Compensatory Mechanisms for Preserving Speech-in-Noise Comprehension Involve Prefrontal Cortex in Older Adults

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Abstract

The capacity of comprehending others amidst noise is essential for human communication. However, it presents significant challenges for the elderly who often face progressive declines in the peripheral auditory system and the whole brain. While previous studies have suggested the existence of neural reserve and neural compensation as potential mechanisms for preserving cognitive abilities in aging, the specific mechanisms supporting speech-in-noise comprehension among the elderly remain unclear. To address this question, the present study employs an inter-brain neuroscience approach by analyzing the neural coupling between brain activities of older adults and those of speakers under noisy conditions. Results showed that the neural coupling encompassed more extensive brain regions of older listeners compared to young listeners, with a notable engagement of the prefrontal cortex. Moreover, the neural coupling from prefrontal cortex was coordinated with that from classical language-related regions. More importantly, as background noise increases, the older listener's speech comprehension performance was more closely associated with the neural coupling from prefrontal cortex. Taken together, this study reveals the compensatory recruitment of neurocognitive resources, particularly within the prefrontal cortex, to facilitate speech processing in the aging brain, and further highlights the critical role of prefrontal cortex in maintaining the elderly's ability to comprehend others in noisy environments. It supports the neural compensation hypothesis, extending the knowledge about the neural basis that underlies cognitive preservation in the aging population.

Introduction

Understanding other people's speech, commonly taking place in environments with background noise in daily life, poses a significant challenge for older adults. This challenge arises from the progressive decline in the auditory system's structure and function (*1*), as well as alterations in the perisylvian language regions that are crucial for processing speech acoustics and mapping them into meaningful content (*2*). To counteract these age-related declines and maintain the cognitive ability in older adults, it is hypothesized that the aging brain may recruit additional neurocognitive resources (*3-5*). The neural reserve hypothesis suggests that the brain's functional network possesses resilience and contains redundancy of neural resources (*6*), which allows it to maintain cognitive function despite age-related degradation or heightened demands imposed by difficult cognitive tasks (*3, 4*). Empirical evidence in support of this hypothesis includes a reserve and even upregulation of the neural activation of the language-related brain regions in older adults (*2, 7-9*), which may serve as a mechanism for preserving speech comprehension abilities. Alternatively, the neural compensation hypothesis proposes that when primary cognitive networks become less efficient, additional brain regions or circuits are recruited to sustain cognitive function (*3, 4, 10*). For instance, the prefrontal cortex, which shows minimal activation in younger adults (*2, 4, 11, 12*), has been reported to be significantly engaged during older adults' speech processing. This compensation is hypothesized to be based on neural plasticity and functional reorganization of the brain, suggesting a dynamic adaptation to cognitive demands (*10*). However, despite these findings and hypotheses, the precise neural mechanisms that facilitate daily-life speech comprehension in older adults remain unclear.

A critical question concerns the extent to which various brain regions are engaged in understanding other's speech in a naturalistic context. Despite significant efforts in exploring this question, most existing studies have focused on reduced speech conditions, using simple language materials like syllables or words. These experimental setups fail to replicate the complexities of real-world speech

comprehension, which often involves more naturalistic speech, e.g., narratives, and is

frequently impeded by environmental noise (*13, 14*). The processing of natural speech

is more complex than that of simple stimuli, requiring more extensive computational

analysis of meaningful content and context, thus engaging a wider network of fronto-

parieto-temporal cortical regions (*13, 14*). Furthermore, adapting to background noise

demands additional neurocognitive resources to mitigate the interference of the

background noise and enhance selective processing of the target speech (*15-17*).

Consequently, previous studies may have significantly underestimated the

neurocognitive demands of processing natural speech in noisy conditions, resulting in

an incomplete understanding of the brain regions involved in speech comprehension

in the aging brain.

Another critical issue is the functional role of various brain regions in natural speech

comprehension among older adults. While previous studies have noted enhanced

activation in the prefrontal cortex and classical language regions (*2, 18*), the specific

regions most influential to speech ability in older adults remain much controversial.

The neural reserve hypothesis supposed that the preservation of older adult's

cognitive ability was achieved based on the functional reserve or reorganization

within the original functional network (*3*). Following this line, the older adult's speech

performance should be closely related to the neural responses within the language

network. In contrast, the neural compensation hypothesis emphasizes the recruitment

of brain regions or networks that is not typically involved in young adults, e.g.,

prefrontal cortex, to facilitate the cognitive maintenance (*3, 19*). Drawing on this, the

older adult's speech ability may be more closely associated with the neural responses

of non-language-specific regions, such as the prefrontal cortex, rather than the

language-related regions. Considering the limited capacity of neural reserve and the

overall decline of the language network within the aging brain (*3, 4*), we hypothesize

that the mechanism of the neural compensation plays a more significant role in

maintaining the speech performance or ability, especially under noisy conditions that

demand more cognitive resources. Specifically, the prefrontal cortical response may

be more predictive of the actual speech-in-noise performance in older adults. Notably,

as the prefrontal cortex may facilitate speech processing by compensating for the

language network rather than replacing it (*20, 21*), we further hypothesize an

enhanced functional integration between them within the aging brain (*22, 23*) for

facilitate the natural speech processing in older adults.

