Hasson, Speaker-listener neural coupling underlies successful communication. *Proc Natl Acad Sci U S A* **107**, 14425-14430 (2010).
31. Z. Li, B. Hong, D. Wang, G. Nolte, A. K. Engel, D. Zhang, Speaker-listener neural coupling reveals a right-lateralized mechanism for non-native speech-in-noise comprehension. *Cereb Cortex* **33**, 3701-3714 (2023).
32. Z. R. Li, J. W. Li, B. Hong, G. Nolte, A. K. Engel, D. Zhang, Speaker-Listener Neural Coupling Reveals an Adaptive Mechanism for Speech Comprehension in a Noisy Environment. *Cerebral Cortex* **31**, 4719-4729 (2021).
33. U. Hasson, A. A. Ghazanfar, B. Galantucci, S. Garrod, C. Keysers, Brain-to-brain coupling: a mechanism for creating and sharing a social world. *Trends Cogn Sci* **16**, 114-121 (2012).
34. J. Chen, P. Qian, X. Gao, B. Li, Y. Zhang, D. Zhang, Inter-brain coupling reflects disciplinary differences in real-world classroom learning. *NPJ Sci Learn* **8**, 11 (2023).
35. Y. Benjamini, Y. Hochberg, Controlling the False Discovery Rate - a Practical and Powerful Approach to Multiple Testing. *J R Stat Soc B* **57**, 289-300 (1995).
36. O. Abbasi, N. Steingraber, N. Chalas, D. S. Kluger, J. Gross, Spatiotemporal dynamics characterise spectral connectivity profiles of continuous speaking and listening. *PLoS Biol* **21**, e3002178 (2023).
37. B. Yuan, H. Xie, Z. Wang, Y. Xu, H. Zhang, J. Liu, L. Chen, C. Li, S. Tan, Z. Lin, X. Hu, T. Gu, J. Lu, D. Liu, J. Wu, The domain-separation language network dynamics in resting state

support its flexible functional segregation and integration during language and speech processing. *Neuroimage* **274**, 120132 (2023).

38. G. Hickok, D. Poeppel, The cortical organization of speech processing. *Nat Rev Neurosci* **8**, 393-402 (2007).

39. P. A. Reuter-Lorenz, K. A. Cappell, Neurocognitive aging and the compensation hypothesis. *Curr Dir Psychol Sci* **17**, 177-182 (2008).

40. L. K. Ferreira, G. F. Busatto, Resting-state functional connectivity in normal brain aging. *Neurosci Biobehav Rev* **37**, 384-400 (2013).

41. J. Stumme, C. Jockwitz, F. Hoffstaedter, K. Amunts, S. Caspers, Functional network reorganization in older adults: Graph-theoretical analyses of age, cognition and sex. *Neuroimage* **214**, 116756 (2020).

42. D. Meunier, E. A. Stamatakis, L. K. Tyler, Age-related functional reorganization, structural changes, and preserved cognition. *Neurobiol Aging* **35**, 42-54 (2014).

43. R. Sala-Llonch, D. Bartres-Faz, C. Junque, Reorganization of brain networks in aging: a review of functional connectivity studies. *Front Psychol* **6**, 663 (2015).

44. P. C. M. Wong, M. Ettlinger, J. P. Sheppard, G. M. Gunasekera, S. Dhar, Neuroanatomical Characteristics and Speech Perception in Noise in Older Adults. *Ear Hearing* **31**, 471-479 (2010).

45. J. Li, B. Hong, G. Nolte, A. K. Engel, D. Zhang, EEG-based speaker-listener neural coupling reflects speech-selective attentional mechanisms beyond the speech stimulus. *Cereb Cortex* **33**, 11080-11091 (2023).

46. S. Wang, Y. Chen, Y. Liu, L. Yang, Y. Wang, X. Fu, J. Hu, E. Pugh, S. Wang, Aging effects on dual-route speech processing networks during speech perception in noise. *Hum Brain Mapp* **45**, e26577 (2024).

47. L. Yang, S. Wang, Y. Chen, Y. Liang, T. Chen, Y. Wang, X. Fu, S. Wang, Effects of Age on the Auditory Cortex During Speech Perception in Noise: Evidence From Functional Near-Infrared Spectroscopy. *Ear Hear*, (2024).

