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

Zhuoran Li[1, 2, 3, 4] [†], Yi Liu[5, †], Xinmiao Zhang[1,2], Nuonan Kou[5], Xiaoying Zhao[5], Xiangru Jiang[5], Andreas K. Engel[6], Dan Zhang[1, 2, ‡], Shuo Wang[5, ‡]

[1] Department of Psychological and Cognitive Sciences, Tsinghua University, Beijing, China
[2] Tsinghua Laboratory of Brain and Intelligence, Tsinghua University, Beijing, China
[3] Department of Psychiatry, University of Iowa Carver College of Medicine, Iowa, United States
[4] Stead Family Department of Pediatrics, University of Iowa Carver College of Medicine, Iowa, United States
[5] Beijing Institute of Otolaryngology, Otolaryngology-Head and Neck Surgery, Beijing Tongren Hospital, Capital Medical University, Beijing, China
[6] Department of Neurophysiology and Pathophysiology, University Medical Center Hamburg-Eppendorf, 20246 Hamburg, Germany

† These authors contributed equally to this work.

‡ Corresponding authors:

Shuo Wang, shannonwsh@aliyun.com

Dan Zhang, dzhang@tsinghua.edu.cn

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

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

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

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

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

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

84   demands additional neurocognitive resources to mitigate the interference of the

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

86   Consequently, previous studies may have significantly underestimated the

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

88   an incomplete understanding of the brain regions involved in speech comprehension

89   in the aging brain.

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

91   comprehension among older adults. While previous studies have noted enhanced

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

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

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

95   cognitive ability was achieved based on the functional reserve or reorganization

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

112   facilitate the natural speech processing in older adults.

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

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

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

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

117   +2 dB, -6 dB, and -9 dB. This design allowed us to explore how various brain regions

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

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

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

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

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

123   (*25-27*). This approach analyzes the coupling between the neural activities of old

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

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

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

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

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

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

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

131   to further highlight age-specific neural mechanisms.

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

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

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

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

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

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

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

139 relationship demonstrates the functional role of the prefrontal cortex in compensating

140 for reduced auditory input and to maintain speech comprehension, highlighting the

141 functional role of neural compensation in preserving the speech-in-noise

142 comprehension ability among the older adults. Moreover, the older listener's neural

143 coupling of prefrontal cortex was robustly correlated to that of the language regions

144 across noise levels, which was not observed in the young listeners. These results

145 suggest that the prefrontal cortex was closely integrated with the classical language

146 network in the aging brain. Taken together, our study elucidates the neural

147 mechanisms that support natural speech comprehension in noise among older adults.

148 It highlights the critical role of the prefrontal cortex in the cognitive preservation of

149 speech(-in-noise) comprehension ability, shedding lights on potential interventions to

150 promote successful cognitive aging.

151

Results

Noise impacts old listener's perception and speech comprehension

154 Figure 1A illustrates the experimental design of this study. A group of older adults

155 with normal or close-to-normal hearing threshold were recruited to listen to narratives

156 pre-recorded from a group of younger speakers (*35*). The listener's experiment was

157 conducted separately after the speaker's experiment, for the convenience of

158 controlling the speaking quality of speakers and incorporating noise into the speaker's

159 narrative audios (*33, 35, 36*). The neural activities from the speakers and the listeners

160 were measured by fNIRS with the same coverage of brain regions, including

161 prefrontal cortex and classical language regions (Figure 1B, see Methods for more

162 details). The listeners' subjective ratings of the narratives' clarity and intelligibility

163 and their comprehension scores were collected. Results are shown in Figure 2A. The

164 repeated-measures analysis of variance (rmANOVA) revealed that noise level

165 significantly affected the old listeners' perception and comprehension to the speech

166 (clarity: $F(3, 84) = 76.17$, $p < .001$, partial $\eta^2 = .73$; intelligibility: $F(3, 84) = 51.15$, p

167 $< .001$, partial $\eta^2 = .65$; comprehension: $F(3, 84) = 19.69$, $p < .001$, partial $\eta^2 = .41$).

168   Post hoc analysis showed that, for the clarity and the intelligibility ratings, all
169   pairwise comparisons between noise levels were significant (post hoc t-test, ps < .001,
170   corrected by false discovery rate (FDR), (*37*)), with a lower rating when noise
171   increased. For the comprehension score, except for the comparison between NN and 2
172   dB (post hoc t-test, p > .999), the other pairwise comparisons were significant (post
173   hoc t-test, ps < .05, FDR corrected). Notably, the comprehension scores of all the
174   listeners are substantially higher that the random level (25%) in all conditions. Even
175   in the strongest noise level (-9 dB), the average score was $65.3 \pm 2.6\%$ (mean $\pm$ SE),
176   suggesting a pretty good preservation of speech-in-noise comprehension ability for
177   the old listeners in this study.

178   To examine the relationship between the perceptual ratings and comprehension
179   performance, the correlation coefficients were computed across these behavioral
180   measures. Results showed that the average ratings of clarity and intelligibility was
181   significantly correlated (Spearman r = .40, p = .03). In contrast, the correlation
182   between these two ratings and the comprehension score was not significant (ps > .23),
183   suggesting a dissociation between the old listener's subjective percept and the actual
184   comprehension of speech. Besides, no significant correlation between these
185   behavioral measures and the old listener's hearing thresholds was found (ps > .14).

186

Old listener's neural activities are coupled to the speaker

188   To examine how old listener's neural activities were coupled to the speaker, we
189   conducted an rmANOVA on the speaker-listener neural coupling for all four noise
190   levels and the resting-state baseline. This allowed to test for significant differences in
191   neural coupling between any of the noise levels and the baseline as well as significant
192   differences in coupling strength across different noise levels. A non-parametric
193   cluster-based method (see Methods for more details) identified 57 clusters where
194   speaker-listener neural coupling differed among the five conditions. These clusters
195   covered the bilateral superior temporal gyrus (STG), middle temporal gyrus (MTG)
196   (CH19/21/29/31) and right inferior frontal gyrus (IFG) (CH27) at the speaker's side,
197   which were likely to be speech-production-related brain regions (*32, 38*). At the

198   listener's side, the clusters covered an extensive range of brain regions, including the

199   wide range of the prefrontal cortex (CH2, CH5-16) and the classical language regions.

