

# Reduced Listener-speaker Neural Coupling Underlies Speech Understanding Difficulty in Older Adults

Ianfang liu (✉ [liulanfang11@mail.bnu.edu.cn](mailto:liulanfang11@mail.bnu.edu.cn))

Sun Yat-Sen University <https://orcid.org/0000-0002-1448-9009>

Xiaowei Ding

Sun Yat-Sen University

Hehui Li

Shenzhen University

Qi Zhou

Beijing Normal University

Dingguo Gao

Sun Yat-Sen University

Chunming Lu

Beijing Normal University

Guosheng Ding

Beijing Normal University

---

## Research Article

**Keywords:** Healthy aging, neural coupling, speech comprehension, fMRI

**Posted Date:** March 13th, 2021

**DOI:** <https://doi.org/10.21203/rs.3.rs-283844/v1>

**License:**  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

---

**Version of Record:** A version of this preprint was published at Brain Structure and Function on April 11th, 2021. See the published version at <https://doi.org/10.1007/s00429-021-02271-2>.

# Abstract

An increasing number of studies have highlighted the importance of listener-speaker neural coupling in successful verbal communication. Whether the brain-to-brain coupling changes with healthy aging and the possible role of this change in the speech comprehension of older adults remain unexplored. In this study, we scanned with fMRI a young and an older speaker telling real-life stories, and then played the audio recordings to a group of young ( $N = 28$ , aged 19-27y) and a group of older adults during scanning ( $N = 27$ , aged 53-75y), respectively. The older listeners understood the speech less well than did the young listeners, and the age of the older listeners was negatively correlated with their level of speech understanding. Compared to the young listener-speaker dyads, the older dyads exhibited reduced neural couplings in both linguistic and extra-linguistic areas. Moreover, within the older group, the listener's age was negatively correlated with the overall strength of interbrain coupling, which in turn was associated with reduced speech understanding. These results reveal the deficits of older adults in achieving neural alignment with other brains, which may underlie the age-related decline in speech understanding.

## 1. Introduction

Narratives, especially real-life stories, are the most ancient and effective tools for communicating personal experiences, emotions, and beliefs between people in daily life. To successfully understand spoken narratives requires a set of complex cognitive and neural computations. A listener needs to not only segregate audio streams into linguistic units and retrieve semantic information, but also simultaneously maintain the decoded information in working memory, integrate it with preceding information and the knowledge base, build situation models, make inferences and predictions, and beyond. Despite these cognitive requirements, young adults usually understand well the information intended by a speaker. However, the older adults typically understand spoken narratives slower, make more errors, and remember less information (1-3), even though their basic linguistic functions (such as semantic and syntactic processing) are thought to be preserved (4,5).

Currently, neuroimaging studies on language processing in older adults have primarily focused on cortical responses to isolated, decontextualized phonemes, words, or sentences within isolated brains (e.g, 6,7,8). Little is known about the neural processes underlying speech comprehension during naturalistic verbal communication in aged brains. According to the interactive alignment model, originally proposed by Pickering & Garrod (2004), individuals engaged in verbal communication interactively coordinate their mental representations at multiple levels (e.g., phonology, syntax, semantics, situation models) (9). This alignment process is suggested to be the major driver of mutual understanding (9-11). In line with this model, it has been demonstrated that neural activities associated with the phonological (12), lexical (13), and syntactic (14) processing during speaking and listening are closely related, supporting the representational parity between language production and comprehension (15). Moving beyond single brains, recent studies applying fMRI (16-19), fNIRS (20-24) or EEG (25,26) directly measured the brain activities from both speakers and listeners engaged in verbal communication. These studies consistently demonstrated that the brain activities between the speaker and listener were tightly coupled (i.e.,

variations in the amplitude or phase of brain signals are correlated) when communication succeeded. Significant interbrain couplings were found both in areas associated with linguistic analyses (such as the inferior frontal gyrus, and the superior temporal gyrus) and in areas associated with social cognition (such as the precuneus and the media prefrontal cortex) (16,17). Moreover, the tighter listener-speaker neural coupling was associated with better speech understanding (16,19). The brain-to-brain coupling is thought to reflect the listener-speaker alignment at different levels of linguistic and extra-linguistic representations, and to be an important neural mechanism underlying successful verbal communication (15,27).