48. N. Golestani, A. Hervais-Adelman, J. Obleser, S. K. Scott, Semantic versus perceptual interactions in neural processing of speech-in-noise. *Neuroimage* **79**, 52-61 (2013).

49. E. Buss, S. E. Hodge, L. Calandruccio, L. J. Leiboid, J. H. Grose, Masked Sentence Recognition in Children, Young Adults, and Older Adults: Age-Dependent Effects of Semantic Context and Masker Type. *Ear Hearing* **40**, 1117-1126 (2019).

50. J. L. Schwartz, A. Basirat, L. Menard, M. Sato, The Perception-for-Action-Control Theory (PACT): A perceptuo-motor theory of speech perception. *J Neurolinguist* **25**, 336-354 (2012).

51. G. Hickok, J. Houde, F. Rong, Sensorimotor Integration in Speech Processing: Computational Basis and Neural Organization. *Neuron* **69**, 407-422 (2011).

52. M. L. Barnaud, P. Bessiere, J. Diard, J. L. Schwartz, Reanalyzing neurocognitive data on the role of the motor system in speech perception within COSMO, a Bayesian perceptuo-motor model of speech communication. *Brain and Language* **187**, 19-32 (2018).

53. Y. Du, B. R. Buchsbaum, C. L. Grady, C. Alain, Increased activity in frontal motor cortex compensates impaired speech perception in older adults. *Nat Commun* **7**, 12241 (2016).

54. L. Zhang, X. Wang, C. Alain, Y. Du, Successful aging of musicians: Preservation of sensorimotor regions aids audiovisual speech-in-noise perception. *Sci Adv* **9**, eadg7056 (2023).

55. V. Stenback, E. Marsja, M. Hallgren, B. Lyxell, B. Larsby, The Contribution of Age, Working

Memory Capacity, and Inhibitory Control on Speech Recognition in Noise in Young and Older Adult Listeners. *J Speech Lang Hear Res* **64**, 4513-4523 (2021).

56. L. Aron, J. Zullo, B. A. Yankner, The adaptive aging brain. *Curr Opin Neurobiol* **72**, 91-100 (2022).

57. M. Pronk, D. J. H. Deeg, J. M. Festen, J. W. Twisk, C. Smits, H. C. Comijs, S. E. Kramer, Decline in Older Persons' Ability to Recognize Speech in Noise: The Influence of Demographic, Health-Related, Environmental, and Cognitive Factors. *Ear Hearing* **34**, 722-732 (2013).

58. X. X. Fu, R. H. Eikelboom, B. Liu, S. Wang, D. M. P. Jayakody, The longitudinal relationship between hearing loss and cognitive decline in tonal language-speaking older adults in China. *Frontiers in Aging Neuroscience* **15**, (2023).

59. K. Slade, C. J. Plack, H. E. Nuttall, The Effects of Age-Related Hearing Loss on the Brain and Cognitive Function. *Trends Neurosci* **43**, 810-821 (2020).

60. D. Yang, D. Zhang, X. Zhang, X. Li, Tinnitus-associated cognitive and psychological impairments: a comprehensive review meta-analysis. *Front Neurosci* **18**, 1275560 (2024).

61. G. Bubbico, P. Chiacchiaretta, M. Parenti, M. di Marco, V. Panara, G. Sepede, A. Ferretti, M. G. Perrucci, Effects of Second Language Learning on the Plastic Aging Brain: Functional Connectivity, Cognitive Decline, and Reorganization. *Front Neurosci* **13**, 423 (2019).

62. S. Knight, A. Heinrich, Visual Inhibition Measures Predict Speech-in-Noise Perception Only in People With Low Levels of Education. *Front Psychol* **9**, 2779 (2018).

63. R. Li, N. Mayseless, S. Balters, A. L. Reiss, Dynamic inter-brain synchrony in real-life inter-personal cooperation: A functional near-infrared spectroscopy hyperscanning study. *Neuroimage* **238**, 118263 (2021).

64. X. Shen, L. Tao, X. Chen, S. Song, Q. Liu, D. Zhang, Contrastive Learning of Shared Spatiotemporal EEG Representations Across Individuals for Naturalistic Neuroscience. *arXiv preprint* **2402.14213**, (2024).