200   Based on the anatomical localization and functional organization within the language

201   network (*35, 36, 39, 40*), these language regions were divided into ventral language

202   regions, including right STG, MTG (CH29/31/35), bilateral inferior parietal lobe (IPL,

203   CH23/24/26/33/34/36), and dorsal language regions, including bilateral IFG

204   (CH17/27), bilateral pre- and post-central gyrus (pre-/postCG, CH18/20/22/28/30/31).

205   The channel and localization of these channel combinations are shown in Figure 3A

206   and S1A. The strength of the neural coupling for each cluster is shown in Figure S2.

207   For all these clusters, the frequency band was around 0.01-0.03 Hz, as shown in

208   Figure S1B. It was in the same frequency band as discovered in our previous studies

209   on young listeners (*35, 36*). The specific information of all the clusters, including the

210   channels of speaker and listener, frequency band, and cluster-level statistics, are listed

211   in Table S1.

212   Based on the brain region at the listener's side, these inter-brain clusters were grouped

213   into three patterns (Figure 3A), i.e., O-Prefrontal (prefrontal cortex, "O" refers to

214   clusters from the old listeners), O-Ventral (ventral language regions) and O-Dorsal

215   (dorsal language regions). The neural coupling for these three inter-brain patterns was

216   derived by averaging the coupling values across clusters within the same group. These

217   results at the pattern level are illustrated in Figure 3C. Post hoc analysis showed that

218   for all of these three patterns, the neural coupling at the four noise levels were

219   significantly higher than the resting-state condition (post hoc *t*-test, *p*s < .05, FDR

220   corrected), indicating that the neural activities of old listeners were significantly

221   coupled to the speaker in both quiet and noisy conditions. Besides, the neural

222   coupling of the O-Prefrontal pattern at NN is higher than -9 dB (post hoc *t*-test, *p*

223   = .016, FDR corrected), and marginally higher than that at 2 dB and -6 dB (post hoc *t*-

224   test, *p*s = .052, .052, FDR corrected), suggesting its sensitivity to the appearance of

225   background noise. However, no significant difference was observed between the

226   neural coupling of the O-Prefrontal pattern and that from the O-Ventral or O-Dorsal

227   patterns, even in the noisy conditions (*p*s > .10, FDR corrected).

228

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, ts = 2.25, 3.48; ps = .032, .005, FDR corrected; Cohen's ds = 0.42, 0.65), -6 dB and -9 dB was marginally higher than the resting-state (Paired samples t-test, ts = 1.77, 1.57; ps = .054, .063, FDR corrected; Cohen's ds = 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, ts = 3.16, 3.17; ps = .005, .005, FDR corrected; Cohen's ds = 0.59, 0.59), +2 dB and -6 dB were marginally higher than resting-state (Paired samples t-test, ts = 1.83, 1.73; ps = .054, .054, FDR corrected; Cohen's ds = 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, ts > 3.00; ps < .05,

258 FDR corrected; Cohen's $ds > 0.91$).

259 To examine the specificity of these neural patterns for particular listener groups, we

260 compared the strength of these inter-brain neural coupling between the old and the

261 young listeners. The coherence of the resting-state baseline was first subtracted from

262 that of the four noise levels, and then devoted to a two-way mixed-design ANOVA

263 (between-participant factor: listener group/age; within-participant factor: SNR) to

264 analyze how age impacted the neural coupling. Results showed that, for all the five

265 patterns, the main effect of listener group was significant ($Fs > 4.11$, $ps < .05$, FDR

266 corrected). For the O-Prefrontal, O-Ventral and O-Dorsal patterns, the neural coupling

267 of the old listener was significantly higher than that of young listener. In contrast, for

268 the Y-Ventral and Y-Dorsal patterns, the neural coupling of the young listener was

269 significantly higher than that of the old listener. The main effect of SNR and the

270 interaction effect between the listener group and SNR were not significant ($Fs < 1.84$,

271 $ps > .14$). The group comparisons of the neural coupling are shown in Figure S4.

272 Furthermore, we compared the inter-brain neural coupling between two types of inter-

273 brain neural patterns (O-Prefrontal/Ventral/Dorsal vs. Y-Ventral/Dorsal). A two-way

274 rmANOVA (within-participant factors: inter-brain pattern, SNR) was conducted for

275 each listener group. Results showed that the main effect of the inter-brain pattern was

276 significant for both listener groups (old listener: $F(4, 112) = 16.46$, $p < .001$; young

277 listener: $F(4, 56) = 4.51$, $p = .003$). Post hoc analysis further showed that, for the old

278 listeners, the neural coupling from the O-Prefrontal, O-Ventral and O-Dorsal patterns

279 was significantly higher than that from both the Y-Ventral and Y-Dorsal patterns (post

280 hoc t-test, $ps < .05$, FDR corrected). In contrast, for the young listeners, the neural

281 coupling from the O-Prefrontal, O-Ventral and O-Dorsal patterns was significantly

282 lower than that from the Y-Dorsal pattern (post hoc t-test, $ps = .040$, $.003$, $.007$, FDR

283 corrected), but not the Y-Ventral pattern (post hoc t-test, $ps > .05$, FDR corrected). The

284 main effect of SNR and interaction effect between inter-brain pattern and SNR were

285 not significant ($Fs < 1.56$, uncorrected $ps > .10$). These findings suggested distinct

286 inter-brain neural patterns for speech(-in-noise) processing in the old versus young

287 listeners.

288

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

318   = .49, p = .007, uncorrected), but not in the other three conditions (ps > .12).

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

320   cluster level (ps > .10, FDR corrected) or at the pattern level (ps > .10). For the Y-

321   Dorsal pattern, at the cluster level, the r-values at NN and -6 dB were higher than

322   those at +2 dB and -9 dB (Paired samples t-test, ts > 2.48; ps < .05, FDR corrected;

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

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

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

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

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

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

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

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

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

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

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

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

335   shown in Figure 4C.