To address these questions and test our hypotheses, we conducted a study with a

cohort of older adults aged 59-71 years, who listened to pre-recorded narratives

spoken by young adults. To simulate real-life speech scenarios with environmental

noise, we added white noise to the narrative audios at four different levels: no noise,

+2 dB, -6 dB, and -9 dB. This design allowed us to explore how various brain regions

adapt and function under different noise conditions. Neural activities from both the

old adults and young speakers were recorded by functional near-infrared spectroscopy

(fNIRS), chosen for its motion insensitivity and low operational noise than functional

magnetic resonance imaging (*24*). To elucidate the involvement of different brain

regions in natural speech processing, we adopted an inter-brain neuroscience approach

(*25-27*). This approach analyzes the coupling between the neural activities of old

adults and those of the speakers, with the latter providing a reference for

understanding the neural response to speech. This method avoids the difficulty of

disentangling the interdependent speech features (*13, 28*) and captures additional

information beyond common speech features, such as acoustics and semantics (*29-33*).

Based on this approach, we examined the speaker-listener neural coupling from

various brain regions across different noise levels (*14, 34, 35*). Furthermore, we

compared the neural coupling of old listeners to a control group of young listeners (*35*)

to further highlight age-specific neural mechanisms.

Our findings reveal that the neural activity in the prefrontal cortex and language-

related regions of old listeners was significantly coupled with the speaker's brain

activity, regardless of the noise level. These couplings involved a wider range of brain

regions in old listeners compared to young listeners, suggesting both neural reserve

and neural compensation mechanisms within the aging brain. Notably, with the

increasing of background noise, the old listener's comprehension performance was

more closely associated with their neural coupling from the prefrontal cortex. This

relationship demonstrates the functional role of the prefrontal cortex in compensating for reduced auditory input and to maintain speech comprehension, highlighting the functional role of neural compensation in preserving the speech-in-noise comprehension ability among the older adults. Moreover, the older listener's neural coupling of prefrontal cortex was robustly correlated to that of the language regions across noise levels, which was not observed in the young listeners. These results suggest that the prefrontal cortex was closely integrated with the classical language network in the aging brain. Taken together, our study elucidates the neural mechanisms that support natural speech comprehension in noise among older adults. It highlights the critical role of the prefrontal cortex in the cognitive preservation of speech(-in-noise) comprehension ability, shedding lights on potential interventions to promote successful cognitive aging.

Results

Noise impacts old listener's perception and speech comprehension

Figure 1A illustrates the experimental design of this study. A group of older adults with normal or close-to-normal hearing threshold were recruited to listen to narratives pre-recorded from a group of younger speakers (*35*). 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 (*33, 35, 36*). The neural activities from the speakers and the listeners were measured by fNIRS with the same coverage of brain regions, including prefrontal cortex and classical language regions (Figure 1B, see Methods for more details). The listeners' subjective ratings of the narratives' clarity and intelligibility and their comprehension scores were collected. Results are shown in Figure 2A. 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, ps < .001,
corrected by false discovery rate (FDR), (*37*)), 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, ps < .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 $65.3 \pm 2.6\%$ (mean $\pm$ 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 (Spearman 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 old listener's subjective percept and the actual
comprehension of speech. Besides, no significant correlation between these
behavioral measures and the old listener's hearing thresholds 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 for all four noise
levels and the resting-state baseline. This allowed to test for significant differences in
neural coupling between any of the noise levels and the baseline as well as significant
differences in coupling strength across different noise levels. A non-parametric
cluster-based method (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 (*32, 38*). 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 (*35, 36, 39, 40*), 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 3A

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 (*35, 36*). 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 (Figure 3A), i.e., O-Prefrontal (prefrontal cortex, "O" refers to

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 3C. 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, ps < .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, ps = .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 (ps > .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 participants (Figure 3B) who listened to the same narratives (*35*). As illustrated in Figure 3A/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" refers to 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 also examined whether the neural coupling from the Y-Ventral and Y-Dorsal patterns was significant in the old listeners (Figure 3C). 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 $ds > 0.91$).