65. A. Perez, M. H. Davis, Speaking and listening to inter-brain relationships. *Cortex* **159**, 54-63 (2023).

66. F. Faul, E. Erdfelder, A. Buchner, A. G. Lang, Statistical power analyses using G*Power 3.1: tests for correlation and regression analyses. *Behav Res Methods* **41**, 1149-1160 (2009).

67. A. K. Singh, M. Okamoto, H. Dan, V. Jurcak, I. Dan, Spatial registration of multichannel multi-subject fNIRS data to MNI space without MRI. *Neuroimage* **27**, 842-851 (2005).

68. D. W. Shattuck, M. Mirza, V. Adisetiyo, C. Hojatkashani, G. Salamon, K. L. Narr, R. A. Poldrack, R. M. Bilder, A. W. Toga, Construction of a 3D probabilistic atlas of human cortical structures. *Neuroimage* **39**, 1064-1080 (2008).

69. J. C. Ye, S. Tak, K. E. Jang, J. Jung, J. Jang, NIRS-SPM: statistical parametric mapping for near-infrared spectroscopy. *Neuroimage* **44**, 428-447 (2009).

70. T. J. Huppert, S. G. Diamond, M. A. Franceschini, D. A. Boas, HomER: a review of time-series analysis methods for near-infrared spectroscopy of the brain. *Appl Opt* **48**, D280-298 (2009).

71. M. A. Yucel, J. Selb, R. J. Cooper, D. A. Boas, Targeted Principle Component Analysis: A New Motion Artifact Correction Approach for near-Infrared Spectroscopy. *J Innov Opt Health Sci* **7**, (2014).

72. F. Scholkmann, S. Spichtig, T. Muehlemann, M. Wolf, How to detect and reduce movement

artifacts in near-infrared imaging using moving standard deviation and spline interpolation. *Physiol Meas* **31**, 649-662 (2010).

73. A. Grinsted, J. C. Moore, S. Jevrejeva, Application of the cross wavelet transform and wavelet coherence to geophysical time series. *Nonlinear Proc Geoph* **11**, 561-566 (2004).

74. S. Tak, J. C. Ye, Statistical analysis of fNIRS data: a comprehensive review. *Neuroimage* **85 Pt 1**, 72-91 (2014).

75. E. Maris, R. Oostenveld, Nonparametric statistical testing of EEG- and MEG-data. *J Neurosci Methods* **164**, 177-190 (2007).

Fig. 1. Experimental design and behavioral results. (A) Overview of the experimental design. (B) The fNIRS optode probe set. The red dots represent the source optode; the blue dots represent the detection optode. Channels of 21 and 31 were placed at T3 and T4, and the center of the prefrontal probe set was placed at FPz, in accordance with the international 10-20 system. The probe set covered the prefrontal cortex and classical language-related regions in both hemispheres. (C) Behavioral performance of the old listeners. Results of repeated measures ANOVA showed that the noise significantly impacted the old listener's clarity, intelligibility ratings and comprehension scores. Post hoc analysis revealed that for the clarity and intelligibility ratings all pairwise comparisons between four noise levels were significant. For the comprehension score, except for the comparison between NN and +2 dB, the other pairwise comparisons were significant. (D) The average pure-tone hearing thresholds of the old listeners. The error bar means the standard error. The asterisk (*) means significant result ($p < .05$ after FDR correction).