336

337   **Neural coupling from prefrontal cortex integrates with language regions in old**

338   **listener**

339   To figure out how the prefrontal cortex was functionally connected with the language

340   regions within the aging brain, the Spearman correlation between the neural coupling

341   from these regions was computed under various noise levels and for both the old

342   versus young listeners. For the old listeners, the inter-brain neural patterns of the O-

343   Prefrontal, O-Ventral and O-Dorsal patterns were interconnected. At all the four noise

344   levels, the neural coupling from the O-Prefrontal pattern was positively correlated

345   with that from the O-Ventral pattern (Spearman rs = 45, .48, .38, .58; ps

346   = .014, .008, .043, .001, FDR corrected), and the O-Dorsal pattern (Spearman rs =

347   50, .51, .43, .38; ps = .006, .006, .022, .042, FDR corrected). The coupling strength

348   from the O-Ventral pattern was also positively correlated with the that from the O-

349   Dorsal pattern in all the four noise levels (Spearman rs = 76, .69, .46, .43; ps < .001,

350   < .001, .013, .021, FDR corrected). These results suggested a close within-network

351   connectivity of the language regions and the possible integration of the prefrontal

352   cortex into the language network in older adults (Figure 5A/B).

353   For the young listeners, the neural coupling from the O-Ventral and the O-Dorsal

354   patterns was also correlated at all the four noise levels (Spearman rs

355   = .69, .72, .87, .61; ps = .006, .004, < .001, .018, FDR corrected). However, the neural

356   coupling from the O-Prefrontal pattern was only correlated with that from the O-

357   Ventral and O-Dorsal patterns at -6 dB (Spearman rs = .65, .87; ps = .005, .010, FDR

358   corrected), but not at the other noise levels (ps > .05, FDR corrected). These results

359   indicated the prefrontal cortex might be less connected to the classical language

360   regions for the young listeners. Interestingly, for both the old listeners or the young

361   listeners, the correlation between the neural coupling from the Y-Ventral and the Y-

362   Dorsal patterns were not significant at any noise levels (ps > .05, FDR corrected).

363   Besides, we also observed some correlation across two types of inter-brain neural

364   patterns (Figure S5). For the old listeners, the neural coupling from the Y-Ventral

365   pattern was positively correlated with that from the O-Prefrontal pattern at +2 dB

366   (Spearman r = .44, p = .048, FDR corrected), and the O-Ventral pattern at NN and +2

367   dB (Spearman rs = .37, .44; ps = .017, .017, FDR corrected). The neural coupling

368   from the O-Dorsal was negatively correlated with that from the Y-Dorsal pattern

369   (Spearman r = -.51, p = .006, FDR corrected). For the young listeners, the neural

370   coupling from the Y-Ventral pattern was correlated with that from the O-Ventral

371   pattern at NN and -9 dB (Spearman rs = .53, .54; ps = .045, .042, FDR corrected), and

372   the O-Dorsal pattern at -6 dB (Spearman r = .60, p = .021, FDR corrected). The neural

373   coupling from the Y-Dorsal pattern was correlated with that from both the O-

374   Prefrontal and O-Ventral patterns at NN (Spearman rs = .57, .54; ps = .030, .042, FDR

375   corrected). These results might reflect a complex relationship between the two types

376   of the inter-brain neural patterns.

377

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

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

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

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

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

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

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

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

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

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

416 neurocognitive resources from the prefrontal cortex to facilitate their natural speech

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

418 comprehension performance was more closely associated with the neural coupling in

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

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

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

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

423 mechanism centered around the prefrontal cortex for supporting the cognitive

424 preservation of speech ability in older adults.

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

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

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

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

429 classical language networks but also additionally engaged the prefrontal cortex to

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

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

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

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

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

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

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

437   *6*), and neural compensation hypothesis, which proposes the involvement of

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

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

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

441   consistently contribute to speech processing across diverse listening environments.

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

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

444   coupling and the comprehension performance suggests that the neural mechanisms

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

446   environmental noise.

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

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

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

450   contribution to the preservation of speech functions remains controversial. Drawing

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

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

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

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

455   the speech comprehension performance of the old listeners was more closely

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

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

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

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

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

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

462   compensatory recruitment of resources beyond the language network to meet the

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

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

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

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

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

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

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

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

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

472   coordinated for compensation with the classical language regions within the aging

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

490   integration perspective by showing that neural activities from both the prefrontal

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

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

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

494   remains unresolved and requires further research.

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

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

497　regions, this relationship was not observed in our study. One possible explanation for

498　this discrepancy may lie in the more naturalistic speech material used in our study.

499　Most previous studies have used simplified language materials, such as syllables or

500　words (*2, 11, 22, 41, 51*), which cannot fully capture how the brain processed natural

501　speech, such as narratives or stories, in more realistic settings. In particular, the dorsal

502　language regions could facilitate the speech-in-noise processing by generating an

503　internal representation of speech (*52, 53*), e.g., enabling the clear phonological

504　structures of the noise-masked speech by referring to pre-acquired phonological

505　knowledge (*54*). Despite the essential role of dorsal language regions in identifying

506　phonological units under noisy conditions (*9, 55*), the comprehension of natural

507　speech is more closely associated with the processing of content and contextual

508　information, especially for the older adults with a poor hearing ability (*56*). In this

509　way, as found in our study, the natural speech-in-noise comprehension ability of older

510　adults may be more closely related to brain regions responsible for processing

511　meaning or content, which are predominantly located in ventral language regions as

512　well as the prefrontal cortex, rather than the dorsal language regions (*57*). This

513　discrepancy between our study and previous studies also highlights the importance of

514　employing more naturalistic paradigms to understand the behavior, cognition and

515　brain function of older adults in everyday settings.

516　It should be noted that neither the neural reserve nor neural compensation can fully

517　restore the cognitive ability of older adults to the levels of young adults (*3, 4*).