Up to now, the investigation of human brains in communicative settings has been mainly limited to the young cohorts. Whether the brain-to-brain coupling changes with healthy aging and the possible role of this change in the speech comprehension of older adults remain unexplored. Two possibilities exist. First, due to impaired auditory temporal processing (28) and slowing in cognitive processing, as well decline in high-level cognitive functions (e.g., sustained attention), an older listener may have difficulties in tracking the fleeting linguistic input and therefore fail to achieve alignment with a speaker on neural activities and mental representations. This failure may in turn lead to poorer speech understanding. Alternatively, according to the interactive brain hypothesis, interactive experience and skills play enabling roles in both the development and current function of social brain mechanisms (29). In relation to aging, this experience-driven model would predict that the older listeners will exhibit preserved or even tighter neural alignment with the speaker during communication, due to their life-long experience of social interactions through verbal language. The preserved or strengthened ability to achieve alignment with other brains (and minds) may serve as a compensation mechanism to alleviate the adverse effect of cognitive and auditory declines during aging.

To test the above possibilities, we recorded a young and an older speaker telling real-life stories during fMRI scanning, and then played the audio recordings to a group of young adults and a group of older adults, respectively, while undergoing fMRI scanning. We choose to have the speaker and listeners age-matched, rather than exposing the same speaker to both young and older adults, for two considerations. First, in daily-life situations, verbal communication among older adults differs substantially from that among young adults in terms of topics, speech rate, vocabulary, and organizational structure (30,31). Thus, age-matched dyads are likely to communicate better than young-old dyads. Second, the rate of blood flow, metabolism, and neurovascular coupling in the aging brain are quite different from those in young brains (32-34); thus, age-matched brains should be more alike in neural dynamics. Given these two points, we presume age-matched listener-speaker dyads are more likely to achieve neural alignment than young-old dyads.

Neural couplings between the speaker and each listener were assessed by calculating the temporal correlation between their BOLD signals in spatially corresponding cortical regions. Listeners' level of speech understanding was assessed mainly by a story-retelling task (16). However, listeners' performance on this task may depend not only on their speech comprehension but also on their memory capacity, and healthy aging is accompanied by decreased working memory (35,36). To reduce the impact of memory

capacity on language comprehension, we measured listeners' phonological working memory using WISC-III forward and backward digit span tests and regressed out their digit spans when analyzing the relationship between comprehension scores and other variables. To determine the potential effect of age on brain-to-brain coupling, we compared the older listener-speaker dyads with the young dyads and further examined the correlation between the age of older listeners and their neural alignments with the speaker. Next, we investigated whether change in the interbrain coupling played a role in the age-related change in speech understanding. To this end, we examined the correlations among age, interbrain coupling, and the level of speech understanding, and then conducted a mediation analysis. If interbrain coupling decreases with healthy aging and this neural decline accounts (partially) for the age-related decline in speech comprehension, the older dyads would exhibit reduced neural coupling compared to the young, and the age of the older listeners would be negatively correlated with their neural alignments with the speaker. Moreover, the reduced neural alignment would in turn be linked to poorer speech understanding. Alternatively, if life-long experience of verbal interactions plays a protective role, the older listener-speaker dyads would exhibit comparable or tighter interbrain coupling than the young dyads. Moreover, the interbrain coupling may positively correlate with speech comprehension in the older group. Note, even with such a compensation effect, the older adults may still understand the speech less well than the young adults, given that a set of adverse factors (such as age-related decline in hearing acuity and working memory) can contribute greater to speech comprehension than does the protective factor.