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 and the

young listeners. 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 effect of listener group was significant ($Fs > 4.11$, $ps < .05$, 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. 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 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 4A) and at the pattern level (Figure 4B). 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, ts = 5.84, 4.14; ps < .001, FDR corrected; Cohen's ds = 1.12,

0.80), but not at NN and +2 dB (ps > .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, ts < -3.21; ps < .05, FDR corrected; Cohen's ds > 0.61), and the r-values at +2 dB

were lower than those at -6 dB and -9 dB (Paired samples t-test, ts = -2.60, -2.06; ps

= .023, .059, FDR corrected; Cohen's ds = 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 (Spearman rs = .39, .37; ps

= .035, .047, uncorrected), but not at NN and +2 dB (ps > .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, ts = 3.92, 3.89; ps = .001, .001, FDR corrected; Cohen's ds =

0.92, 0.91), but not at NN and +2 dB (ps > .13). However, no significant results were

found when comparing the results between any noise levels (ps > .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 (Spearman r

= .49, p = .007, uncorrected), but not in the other three conditions (ps > .12).

For the O-Dorsal and Y-Ventral patterns, no significant results were found at the

cluster level (ps > .10, FDR corrected) or at the pattern level (ps > .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, ts > 2.48; ps < .05, FDR corrected;

Cohen's ds > 0.64). However, these r-values were neither significant at the cluster

level (ps > .07, FDR corrected) or at the pattern level (ps > .10).

To examine the functional role of the prefrontal cortex in younger listeners, the

correlation between the younger listeners' neural coupling from the O-Prefrontal

pattern and speech comprehension scores were also analyzed (Figure 4C). At the

cluster level, r-values at +2 dB were higher than those at the other three conditions

(Paired samples t-test, ts > -2.55; ps < .05, FDR corrected; Cohen's ds > 0.66), and r-

values at NN were lower than -6 dB (Paired samples t-test, t = -3.21; p = .025, FDR

corrected; Cohen's d = 0.49). However, these correlations were neither significant at

the cluster level (ps > .11, FDR corrected) or at the pattern level (ps > .29). In contrast,

the young listener's speech comprehension score was associated with the neural

coupling from the Y-Dorsal at both the cluster level and the pattern level (*35*), as

shown in Figure 4C.

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 (Spearman rs = 45, .48, .38, .58; ps

= .014, .008, .043, .001, FDR corrected), and the O-Dorsal pattern (Spearman rs =

50, .51, .43, .38; ps = .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 (Spearman rs = 76, .69, .46, .43; ps < .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 5A/B).

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 (Spearman rs = .69, .72, .87, .61; ps = .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 (Spearman rs = .65, .87; ps = .005, .010, FDR corrected), but not at the other noise levels (ps > .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 (ps > .05, FDR corrected).

Besides, we also observed some correlation across two types of inter-brain neural patterns (Figure S5). 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 (Spearman r = .44, p = .048, FDR corrected), and the O-Ventral pattern at NN and +2 dB (Spearman 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 (Spearman 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 (Spearman rs = .53, .54; ps = .045, .042, FDR corrected), and the O-Dorsal pattern at -6 dB (Spearman 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 (Spearman 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 have a comprehensive 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 in addition to the inter-brain analyses. As shown in Figure S6, 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 S7). 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 (Spearman rs = .38, .38; ps = .041, .045, uncorrected). The correlations in the other noise levels and in the dorsal language regions were not significant (ps > .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 (Spearman r = .03, p = .86). The correlation in various noise levels and from other brain regions are further shown in Figure S8.

Discussion

This study utilized an inter-brain neuroscience approach to investigate the neural

mechanisms of natural speech-in-noise comprehension among the older adults.

Through an analysis of speaker-listener neural coupling, we discovered that the neural

activities of old listeners from many brain regions in the prefrontal cortex and

classical language networks were coupled with the neural activities of the speaker.

Compared to the young listeners, the neural coupling of the old listeners engaged

more extensive brain regions, particularly in the prefrontal cortex. Besides, the neural

coupling from the prefrontal cortex was reliably correlated to that from the language-

related regions across different noise levels, which was not observed in young

listeners. These results imply that older adults engage and integrate more

neurocognitive resources from the prefrontal cortex to facilitate their natural speech

processing in noisy environments. More importantly, the old listener's speech

comprehension performance was more closely associated with the neural coupling in

prefrontal cortex as background noise increased, highlighting the functional role of

the prefrontal cortex for older adults to maintain their speech comprehension under

more acoustically challenging scenarios. In conclusion, this study examined how the

aging brain processed natural speech in noise, and highlighted the compensatory

mechanism centered around the prefrontal cortex for supporting the cognitive

preservation of speech ability in older adults.