518　Actually, the additional cognitive or neural resources recruited reflect a reduced

519　computational efficiency in the aging brain (*19, 58*). This study provides evidence for

520　this from the inter-brain neural patterns observed on the speaker's side. While the old

521　listeners recruit a wide range of brain regions than the young listeners, their neural

522　coupling at the speaker's brain is limited to a smaller set of regions. Conversely,

523　young listeners demonstrate neural coupling with a more extensive network of regions

524　within the speaker's brain, including bilateral temporo-parietal cortex and prefrontal

525　cortex. The neural coupling between speakers and listeners from specific brain

526　regions reflects the specific speech processing (*29, 59*). For example, coupling from

527   the primary auditory cortex is associated with early acoustic processing (*32*), whereas

528   coupling from higher-level regions like the posterior temporal lobe and frontal cortex

529   is associated with more complex processes such as semantic and contextual

530   interpretation (*29*). Therefore, given the inter-brain neural patterns showing limited

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

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

533   capacity for high-level speech processing and potentially low computational

534   efficiency in the brain.

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

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

537   related regions exhibited significant activation across different noise levels.

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

539   activities from the prefrontal cortex and ventral language regions were positively

540   correlated with speech comprehension performance. However, the correlation

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

542   significant, suggesting a dissociation between the specific speech processing within

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

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

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

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

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

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

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

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

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

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

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

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

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

556   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

587   age, future research might incorporate and analyze a broader spectrum of cognitive

588   tasks. This would enable a more nuanced view of the cognitive and neural alterations

589   in older adults.

590

Methods

591

Participants

592

593   Thirty older adults (15 males, 15 females; age 59 to 71 years old) participated in the

594   study. The sample size was determined by a prior power analysis using G*Power (*70*),

595   with the repeated measures *F*-test was employed (number of measurements = 4). The

596   effect size was designed at the medium level of 0.25. The significance level (alpha)

597   was set as 0.05, and the power was set as 0.9. All participants were native Chinese

598   speakers, right-handed, and had an educational level equivalent to or higher than high

599   school, ensuring basic reading proficiency. All participant passed the Chinese version

600   of the Mini-Mental State Examination (MMSE) (> 26 scores). Based on the definition

601   of   hearing   loss   (World   Report   on   Hearing   by   WHO,

602   https://www.who.int/publications/i/item/9789240020481), one female participant was

603   excluded due to a mild to moderate hearing loss as assessed by pure-tone audiometry

604   (34 dB hearing level, average pure tone threshold between 500 and 4000 Hz). For the

605   remaining twenty-nine participants, twenty-seven of them have a normal hearing

606   threshold (≤20 dB), the rest two of them have a close-to-normal hearing threshold (22,

607   23 dB). Figure 2B shows the group average and standard deviation of their hearing

608   levels.

609   The study was conducted in accordance with the Declaration of Helsinki and was

610   approved by the local Ethics Committee of Tsinghua University and the Institutional

611   Review Board of the Beijing Institute of Otolaryngology and Beijing Tongren

612   Hospital. All participants provided written informed consent prior to the experiment.

613

Experimental Design

614

615   The experimental design is illustrated in Figure 1A. The old listeners were instructed

616   to listen to pre-recorded narrative audios under various noise conditions. These

617   narratives were spoken by a group of young speakers, which were from our previous

618   study (*35*). Both the neural activities of the old listeners and the young speakers were

619   measured by fNIRS.

620

621   *Stimuli*

622   Each participant listened to sixteen narratives, with each lasting for 85 to 90 seconds.

623   These narratives were about daily topics that were adapted from the National

624   Mandarin Proficiency Test, such as favorite movies or travelling experiences. The

625   narratives were spoken by four young adults (2 males, 2 females; 21 to 25 years old),

626   all of whom were native Chinese speakers with professional training in broadcasting

627   and hosting. Two of them (one male, one female) contributed five stories each, and

628   two speakers (one male, one female) contributed three stories each. All narratives

629   were about the speaker's personal experiences, which were unfamiliar to the listeners.

630   These audios were recorded by a regular microphone at a sampling rate of 44,100 Hz

631   in a sound-attenuated room, and were then resampled to the 48,000 Hz to align with

632   the speaker's output frequency for this study.

633   Narrative audios were added with meaningless broadband white noise. For each

634   listener, they were processed into one of four noise levels: no noise (NN) level and

635   three noisy levels with the signal-to-noise ratio (SNR) of +2 dB, -6 dB, and -9 dB.

636   Each noise level included four narratives. All processed audios were normalized for

637   the average root mean square sound pressure level (SPL). For each narrative, four

638   four-choice questions regarding narrative content were prepared to evaluate the

639   listener's comprehension performance. For example, one question was, "What is the

640   relationship between the speaker and her friend? (˙ ˙ 人和朋友是什 ˙ ˙ 系)" and

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

642   (1. ˙ 生 ˙ 系, 2.姐妹 ˙ 系, 3. ˙ 居 ˙ 系, and 4.室友 ˙ 系).

643

644   *Experimental Procedure*

645   The listener's experiment was carried out in a sound-attenuated room. Sixteen

646   narratives are structured into sixteen trials, with one narrative in each trial. During

647   each trial, participants listened to one narrative under one of the four noise levels.

648   After listening, they rated the clarity and intelligibility of the audio using a 7-point

649   Likert scale, and completed a comprehension test based on the four choice questions.

650   The comprehension score was calculated as the accuracy of these questions. Then,

651   they could arrange a rest for a minimum of 10 seconds before proceeding to the next

652   trial. One practice trial was conducted using an additional speech audio stimulus at -2

653   dB SNR level.

654   Before the task session, there is a 3-min resting-state session. Participants were

655   instructed to get relaxed with their eyes closed. This resting-state session serves as the

656   baseline for task session.