Upon finding the aging effect in listener-speaker neural couplings, we conducted additional analyses to explore the potential contribution of three factors to this effect. First, it has been well-documented that older adults have difficulties in sustaining their attention over time (37,38). It is possible that the older listener-speaker dyads presented as tight interbrain coupling as the young dyads at the beginning of the communication, which dropped down gradually because the older listeners could not well sustain their attention on the speech. To test this possibility, we performed a sliding window analysis to capture the time-dependent variations in the interbrain effect. Second, it has been reported that older participants showed more idiosyncratic cortical responses during movie-watching (39). Since the listener-speaker neural coupling can be regarded as a special case of neural similarity, it is possible that the age-related reduction in neural coupling was merely an epiphenomenon of age-related decline in intersubject neural similarity. To test this possibility, we computed the neural correlation between each listener with other listeners exposed to the same story. Then the listener-listener correlation was taken as a covariate during the between-group comparison and the correlation analysis for age and neural coupling. Finally, we explored whether the deficits of aged brain in "tuning into" other brains were associated with age-related gray matter atrophy. We first tested whether those cortical regions showing age-related decline in neural coupling also exhibited age-related reduction in gray matter volume (GMV). We then examined for each cortical region whether the strength of interbrain coupling was correlated with the GMV of this region across the participants.

## 2. Method

## 2.1 Participants

Two females (aged 23y and 62y, respectively) participated in this study as the speakers. They were chosen from several candidates because they talked fluently and vividly, moved their heads very little, and output clear audio recordings during the fMRI scanning. Details on the selection of speakers are provided in the supplementary material. Thirty-two young adults (16 females, aged 19-27y) and 30 older adults (18 females, aged 53-75y) participated in this study as listeners. The young participants were college students from the Southwest University, China. The older participants were recruited from several communities nearby the campus. All participants were paid for their participation. The datasets of four young and three older participants were discarded due to excessive head movements (more than 3mm or 3 degrees) during the fMRI scanning.

All participants were right-handed based on the Edinburgh Handedness Inventory (40) and reported no mental or neurological disorders. For the older group, a Mini-Mental State Examination was administered by a researcher, and all older adults scored above 26. To exclude participants with potential hearing loss, pure tone audiometry was conducted. The threshold of < 30 dB HL in the better ear across 0.5, 1.0, 2.0, and 4.0 kHz, which cover the most range of human speech (41), was employed to filter participants (42). All participants in the young group met this criterion at every frequency. In the older group, all met this criterion at 0.5, 1, and 2 kHz, and all but two met at 4 kHz. Written informed consent was obtained from all participants under the protocol approved by the Reviewer Board of Southwest University. The data of the older group were also used in another study which addressed a different question (19).

## 2.2 Experimental Design

During the fMRI scanning, the two speakers told stories based on their personal experience, with each story lasting 10 min. To obtain audio recordings with good quality, we used a noise-canceling microphone (FOMRI-III, Optoacoustics Ltd., Or-Yehuda, Israel) positioned above the mouth of the speaker, and further de-noised the audio recordings offline using Adobe Audition 3.0 (Adobe Systems Inc., USA). Two groups of college students ( $N_1 = 32$ ,  $N_2 = 31$ ) assessed the complexity and vividness of the stories told by the young and older speakers, respectively, on a scale of 1.0-10. The results showed, different stories told by the same speaker did not differ in either vividness or complexity. Compared to the stories told by the young speaker, the stories told by the older speaker were more vivid ( $p < 0.001$ ) but did not differ in complexity ( $p = 0.25$ ).

When checking the quality of audio recordings, we detected a sudden cough at the last minute in one of the stories told by the older speaker. In addition, our pilot experiment on several older adults showed that the 10-min story was too long for them to keep sustained attention and memorize well. We thus played back only the first 7-min recordings to the older listeners during the fMRI scanning. For the young group, the full-length (10 min) recordings were played back. The audio stimuli were presented through an MR-compatible headphone with noise-cancellation (OptoACTIVE, Optoacoustics Ltd., Or-Yehuda, Israel) at a

volume comfortably audible for all listeners. A fixation cross lasting for 20s and then an icon of a horn lasting until the end of the scanning were presented to both speakers and listeners (Fig.1). The participants were informed to start speaking or listening immediately upon seeing the horn. To make the participants focus their attention on the speech, they were informed beforehand that an interview about the content of the story would be given after the scanning.