This study elucidates how different brain regions are involved during speech-in-noise

processing in older adults. Our findings showed that the old listeners' neural activities

across a wide range of brain regions and in both hemispheres were coupled to the

speaker. Specifically, the older listeners not only recruited brain regions within the

classical language networks but also additionally engaged the prefrontal cortex to

facilitate speech processing. Furthermore, the neural coupling in the older listeners

extended beyond the language-dominant hemisphere (i.e., the left hemisphere) to

include homologous regions in the right hemisphere (*41-43*). It contrasts with the

more localized neural coupling observed in young listeners, which only involved a

few critical brain hubs in the language networks (*35, 36*). This evidence supports both

the neural reserve hypothesis, which presumes the existence of resilience and resource

redundancy within the primary functional network to adapt to aging or pathology (*3, 4,*

6), and neural compensation hypothesis, which proposes the involvement of

additional brain regions or circuits for facilitating cognitive maintenance (*3, 4, 10*).

Notably, the neural coupling observed in older listeners remained robust in both quiet

and noisy conditions, indicating that the prefrontal cortex and language networks can

consistently contribute to speech processing across diverse listening environments.

Likewise, the older listeners in this study also exhibited a relatively stable

comprehension performance in noisy conditions. The stability of both the neural

coupling and the comprehension performance suggests that the neural mechanisms

supporting speech processing in the aging brain may be resilient to varying levels of

environmental noise.

More importantly, this study highlights the functional role of the prefrontal cortex in

older adults. Although prior studies have widely reported the activation of the

prefrontal cortex during speech processing in older adults (*2, 11, 22, 41*), its specific

contribution to the preservation of speech functions remains controversial. Drawing

on the neural compensation hypothesis, the older adult's speech performance would

be more closely associated with the neural response within the prefrontal cortex,

particularly under noisy conditions with a heightened cognitive demand (*3, 4, 10*).

Our findings provide the first empirical evidence for this hypothesis by showing that

the speech comprehension performance of the old listeners was more closely

correlated with the neural coupling from prefrontal cortex as the noise increased.

Meanwhile, we also observed a significant correlation between the older adults'

speech performance and the neural coupling from the ventral language regions.

However, it was only observed at moderate noise level, not at high noise level. This

indicates that while the language network's functionality is preserved in the aging

brain, its adaptability is limited (*3, 4*). Consequently, older adults may rely on

compensatory recruitment of resources beyond the language network to meet the

cognitive challenges of increasing age or more complex tasks, such as increasing

background noise intensity. Taken together, these findings highlight the importance of

the neural compensation based on the prefrontal cortex for older adults to adapt to

various noise conditions. Our results align with and extend existing theories that

emphasize the compensatory role of the frontal lobe in successful aging, such as the

Scaffolding Theory of Aging and Cognition (STAC) (*44, 45*) and the Posterior-

Anterior Shift in Aging (PASA) (*46*), by demonstrating the compensatory role of the

prefrontal cortex in natural speech(-in-noise) processing.

Our study also provides valuable insights into how the prefrontal cortex was

coordinated for compensation with the classical language regions within the aging

brain. By analyzing the correlation of speaker-listener neural couplings across various

brain regions, we found that within the language network, coupling between ventral

and dorsal language regions was consistently correlated across noise levels in both

young and older adults. Notably, a robust correlation between the prefrontal cortex

and the language network was observed exclusively in older adults, but not in young

adults, suggesting an enhanced connectivity to facilitate speech processing in the

aging brain. Our findings are consistent with existing discoveries of increasing global

connectivity in older adults (*22, 47, 48*), which is thought to reflect a neural

reorganization serving to offset the widespread neural deterioration (*48-50*). However,

there explanation for this age-related increase in connectivity between the prefrontal

cortex and the classical language network is controversial. The "interaction" view

posits that the prefrontal cortex is involved in domain-general processing, such as

inhibitory control and working memory, rather than language-specific functions,

supported by evidence that its neural activity does not encode specific language or

speech information (*20, 21*). Conversely, the "integration" perspective suggests that

the prefrontal cortex acts as an extension of the language network following neural

reorganization in the aging brain. Our study provides partial support for the

integration perspective by showing that neural activities from both the prefrontal

cortex and the language network are coupled to the same neural activities at the

speaker's side. This indicates that the prefrontal cortex may be involved in similar

speech processing activities as the language network. Nevertheless, this debate

remains unresolved and requires further research.

Interestingly, while some existing studies have found a relationship between the old

listeners' speech-in-noise ability and neural responses from the dorsal language

regions, this relationship was not observed in our study. One possible explanation for this discrepancy may lie in the more naturalistic speech material used in our study. Most previous studies have used simplified language materials, such as syllables or words (*2, 11, 22, 41, 51*), which cannot fully capture how the brain processed natural speech, such as narratives or stories, in more realistic settings. In particular, the dorsal language regions could facilitate the speech-in-noise processing by generating an internal representation of speech (*52, 53*), e.g., enabling the clear phonological structures of the noise-masked speech by referring to pre-acquired phonological knowledge (*54*). Despite the essential role of dorsal language regions in identifying phonological units under noisy conditions (*9, 55*), the comprehension of natural speech is more closely associated with the processing of content and contextual information, especially for the older adults with a poor hearing ability (*56*). In this way, as found in our study, the natural speech-in-noise comprehension ability of older adults may be more closely related to brain regions responsible for processing meaning or content, which are predominantly located in ventral language regions as well as the prefrontal cortex, rather than the dorsal language regions (*57*). This discrepancy between our study and previous studies also highlights the importance of employing more naturalistic paradigms to understand the behavior, cognition and brain function of older adults in everyday settings.