657

658   *Neural measurement*

659   The listeners' neural activities were recorded from 36 channels using an fNIRS

660   system (NirScan Inc., HuiChuang, Beijing). The fNIRS signals were collected at a

661   sampling rate of 11 Hz, utilizing near-infrared light of two different wavelengths (730

662   and 850 nm). The concentration change of oxy-hemoglobin (HbO) and deoxy-

663   hemoglobin (HbR) for each channel was then obtained based on the modified Beer–

664   Lambert law.

665   Three sets of optode probes were positioned to cover the prefrontal cortex and

666   bilateral inferior frontal, pre- and post-central, inferior parietal, middle and superior

667   temporal gyrus, etc. As shown in Figure 1B, the positions of CH21 and CH31 were

668   aligned with T3 and T4, respectively, as per the international 10-20 system. The

669   central point of the prefrontal probe set was placed at the FPz position. To obtain a

670   probabilistic reference to specific cortical region for each fNIRS channel, the

671   topographic data was mapped onto a standardized MNI-space (Montreal Neurological

672   Institute) (*71, 72*) by using NIRS_SPM (*73*). The MNI coordinates and anatomical

673   labels for each channel are listed in Table S3.

674

675   *Neural data of speaker and young listeners*

676   The neural data of the speakers and a group of young listeners were from our previous

677   study (*35*). The speakers' neural activities were recorded from the same coverage of

678   brain regions, but by another fNIRS system (NirScan Inc., HuiChuang, Beijing) with

679   a sampling rate of 12 Hz and using near-infrared light at three different wavelengths

680   (785, 808, and 850 nm). These data were downsampled to 11 Hz to match the

681   sampling rate of the old listener in this study.

682   The young listeners comprised fifteen young adults (7 males, 8 females; ages 18 to 24

683   years old). Their neural signals were obtained using the same fNIRS system, with the

684   same brain coverage as the speakers. The experimental design for the young listeners

685   were the same as that for old listeners in this study. However, they listened to a larger

686   number of narratives (thirty-two narratives, with eight narratives in each noise level).

687   Only neural data from the same sixteen narratives as used in this study were selected

688   for the comparison between the young listeners versus the old listeners.

689

Data analysis

691   *Preprocessing*

692   A two-step preprocessing method based on HoMER2 software package (*74*) was

693   employed to remove possible motion artifacts. The first step utilized an algorithm

694   grounded   in   target   principal   component   analysis   (function:

695   hmrMotionCorrectPCArecurse; input parameters: tMotion = 0.5, tMask = 1,

696   STDthresh = 30, AMPthresh = 0.5, nSV = 0.97, maxIter = 5). This algorithm

697   discerned artifact-associated principal components and then reconstructed the cleaned

698   signals using the remaining components (*75*). Subsequently, the second step adopted a

699   linear interpolation method (*76*), which identified the motion artifacts based on a

700   predetermined threshold (function: hmrMotionArtifactByChannel; input parameters:

701   tMotion = 0.5, tMask = 1, STDEVthresh = 30, AMPthresh = 0.5), and then corrected

702   these artifacts through cubic spline interpolation (function hmrMotionCorrectSpline;

703   input parameters: p = 0.99). The above algorithms and parameters were all in

704   consistence with that for young listeners (*35*).

705

706 *Inter-brain neural coupling analysis*

707 The Wavelet Transform Coherence (WTC) was employed to analyze the relationship

708 between the speaker's and listener's neural activity. WTC allows for the assessment of

709 cross-correlation between two physiological signal series across frequency and time

710 dimensions (*77*). Each trial during the task sessions was initially segmented and

711 further extended to a duration of 300 seconds, which included the 90-second trial and

712 two additional 105-second periods both preceding and following the trial. This

713 extension aimed to facilitate a reliable computation of inter-brain couplings across the

714 desired frequency range. WTC was computed over the 300-second fNIRS signal

715 segments from both the listener and the corresponding speaker, resulting in a

716 coherence matrix organized across time and frequency domains. In the time domain,

717 coherence values were averaged across the entire 90-second trial and subsequently

718 converted to Fisher-z values. In the frequency domain, 75 frequency bins ranging

719 from 0.01 to 0.7 Hz were selected for subsequent analysis. Frequencies outside this

720 range were excluded to mitigate aliasing of higher-frequency physiological noise, like

721 cardiac activity (~0.8–2.5 Hz), and very-low-frequency fluctuations (*78*). Next,

722 coherence values from four trials under the same noise levels were averaged. The

723 coherence value for the middle 90 s of the resting-state session were calculated in the

724 same way. The above calculation was conducted for all speaker-listener channel

725 combinations, creating a total of 1296 cross-channel combinations (36 channels from

726 the speaker $\times$ 36 channels from the listener). Consequently, each listener had

727 coherence value under five different conditions, i.e., four speech conditions vs. the

728 resting-state condition, across 1296 channel combinations and 75 frequency bins

729 (0.01-0.07 Hz).

730 At the group level, a repeated-measures analysis of variance (rmANOVA) was applied

731 to examine the modulation of speech condition on the speaker-listener neural coupling

732 for each channel combination and frequency bin. A nonparametric cluster-based

733 permutation method was utilized to address the issue of multiple comparisons (*79*).

734 This method grouped neighboring frequency bins with uncorrected p-values below

735 0.05 into clusters and summed the *F*-statistics of these bins as the cluster statistic. A

736   null distribution was generated with the maximum cluster-level statistics from 1,000

737   permutations. In each permutation, the clusters were calculated with labels of different

738   trials in five conditions shuffled within each participant. Corrected *p*-values for each

739   cluster were derived by comparing the cluster-level statistics to the null distribution. A

740   cluster was significant if the *p*-value was lower than 0.05 level. For each cluster, the

741   speaker-listener neural coupling within the corresponding frequency bins were

742   averaged and subjected to further analysis.

743

744   *Comparison between old listeners and young listeners*

745   A two-factor mixed-design ANOVA (within-subject factor: noise level; between-

746   subject factor: listener group) was used to compare the speaker-listener neural

747   coupling between the old listeners and young listeners. Post hoc analysis was further

748   performed whether the main effect of listener group or the interaction effect between

749   noise level and listener group was significant.