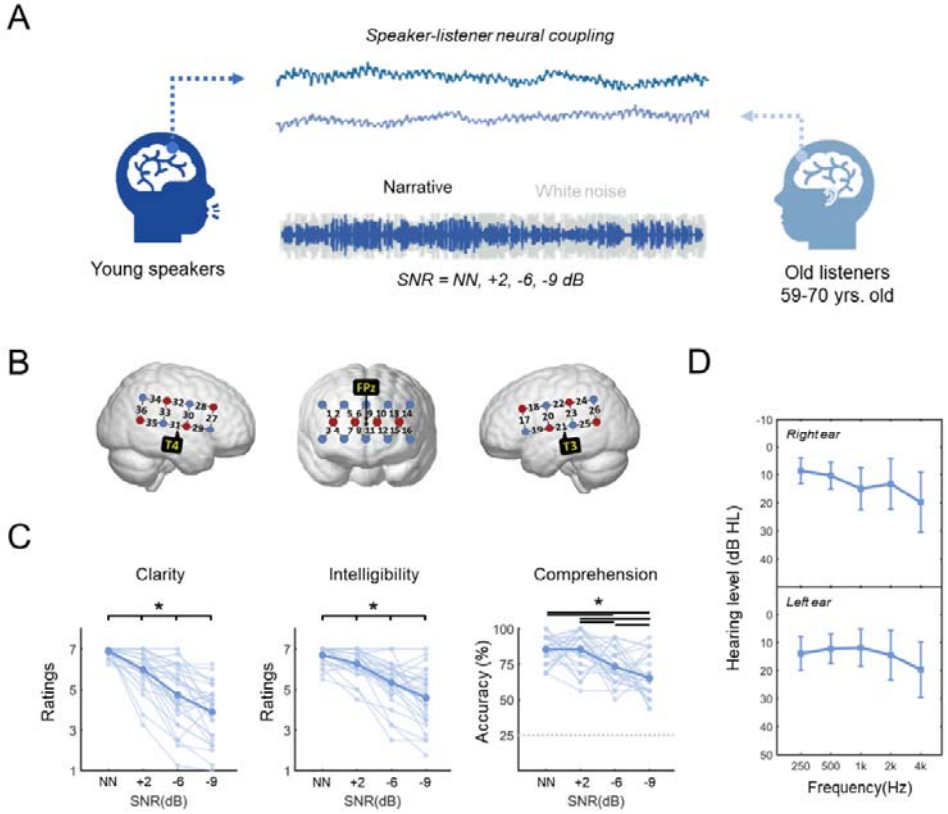

Fig. 2. Speaker-listener neural coupling. (A) Inter-brain neural patterns showing significant speaker-listener neural coupling for the old listeners. The old listener's neural activities from prefrontal cortex, bilateral ventral and dorsal language regions were coupled to the speaker's neural activities from the bilateral STG/MTG and the right IFG, as marked by the frames. Different color means different anatomical brain regions at the listener's side. Yellow means prefrontal cortex; red means the ventral language regions; blue means the dorsal language regions. The inter-brain neural patterns for the young listeners (32) were marked by the patches. (B) The illustration of inter-brain neural patterns from analysis of old listeners (top) and young listeners (bottom). For each circle, the top half nodes represent the brain regions at the speaker's side, and the bottom half represents the regions at the listener's side. (C) The old listener's speaker-listener neural coupling from five inter-brain neural patterns. The first three patterns, i.e., O-Prefrontal, O-Ventral and O-Dorsal, were obtained from the speaker-listener neural coupling analysis of old listeners. The neural coupling in all the four noise levels was higher than the resting-state baseline. Besides, for the O-Prefrontal pattern, the coupling in NN was higher than -9 dB. The right two figures showed the results in patterns of Y-Ventral and Y-Dorsal, which were obtained from the analysis of the young listeners. For the Y-Ventral pattern, the coupling at NN and +2 dB was higher than that at the baseline; for the Y-Dorsal pattern, the coupling at NN and -9 dB was higher than that at the baseline. (D) Comparison of the speaker-listener neural coupling between the old listeners and the young listeners. The coherence from the baseline was first subtracted from the four noise levels and then averaged. For the O-Prefrontal, O-Ventral and O-Dorsal patterns, the coherence of the old listeners was higher than young listeners. In contrast, for the Y-Ventral and Y-Dorsal patterns, the coherence of young listeners was higher than old listeners. The error bar means the standard error. The line and asterisk (*) mean significant result ($p < .05$ after FDR correction).