It should be noted that neither the neural reserve nor neural compensation can fully restore the cognitive ability of older adults to the levels of young adults (*3, 4*). Actually, the additional cognitive or neural resources recruited reflect a reduced computational efficiency in the aging brain (*19, 58*). This study provides evidence for this from the inter-brain neural patterns observed on the speaker's side. While the old listeners recruit a wide range of brain regions than the young listeners, their neural coupling at the speaker's brain is limited to a smaller set of regions. Conversely, young listeners demonstrate neural coupling with a more extensive network of regions within the speaker's brain, including bilateral temporo-parietal cortex and prefrontal cortex. The neural coupling between speakers and listeners from specific brain regions reflects the specific speech processing (*29, 59*). For example, coupling from

the primary auditory cortex is associated with early acoustic processing (*32*), 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 (*29*). Therefore, given the inter-brain neural patterns showing limited

coverage on the speaker's side but extensive engagement of various brain regions on

the listener's side, our study indicates that older adults may have a diminished

capacity for high-level speech processing and potentially low computational

efficiency in the brain.

In addition to examining speaker-listener neural coupling, this study also analyzed

neural activation in various brain regions. Both the prefrontal cortex and language-

related regions exhibited significant activation across different noise levels.

Importantly, similar to the findings from the neural coupling analysis, the neural

activities from the prefrontal cortex and ventral language regions were positively

correlated with speech comprehension performance. However, the correlation

between the strength of speaker-listener neural coupling and neural activation was not

significant, suggesting a dissociation between the specific speech processing within

individual brain regions and the extent of their involvement. Neural coupling and

neural activation capture speech-related neural responses in two different dimensions.

Neural coupling focuses on the temporal dynamics of the listener's neural activity,

using the speaker's brain as a reference, which may better capture the dynamic

processing of natural speech. In contrast, neural activation emphasizes the amplitude

of neural activity, which may reflect the engagement level of individual brain regions.

Therefore, the analysis of speaker-listener neural coupling and single-brain neural

activation can serve as complementary approaches (*33*). Future research could further

explore the relationship between these two metrics and consider combining them to

more fully elucidate the neural basis of speech processing in the brain.

In conclusion, the present study has revealed how natural speech is processed within

the aging brain and has highlighted the compensatory role of the prefrontal cortex in

preserving the speech-in-noise comprehension ability in older adults. Future studies

could build upon our findings in the following aspects. Firstly, this study focused

exclusively on healthy aging adults with normal hearing thresholds and good

cognitive abilities. However, the old adult population exhibits significant

heterogeneity across a broader age range (*60, 61*), regarding diverse hearing loss or

impairments (*62, 63*), varying language experience (*64*), education backgrounds (*65*)

and other traits. 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 (*66*), 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 (*67*). This 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 (*38*) or directly modelled to the temporal dynamics of speaker-listener

neural coupling (*68*). This approach would provide further insights into the specific

computational processing behind those age-related compensatory neural coupling.

Lastly, while the present study indicated the compensatory role of the prefrontal

cortex in older adults' speech-in-noise comprehension ability, it remains to be

explored whether this mechanism also supports or, conversely, hinders cognitive

abilities in other domains. In particular, it has recently been proposed that neural

resources may be deployed for enhancing the cognitive function in one area, e.g., the

age-enhanced involvement of prefrontal cortex in speech-in-noise processing,

reducing their availability for other cognitive functions (*69*). Hence, to thoroughly

examine the role of the prefrontal cortex in cognitive preservation (or decline) during

age, future research might incorporate and analyze a broader spectrum of cognitive
tasks. This would enable a more nuanced view of the cognitive and neural alterations
in older adults.
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Methods

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 (*70*),
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 Chinese version
of the Mini-Mental State Examination (MMSE) (> 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 4000 Hz). For the
remaining twenty-nine participants, twenty-seven of them have a normal hearing
threshold ($\leq$20 dB), the rest two of them have a close-to-normal hearing threshold (22,
23 dB). Figure 2B 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.
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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 (*35*). 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? (ˑˑ人和朋友是什ˑˑ系)" and

the four choices were 1) teacher-student, 2) cousins, 3) neighbors, and 4) roommates

(1.ˑ生ˑ系, 2.姐妹ˑ系, 3.ˑ居ˑ系, and 4.室友ˑ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 1B, 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) (*71, 72*) by using NIRS_SPM (*73*). 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 (*35*). 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 (*74*) 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 (*75*). Subsequently, the second step adopted a

linear interpolation method (*76*), 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 (*35*).