750   Except for the clusters obtained from the old listeners, the clusters showing significant

751   speaker-listener neural coupling in the young listeners was also included into analysis.

752   These clusters centered over the listener's left IFG (CH17), right MTG and IPL

753   (CH35-36). They covered distributed brain areas at the speaker's side, including the

754   bilateral prefrontal cortex (CH4-7/9/11-12/14-15), bilateral postCG (CH22/32) and

755   bilateral IPL (CH23-24/26/30/32-34). The brain regions of these channel

756   combinations are shown in Figure 2A. The channel combination and the frequency

757   band of these clusters are listed in Table S2.

758

759   *Analysis of behavioral relevance*

760   To assess the behavioral relevance of the speaker-listener neural coupling, the

761   Spearman correlation was calculated between the coherence values and old listeners'

762   speech comprehension performance at each noise level.

763

764   *Single-brain activation analysis*

765   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.

Acknowledgments

795   paper are present in the paper and/or the Supplementary Materials. Data supporting

796   this study are available at https://doi.org/10.5061/dryad.sf7m0cgdn

797

798   **Reference**

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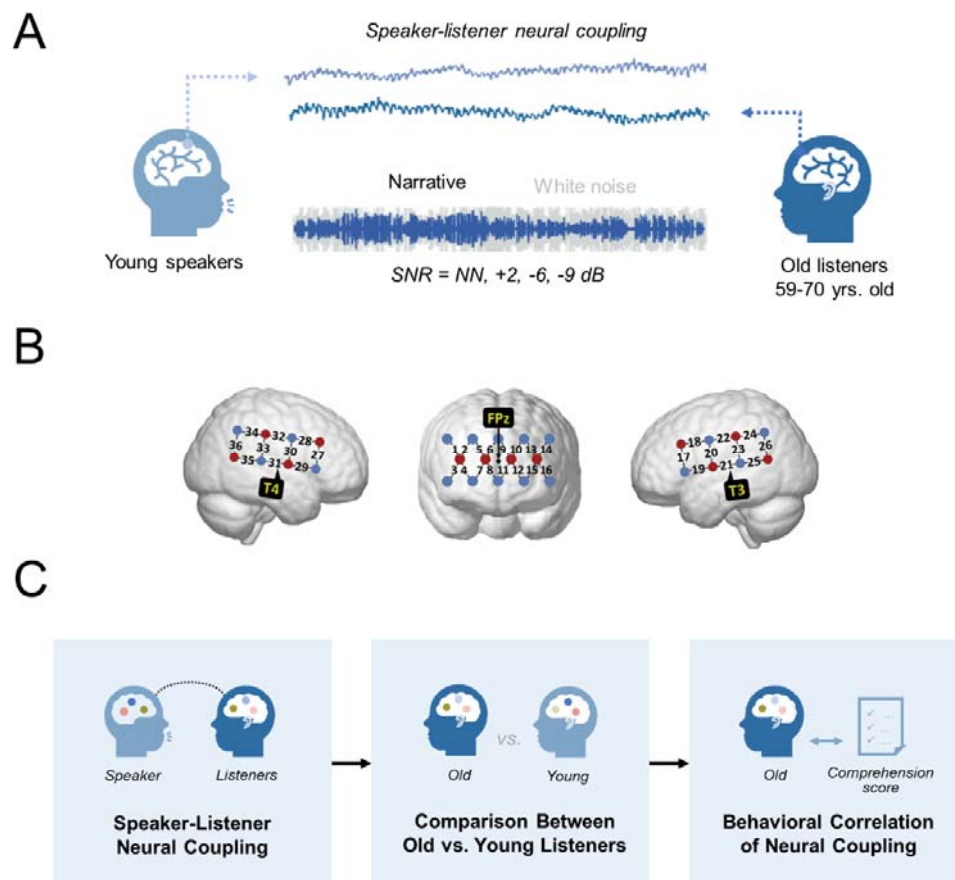
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1008 Fig. 1. Experimental design and behavioral results. (A) Overview of the experimental design.
1009 (B) The fNIRS optode probe set. The red dots represent the source optode; the blue dots
1010 represent the detection optode. Channels of 21 and 31 were placed at T3 and T4, and the
1011 center of the prefrontal probe set was placed at FPz, in accordance with the international 10-
1012 20 system. The probe set covered the prefrontal cortex and classical language-related regions
1013 in both hemispheres. (C) Overview of the analysis framework. The inter-brain neural coupling
1014 between the speaker and old listener was analyzed first. The older listener's neural coupling
1015 was then compared to that from a group of young listeners (*35*) to examine how different
1016 brain regions are compensatorily involved within the aging brain. Moreover, the functional
1017 role of these neural coupling was further exmained by analyzing its correlational relationship