Each young adult listened to one of the three stories told by the young speaker. Each older adult listened to one of the two stories told by the older speaker. As participants listening to the different stories did not differ in their comprehension scores (for young group:  $F_{(2, 29)} = 2.96, p = 0.07$ ; for older group:  $t_{(29)} = -0.18, p = 0.85$ ), their data were collapsed for further analyses.

## 2.3 Behavioral assessment for the level of speech understanding

Two measurements were used to assess the level of speech understanding. First, at the end of the audio play, listeners in the scanner were asked to report to which degree (in the form of percentage) they understood the story. To obtain a more objective assessment, the listeners were required to retell the stories in detail immediately after the scanning. After the free recall, the experimenters asked the participants a few questions regarding the contents not recalled. These questions were from a list (including 9-10 questions for each story) prepared for later scoring, covering important episodes that happened in the different stages of the story (e.g., “please describe the preparation she made for the hiking”, “what happened on her way to the hotel”). Correct answers to these questions contained several key points covering actions, characters, places, time, and motivations et al. Two independent raters scored each listener based on the free call and the answers to the experimenter’s questions. For each question on the list, a score was given according to the information a listener provided about those key points. The percentage of the score received out of the total maximal score was computed for each listener. As the assessments made by the two raters were in high agreement (Spearman’s  $r_{(62)} = 0.85$ ), the mean score between the two raters was used to quantify the listener’s level of speech understanding.

## 2.4 MRI acquisition and preprocessing

Imaging data were acquired with a 3T Siemens Trio scanner in the MRI Center of the Southwest University of China. A gradient echo planar imaging sequence was applied to collect functional images. The parameters were repetition time = 2000 ms, echo time = 30 ms, flip angle = 90°, field of view = 220 mm, matrix size = 64 × 64, slice number = 32 interleaved, voxel size = 3.44 × 3.44 × 3.99 mm<sup>3</sup>. A MPRAGE sequence was adopted to collect T1 structural images with the following parameters: repetition time = 2530 ms, echo time = 3.39 ms, flip angle = 7°, FOV = 256 mm<sup>2</sup>, scan order = interleaved, matrix size = 256 × 256, and voxel size = 1.0 × 1.0 × 1.33 mm<sup>3</sup>.

A total of 310 and 220 volumes were acquired for the young and older participants, respectively. The first ten volumes corresponding to the fixation period were discarded. Image preprocessing was implemented using the DPABI toolkit (43) which is based on SPM12 ([www.fil.ion.ucl.ac.uk/spm/](http://www.fil.ion.ucl.ac.uk/spm/)) modules. First, slice-timing correction was performed to correct for varied sampling time of slices. Next, the corrected images were spatially realigned and co-registered to individual subjects' anatomical images. The resultant images were then spatially normalized to Montreal Neurological Institute (MNI) space, resampled into a  $3 \times 3 \times 3 \text{ mm}^3$  voxel size, and spatially smoothed using a 7mm full-width-half-maximum Gaussian kernel. Finally, the preprocessed images were detrended, nuisance variable regressed, and high-pass filtered (1/128 Hz). The nuisance variables included five principal components of white matter and cerebrospinal fluid within individual subjects' T1 segmentation mask (44), as well as the Friston's 24 motion parameters (45).

## 2.5 Data analysis

### 2.5.1. Analysis of behavioral data

To test whether speech understanding declined with aging, we compared the older adults with the young on self-reports and comprehension scores using two-sample *t*-tests. In addition, we examined whether the increased age of the older adults was associated with a lower comprehension score. As participants' memory capacity may influence their recall for the speech contents, here we applied a Spearman's partial correlation which included the digit spans on the forward and backward memory test as two covariates. In the partial correlation analysis, the digit spans were regressed out separately from age and comprehension scores. Then the residuals of the two models were used to compute the correlation value. Since the directions of between-group differences and the age-behavior correlation had been predicted, a one-tailed test for statistical significance was employed.