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 (*77*). 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 (*78*). 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 $\times$ 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 (*79*). 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 subjected to further 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.

Analysis of behavioral relevance

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.   D. Barulli, Y. Stern, Efficiency, capacity, compensation, maintenance, plasticity: emerging concepts in cognitive reserve. *Trends Cogn Sci* **17**, 502-509 (2013).

4.   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).

5.   M. A. Shafto, L. K. Tyler, Language in the aging brain: The network dynamics of cognitive decline and preservation. *Science* **346**, 583-587 (2014).

6.   P. J. N. Satz, Brain reserve capacity on symptom onset after brain injury: a formulation and review of evidence for threshold theory. **7**, 273 (1993).

7.   G. M. Bidelman, M. S. Mahmud, M. Yeasin, D. W. Shen, S. R. Arnott, C. Alain, Age-related hearing loss increases full-brain connectivity while reversing directed signaling within the dorsal-ventral pathway for speech. *Brain Struct Funct* **224**, 2661-2676 (2019).

8.   Y. Liu, S. Wang, J. Lu, J. Ding, Y. Chen, L. Yang, S. Wang, Neural processing of

speech comprehension in noise predicts individual age using fNIRS-based brain-

behavior models. *Cereb Cortex* **34**, (2024).

9.   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).

10.   A. M. Morcom, W. Johnson, Neural reorganization and compensation in aging. *J*

Cogn Neurosci **27**, 1275-1285 (2015).

11.   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).

12.   W. Kang, J. Wang, A. Malvaso, Inhibitory Control in Aging: The Compensation-

Related Utilization of Neural Circuits Hypothesis. *Front Aging Neurosci* **13**, 771885

(2021).

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.   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).

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. A. Wingfield, M. Grossman, Language and the aging brain: patterns of neural

compensation revealed by functional brain imaging. *J Neurophysiol* **96**, 2830-2839

(2006).

19. L. Aron, J. Zullo, B. A. Yankner, The adaptive aging brain. *Curr Opin Neurobiol* **72**,

91-100 (2022).

20. I. A. Blank, E. Fedorenko, Domain-General Brain Regions Do Not Track Linguistic

Input as Closely as Language-Selective Regions. *J Neurosci* **37**, 9999-10011 (2017).

21. E. Diachek, I. Blank, M. Siegelman, J. Affourtit, E. Fedorenko, The Domain-General

Multiple Demand (MD) Network Does Not Support Core Aspects of Language

Comprehension: A Large-Scale fMRI Investigation. *J Neurosci* **40**, 4536-4550 (2020).

22. 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).

23. 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).

24. A. C. Dieler, S. V. Tupak, A. J. Fallgatter, Functional near-infrared spectroscopy for

the assessment of speech related tasks. *Brain Lang* **121**, 90-109 (2012).

25. L. Kingsbury, W. Hong, A Multi-Brain Framework for Social Interaction. *Trends*

Neurosci **43**, 651-666 (2020).

26.   Y. Farahzadi, Z. Kekecs, Towards a multi-brain framework for hypnosis: a review of

quantitative methods. *Am J Clin Hypn* **63**, 389-403 (2021).

27.   E. Redcay, L. Schilbach, Using second-person neuroscience to elucidate the

mechanisms of social interaction. *Nat Rev Neurosci* **20**, 495-505 (2019).

28.   S. Sonkusare, M. Breakspear, C. Guo, Naturalistic Stimuli in Neuroscience: Critically

Acclaimed. *Trends Cogn Sci* **23**, 699-714 (2019).

29.   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).

30.   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).

31.   J. Jiang, L. Zheng, C. Lu, A hierarchical model for interpersonal verbal

communication. *Soc Cogn Affect Neurosci* **16**, 246-255 (2021).

32.   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).

33.   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).

34.   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).

35.   Z. R. Li, J. W. Li, B. Hong, G. Nolte, A. K. Engel, D. Zhang, Speaker-Listener Neural

884   Coupling Reveals an Adaptive Mechanism for Speech Comprehension in a Noisy

885   Environment. *Cerebral Cortex* **31**, 4719-4729 (2021).

886   36.   Z. Li, B. Hong, D. Wang, G. Nolte, A. K. Engel, D. Zhang, Speaker-listener neural

887   coupling reveals a right-lateralized mechanism for non-native speech-in-noise

888   comprehension. *Cereb Cortex* **33**, 3701-3714 (2023).