1018 to the older listener's speech comprehension performance in noisy conditions.
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1023 Fig. 2. (A) Behavioral performance of old listeners. Results of repeated measures ANOVA
1024 showed that the noise significantly impacted the old listener's clarity, intelligibility ratings
1025 and comprehension scores. Post hoc analysis revealed that for the clarity and intelligibility
1026 ratings all pairwise comparisons between four noise levels were significant. For the
1027 comprehension score, except for the comparison between NN and +2 dB, the other pairwise
1028 comparisons were significant. The asterisk (*) means significant result ($p < .05$, FDR
1029 corrected). (B) The average pure-tone hearing thresholds of the old listeners. The error bar
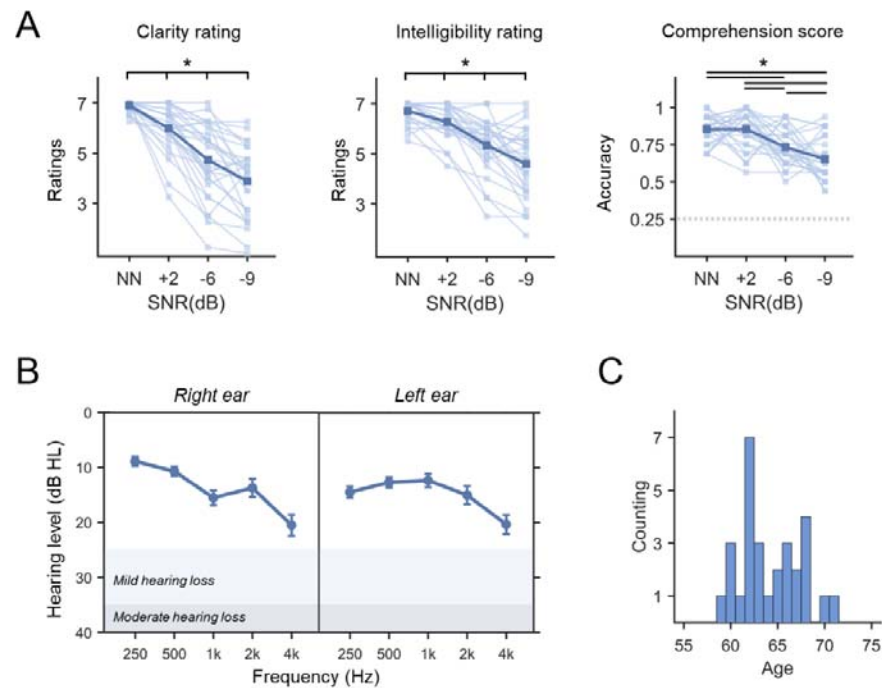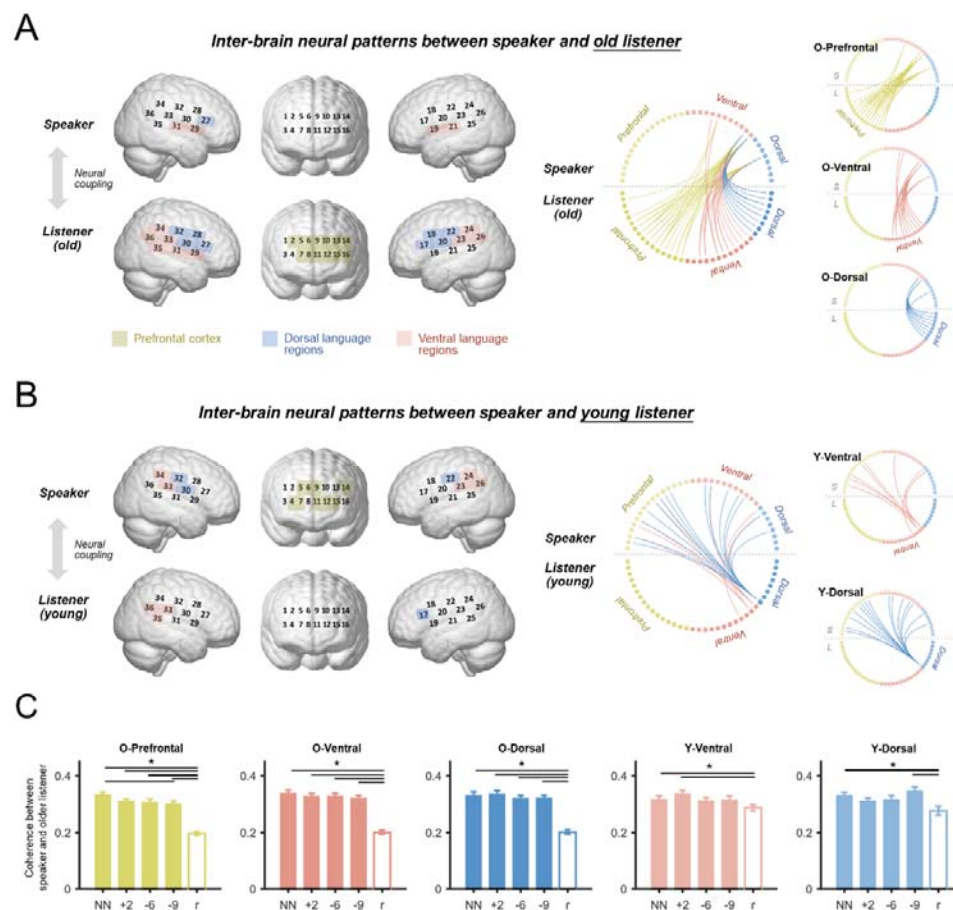1030 means the standard error. (C) The age of the old listeners.
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1035   Fig. 3. Speaker-listener neural coupling. (A) Significant speaker-listener neural coupling for
1036   the old listeners. The old listener's neural activities from prefrontal cortex, bilateral ventral
1037   and dorsal language regions were coupled to the speaker's neural activities. Different color
1038   means different anatomical brain regions: Yellow means the prefrontal cortex; red means the
1039   ventral language regions; blue means the dorsal language regions. Based on the brain region
1040   at the listener's side, these inter-brain neural coupling were divided into three patterns: O-
1041   Prefrontal, O-Ventral, and O-Dorsal. (B) The inter-brain neural patterns for the young
1042   listeners. They were divided into two patterns: Y-Ventral, Y-Dorsal. (C) The old listener's
1043   speaker-listener neural coupling from five inter-brain neural patterns. For O-Prefrontal, O-
1044   Ventral and O-Dorsal, the neural coupling in all the four noise levels was higher than the
1045   resting-state baseline. Besides, for the O-Prefrontal pattern, the coupling in NN was higher
1046   than -9 dB. For the Y-Ventral pattern, the coupling at NN and +2 dB was higher than that at
1047   the baseline; for the Y-Dorsal pattern, the coupling at NN and -9 dB was higher than that at
1048   the baseline. The error bar means the standard error. The lines and asterisks (*) indicate
1049   significant results ($p < .05$, FDR corrected).