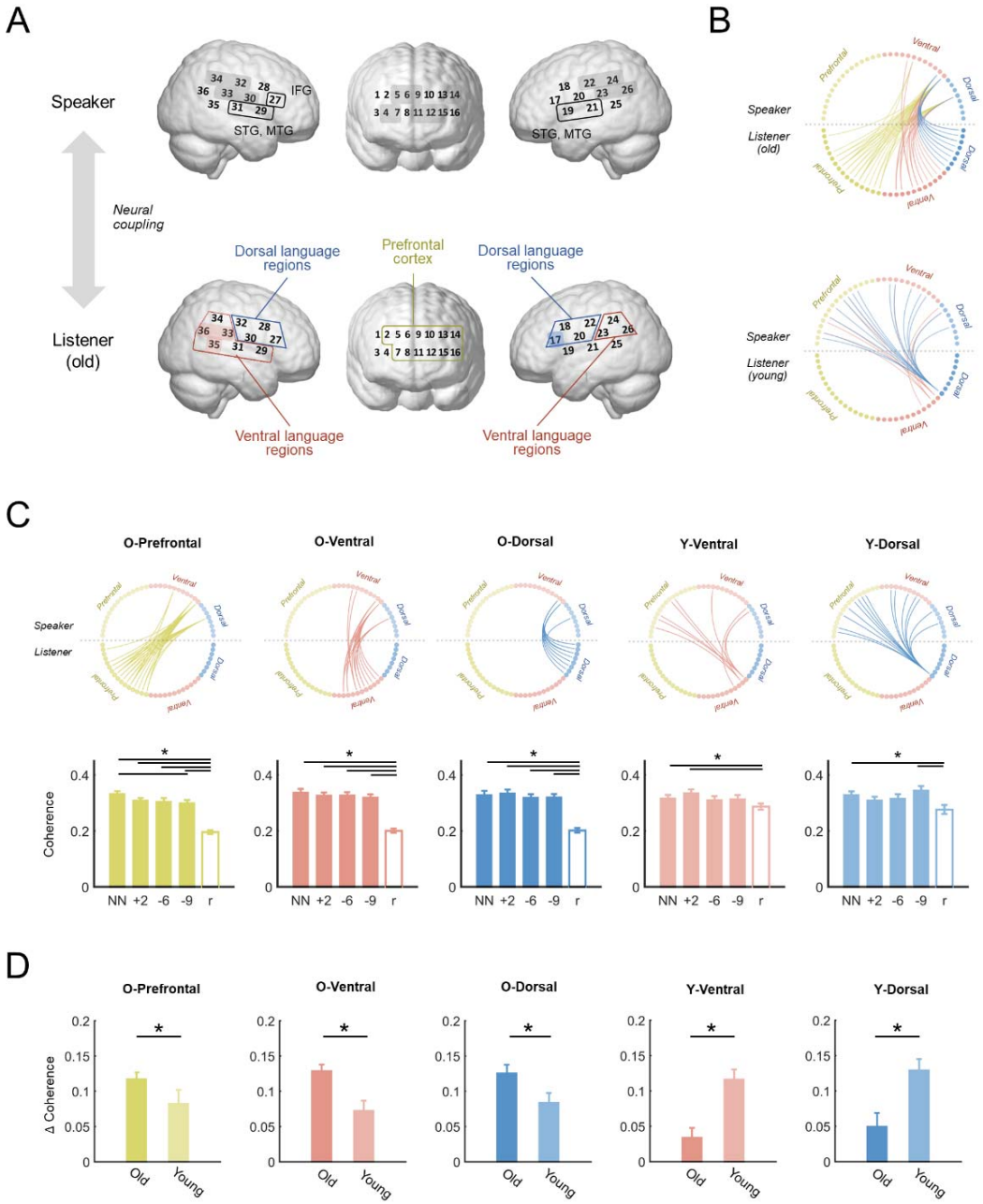

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Fig. 3. Behavioral relevance of speaker-listener neural coupling. (A/C) Correlation between the comprehension score and the coupling from the clusters. Each line represents the correlation r-values (Fisher-z transformed) of one cluster belonging to one particular inter-brain neural pattern. The asterisk means the significant r-values in one particular noise level; the line means a significant pairwise comparison between two noise levels ($p < .05$ after FDR correction). For both the O-Prefrontal and O-Ventral patterns, the r-values in -6 dB and -9 dB were significant. For the O-Prefrontal pattern, the r-values were higher when noise increased. (B/D) Correlation between the comprehension score and average coupling for the inter-brain neural patterns. The neural coupling of the O-Prefrontal pattern was positively correlated with the comprehension score at -6 dB and -9 dB (rs = .39, .37; ps = .035, .047, uncorrected); the neural coupling of the O-Ventral pattern was correlated with the comprehension score at -6 dB (r = .49, p = .007, uncorrected). The other correlations were not significant.