889   37.   Y. Benjamini, Y. Hochberg, Controlling the False Discovery Rate - a Practical and

890   Powerful Approach to Multiple Testing. *J R Stat Soc B* **57**, 289-300 (1995).

891   38.   O. Abbasi, N. Steingraber, N. Chalas, D. S. Kluger, J. Gross, Spatiotemporal

892   dynamics characterise spectral connectivity profiles of continuous speaking and

893   listening. *PLoS Biol* **21**, e3002178 (2023).

894   39.   B. Yuan, H. Xie, Z. Wang, Y. Xu, H. Zhang, J. Liu, L. Chen, C. Li, S. Tan, Z. Lin, X.

895   Hu, T. Gu, J. Lu, D. Liu, J. Wu, The domain-separation language network dynamics in

896   resting state support its flexible functional segregation and integration during

897   language and speech processing. *Neuroimage* **274**, 120132 (2023).

898   40.   G. Hickok, D. Poeppel, The cortical organization of speech processing. *Nat Rev*

899   *Neurosci* **8**, 393-402 (2007).

900   41.   J. Ansado, Y. Marsolais, I. Methqal, F. Alary, Y. Joanette, The adaptive aging brain:

901   evidence from the preservation of communication abilities with age. *Eur J Neurosci*

902   **37**, 1887-1895 (2013).

903   42.   S. Wang, Y. Chen, Y. Liu, L. Yang, Y. Wang, X. Fu, J. Hu, E. Pugh, S. Wang, Aging

904   effects on dual-route speech processing networks during speech perception in noise.

905   *Hum Brain Mapp* **45**, e26577 (2024).

906   43.   L. Yang, S. Wang, Y. Chen, Y. Liang, T. Chen, Y. Wang, X. Fu, S. Wang, Effects of

907   Age on the Auditory Cortex During Speech Perception in Noise: Evidence From

908   Functional Near-Infrared Spectroscopy. *Ear Hear*, (2024).

909   44.   D. C. Park, P. Reuter-Lorenz, The Adaptive Brain: Aging and Neurocognitive

910   Scaffolding. *Annual Review of Psychology* **60**, 173-196 (2009).

911   45.   P. A. Reuter-Lorenz, D. C. J. C. O. i. P. Park, Cognitive aging and the life course: A

912   new look at the Scaffolding Theory. 101781 (2023).

913   46.   S. W. Davis, N. A. Dennis, S. M. Daselaar, M. S. Fleck, R. Cabeza, Que PASA? The

914   posterior-anterior shift in aging. *Cerebral Cortex* **18**, 1201-1209 (2008).

915   47.   L. K. Ferreira, G. F. Busatto, Resting-state functional connectivity in normal brain

916   aging. *Neurosci Biobehav Rev* **37**, 384-400 (2013).

917   48.   J. Stumme, C. Jockwitz, F. Hoffstaedter, K. Amunts, S. Caspers, Functional network

918   reorganization in older adults: Graph-theoretical analyses of age, cognition and sex.

919   *Neuroimage* **214**, 116756 (2020).

920   49.   D. Meunier, E. A. Stamatakis, L. K. Tyler, Age-related functional reorganization,

921   structural changes, and preserved cognition. *Neurobiol Aging* **35**, 42-54 (2014).

922   50.   R. Sala-Llonch, D. Bartres-Faz, C. Junque, Reorganization of brain networks in aging:

923   a review of functional connectivity studies. *Front Psychol* **6**, 663 (2015).

924   51.   P. C. M. Wong, M. Ettlinger, J. P. Sheppard, G. M. Gunasekera, S. Dhar,

925   Neuroanatomical Characteristics and Speech Perception in Noise in Older Adults.

926   *Ear Hearing* **31**, 471-479 (2010).

52.   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).

53. G. Hickok, J. Houde, F. Rong, Sensorimotor Integration in Speech Processing:

Computational Basis and Neural Organization. *Neuron* **69**, 407-422 (2011).

54. 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).

55. 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).

56. 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).

57. 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).

58. 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).

59. 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).

60. 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).

61. 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).

62. 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).

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

64. 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).

65. 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).

66. 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).

67. 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).

68. A. Perez, M. H. Davis, Speaking and listening to inter-brain relationships. *Cortex* **159**,

54-63 (2023).

69. T. D. Griffiths, M. Lad, S. Kumar, E. Holmes, B. McMurray, E. A. Maguire, A. J. Billig,

W. Sedley, How Can Hearing Loss Cause Dementia? *Neuron* **108**, 401-412 (2020).

70. 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).

71. 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).

72. 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).

73. 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).

74. 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).

75. M. A. Yucel, J. Selb, R. J. Cooper, D. A. Boas, Targeted Principle Component

994   Analysis: A New Motion Artifact Correction Approach for near-Infrared Spectroscopy.

995   *J Innov Opt Health Sci* **7**, (2014).