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1054   Fig. 4. Behavioral relevance of speaker-listener neural coupling. (A) Correlation between the
1055   old listener's comprehension score and the coupling from the clusters. Each line represents
1056   the correlation r-values (Fisher-z transformed) of one cluster belonging to one particular inter-
1057   brain neural pattern. The asterisk indicates significant r-values in one particular noise level;
1058   the line indicates a significant pairwise comparison between two noise levels ($p < .05$, FDR
1059   corrected). For both the O-Prefrontal and O-Ventral patterns, the *r*-values in -6 dB and -9 dB
1060   were significant. For the O-Prefrontal pattern, the *r*-values were higher when noise increased.
1061   (B) Correlation between the old listener's comprehension score and average coupling for the
1062   inter-brain neural patterns. The neural coupling of the O-Prefrontal pattern was positively
1063   correlated with the comprehension score at -6 dB and -9 dB (Spearman *r*s = .39, .37; *p*s
1064   = .035, .047, uncorrected); the neural coupling of the O-Ventral pattern was correlated with
1065   the comprehension score at -6 dB (Spearman *r* = .49, *p* = .007, uncorrected). The other
1066   correlations were not significant. (C) Correlation between the young listener's comprehension
1067   score and the couplings. For the O-Prefrontal pattern, the *r*-values under four noise levels
1068   were not significant, although significant differences existed across the different noise levels.
1069   For the Y-Ventral pattern, the *r*-values in -6 dB were significant ($p < .05$, FDR corrected); for
1070   the Y-Dorsal pattern, the *r*-values in -9 dB were significant ($p < .05$, FDR corrected).
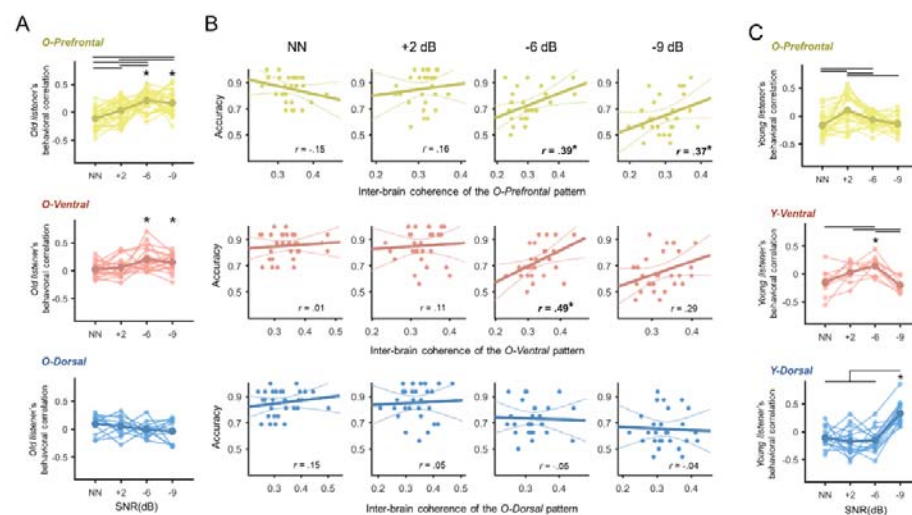1071

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1076   Fig. 5. Integration between inter-brain neural patterns. (A/C) Summary of the integration
1077   between the inter-brain neural patterns of O-Prefrontal, O-Ventral and O-Dorsal for the old
1078   listeners (A) and the young listeners (C). (B/D) The correlation between three inter-brain
1079   neural patterns in four noise levels. Significant correlation were marked by the dark line and
1080   the asterisks ($p < .05$, FDR corrected). For old listeners, the integration between the O-Frontal
1081   pattern and the O-Ventral/O-Dorsal patterns was robust across noise levels. However, they
1082   were only observed in moderate noise level (-6 dB) for the young listeners. The O-Ventral and
1083   the O-Dorsal patterns was closely integrated in all four noise levels, for both the old listeners
1084   and the young listeners.
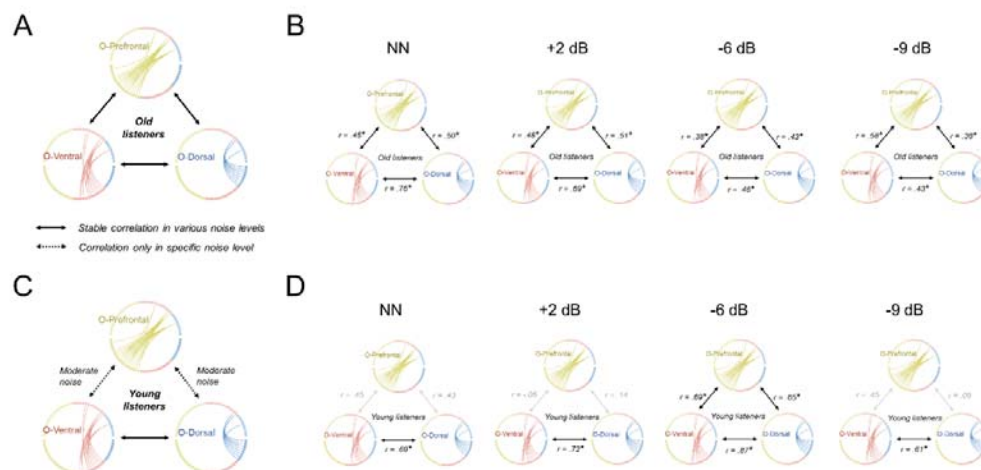

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1089 Fig. 6. Summary of the neural mechanism for natural speech comprehension in different noise
1090 levels and age groups. In young adults, the dorsal and ventral language regions are engaged,
1091 with stable integration facilitating speech-in-noise processing. As noise intensity increases,
1092 the dorsal language regions play a more critical role, as indicated by a stronger correlation
1093 between the speech-in-noise comprehension performance and neural coupling. In contrast,
1094 older adults exhibit a compensatory recruitment of the prefrontal cortex to maintain speech
1095 comprehension abilities. This engagement is characterized by not only robust prefrontal
1096 cortex involvement across noise levels but also by an enhanced integration with language
1097 regions, a phenomenon not observed in young adults. Furthermore, the older adult's speech-
1098 in-noise comprehension is more closely associated with the prefrontal cortex, especially as
1099 noise level increases. Asterisks (*) indicate significant correlational relationship between the
1100 speech comprehension performance and the neural coupling from the particular brain regions.
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