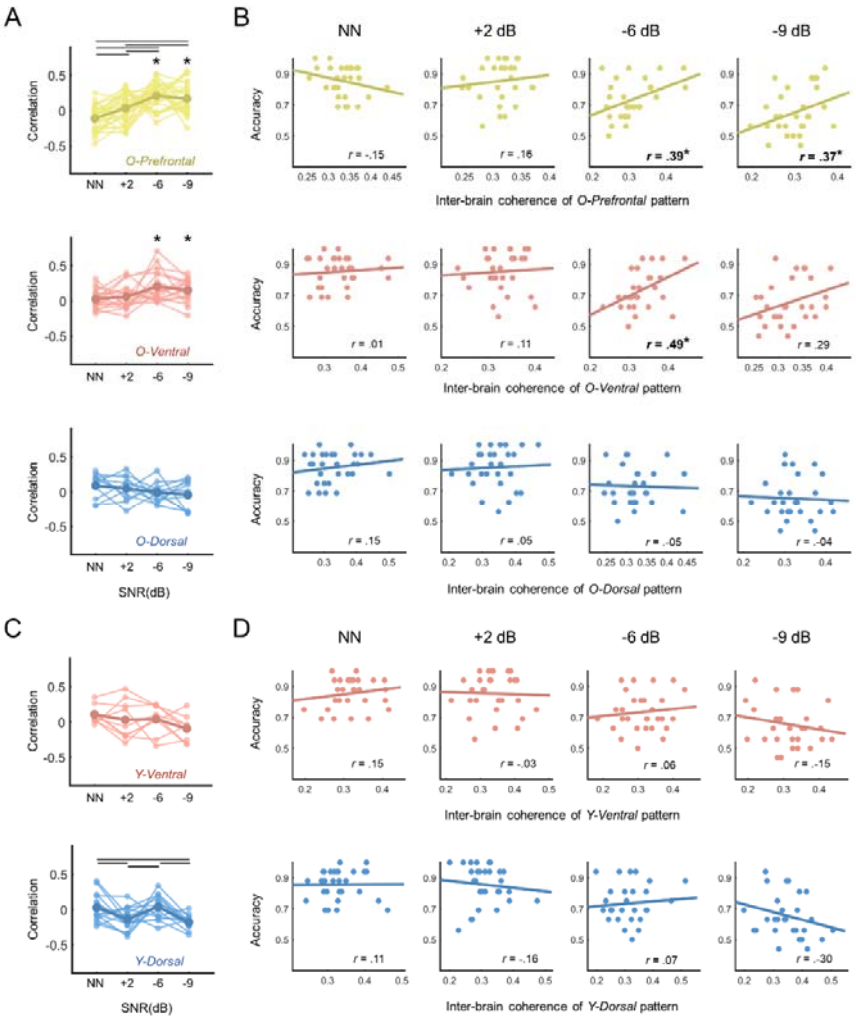

Fig. 4. Integration between inter-brain neural patterns. (A-B) Correlation matrix for all inter-brain neural patterns for the old listeners (A) and the young listeners (B). Significant correlation coefficients were marked by the asterisks ($p < .05$, FDR corrected). (C/D) Summary of the integration between the inter-brain neural patterns of O-Prefrontal, O-Ventral and O-Dorsal. The O-Ventral and O-Dorsal patterns was closely integrated in all four noise levels, for both the old listeners and the young listeners. In contrast, the integration between the O-Frontal pattern and the O-Ventral/O-Dorsal patterns was robust for the old listeners, but was only observed in moderate noise level (-6 dB) for the young listeners.