996   76.   F. Scholkmann, S. Spichtig, T. Muehlemann, M. Wolf, How to detect and reduce

997   movement artifacts in near-infrared imaging using moving standard deviation and

998   spline interpolation. *Physiol Meas* **31**, 649-662 (2010).

999   77.   A. Grinsted, J. C. Moore, S. Jevrejeva, Application of the cross wavelet transform and

1000   wavelet coherence to geophysical time series. *Nonlinear Proc Geoph* **11**, 561-566

1001   (2004).

1002   78.   S. Tak, J. C. Ye, Statistical analysis of fNIRS data: a comprehensive review.

1003   *Neuroimage* **85 Pt 1**, 72-91 (2014).

1004   79.   E. Maris, R. Oostenveld, Nonparametric statistical testing of EEG- and MEG-data. *J*

1005   *Neurosci Methods* **164**, 177-190 (2007).

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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) Overview of the analysis framework. The inter-brain neural coupling
between the speaker and old listener was analyzed first. The older listener's neural coupling
was then compared to that from a group of young listeners (35) to examine how different
brain regions are compensatorily involved within the aging brain. Moreover, the functional
role of these neural coupling was further exmained by analyzing its correlational relationship
to the older listener's speech comprehension performance in noisy conditions.
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Fig. 2. (A) Behavioral performance of 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. The asterisk (*) means significant result ($p < .05$, FDR
corrected). (B) The average pure-tone hearing thresholds of the old listeners. The error bar
means the standard error. (C) The age of the old listeners.
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Fig. 3. Speaker-listener neural coupling. (A) 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. Different color
means different anatomical brain regions: Yellow means the prefrontal cortex; red means the
ventral language regions; blue means the dorsal language regions. Based on the brain region
at the listener's side, these inter-brain neural coupling were divided into three patterns: O-
Prefrontal, O-Ventral, and O-Dorsal. (B) The inter-brain neural patterns for the young
listeners. They were divided into two patterns: Y-Ventral, Y-Dorsal. (C) The old listener's
speaker-listener neural coupling from five inter-brain neural patterns. For O-Prefrontal, O-
Ventral and O-Dorsal, 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. 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. The error bar means the standard error. The lines and asterisks (*) indicate
significant results ($p < .05$, FDR corrected).

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Fig. 4. Behavioral relevance of speaker-listener neural coupling. (A) Correlation between the
old listener's 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 indicates significant r-values in one particular noise level;
the line indicates a significant pairwise comparison between two noise levels ($p < .05$, FDR
corrected). 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) Correlation between the old listener's 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 (Spearman *r*s = .39, .37; *p*s
= .035, .047, uncorrected); the neural coupling of the O-Ventral pattern was correlated with
the comprehension score at -6 dB (Spearman *r* = .49, *p* = .007, uncorrected). The other
correlations were not significant. (C) Correlation between the young listener's comprehension
score and the couplings. For the O-Prefrontal pattern, the *r*-values under four noise levels
were not significant, although significant differences existed across the different noise levels.
For the Y-Ventral pattern, the *r*-values in -6 dB were significant ($p < .05$, FDR corrected); for
the Y-Dorsal pattern, the *r*-values in -9 dB were significant ($p < .05$, FDR corrected).
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Fig. 5. Integration between inter-brain neural patterns. (A/C) Summary of the integration
between the inter-brain neural patterns of O-Prefrontal, O-Ventral and O-Dorsal for the old
listeners (A) and the young listeners (C). (B/D) The correlation between three inter-brain
neural patterns in four noise levels. Significant correlation were marked by the dark line and
the asterisks ($p < .05$, FDR corrected). For old listeners, the integration between the O-Frontal
pattern and the O-Ventral/O-Dorsal patterns was robust across noise levels. However, they
were only observed in moderate noise level (-6 dB) for the young listeners. The O-Ventral and
the O-Dorsal patterns was closely integrated in all four noise levels, for both the old listeners
and the young listeners.

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Fig. 6. Summary of the neural mechanism for natural speech comprehension in different noise levels and age groups. In young adults, the dorsal and ventral language regions are engaged, with stable integration facilitating speech-in-noise processing. As noise intensity increases, the dorsal language regions play a more critical role, as indicated by a stronger correlation between the speech-in-noise comprehension performance and neural coupling. In contrast, older adults exhibit a compensatory recruitment of the prefrontal cortex to maintain speech comprehension abilities. This engagement is characterized by not only robust prefrontal cortex involvement across noise levels but also by an enhanced integration with language regions, a phenomenon not observed in young adults. Furthermore, the older adult's speech-in-noise comprehension is more closely associated with the prefrontal cortex, especially as noise level increases. Asterisks (*) indicate significant correlational relationship between the speech comprehension performance and the neural coupling from the particular brain regions.