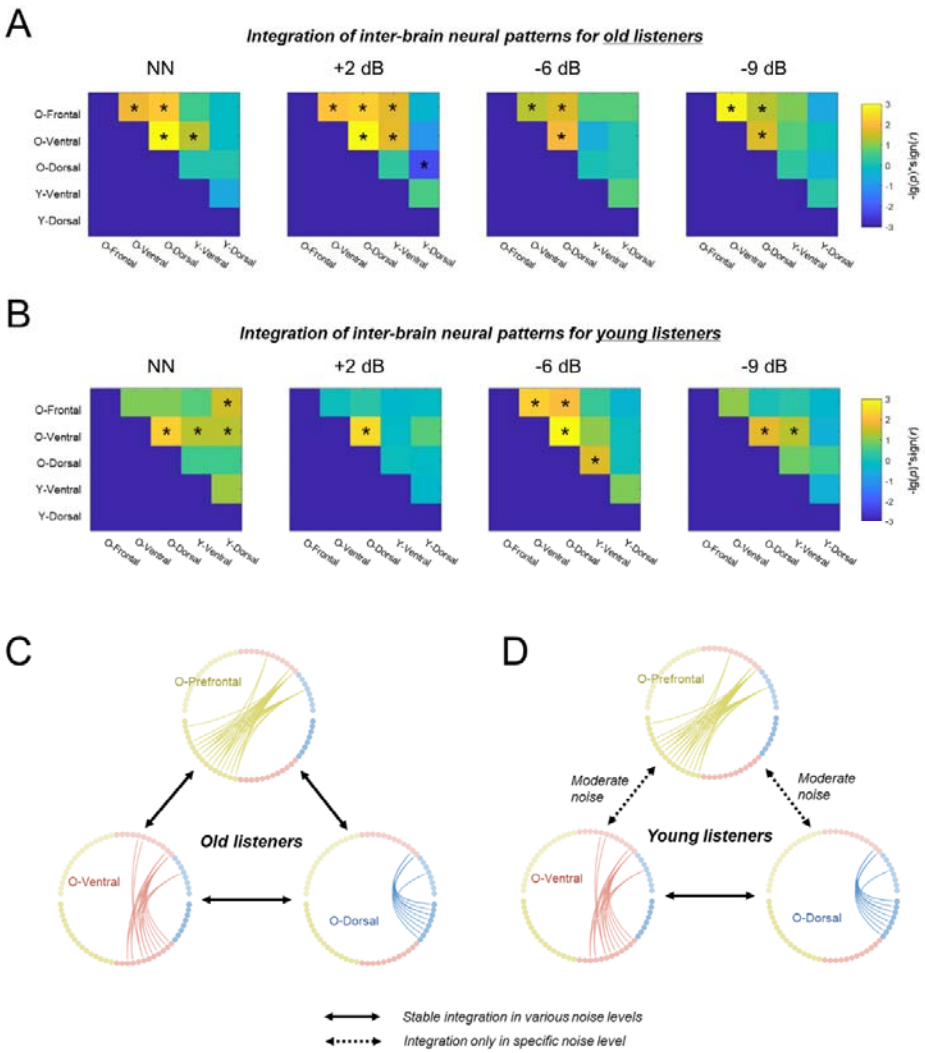
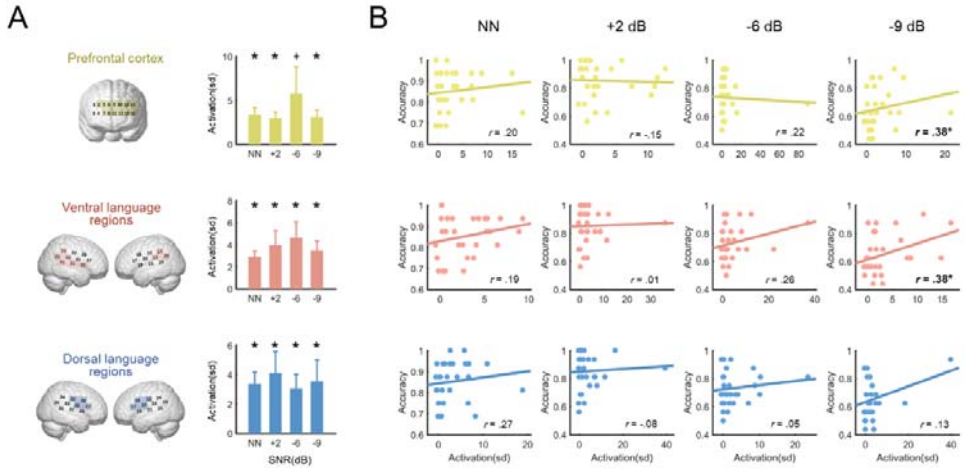
Fig. 5. Single-brain neural activation of the old listeners. (A) Neural activation of these brain regions showing significant speaker-listener neural coupling. The activation of the prefrontal cortex was significant at NN, +2 dB and -9 dB, and marginally significant at -6 dB. The ventral and dorsal language regions were all significantly activated in all four conditions. The error bar means the standard error. The asterisk (*) means significant result ($p < .05$ after FDR correction); the cross (+) means marginal significant result ($p < .10$ after FDR correction). (B) Correlation between the comprehension score and activation of each inter-brain neural pattern. The activation of the prefrontal cortex and the ventral language regions were positively correlated with comprehension score at -9 dB (Pearson rs = .38, .38; ps = .041, .045, uncorrected). The other correlation coefficients were not significant.