### 2.5.2 Measurement for listener-speaker neural coupling

The listener-speaker neural coupling was measured by the Pearson's correlation between the time series of each area in the listener's brain and the time series of the homologous area in the speaker's brain (Fig 1). Since noticeable intersubject variabilities in brain functioning and structural morphometry among older adults have been reported (46-48), functionally similar loci may not correspond well in spatial location across older adults. To alleviate the potential influence of inter-individual variability, we computed the interbrain correlation at the regional level, which is the common practice in studies on intra-brain functional connectivity. For each participant, the brain was partitioned into 246 regions based on the Human Brainnetome Atlas (49). At each region, the time series across all voxels within it were averaged for calculating the interbrain correlation coefficient. To test the robustness of the results, we re-analyzed the data using Craddock's atlas (50) which partitioned the brain into 200 regions (supplementary material).

As listeners might need time to extract high-level information in the speech, their neural activities would lag those in the speaker's brain. Besides, listeners might anticipate the speech content, their neural activities would precede those in the speaker's brain. To capture the temporal asymmetry in neural coupling, we repeated the interbrain correlation analysis by shifting the listener's time course with respect to those of the speaker from -8s (listener preceding) to 8s (listener lagging) in 2s increments. At shift zero, the listener's brain activity was time-locked to the speaker's vocalization. To capture the overall temporal profile of the interbrain coupling and identify the time point wherein this effect reached the peak (referred to as the "peaking time", which was the target of the bellowing analysis), we calculated the mean of the correlation values across the 246 parcels and all participants for each lag.

At each lag, a *t*-test was performed on the interbrain correlation coefficients (the r values) of each brain region, for the young and older groups separately. Considering that the cognitive meaning of negative interbrain correlation is still unclear, here we only focused on positive interbrain correlations, and used the one-tailed p-value as the indicator of significance. The resulting coupling maps were corrected for multiple comparisons using the Benjamini-Hochberg procedure to control the false discovery rate (FDR) at 0.05.

### **2.5.3 Evaluation for the effect of age on listener-speaker neural coupling**

Two folds of analyses were conducted to assess the effect of age on listener-speaker neural coupling. First, we directly compared the older group to the young group at each time lag using a two-sample *t*-test. Nevertheless, the between-group effects could be driven by not only the differences in the listener's age but also the differences in the speaker and the speech contents. To eliminate the confounding effect, we further assessed the correlation between the chronological age of older listeners and their neural alignment with the speaker. To measure the overall strength of neural alignment, we selected the collection of cortical regions showing the most significant listener-speaker neural coupling (for the peaking time) at the group level. Then for each participant, the mean of the correlation values across these regions was calculated. Before averaging, each r-value was transformed to z-value using Fisher's z transformation to normalize its distribution. The averaged z values were then inverse transformed (z-to-r) to produce average r values. To ensure that the number of selected cortical regions did not have an undue influence on the results, we repeated the correlation analysis over a wide range of thresholds: from the top 10 regions showing the strongest interbrain couplings (corresponding  $t_{(26)} >= 2.85$ ) to the top 44 regions (corresponding to  $t_{(26)} >= 1.65$ ). The MNI coordinates and anatomical labels for the 44 regions were reported in the supplementary material (table S1).

### **2.5.4 Brain-behavior correlation**

To assess the association of listener-speaker coupling with the listener's level of speech understanding, we computed the Spearman's rank correlation between the comprehension score and the overall strength

of interbrain coupling, controlling for the listeners' memory spans. Consistent as above, we took the mean value from the collection of cortical regions demonstrating the most significant interbrain coupling and repeated the correlation analyses over a wide range of thresholds.

## 2.5.5 Mediation analysis

To test whether the interbrain coupling mediated the relationship between the older listener's age and the level of speech understanding, we performed a mediation analysis using the Hayes' PROCESS macro in SPSS. In the analysis, the age of the older listeners and their comprehension scores were entered as the causal variable and the outcome, respectively, and the overall strength of listener-speaker neural coupling was entered as the mediating variable. A series of linear regression were used to assess (1) the effect of age on interbrain coupling (denoted as  $a$ ); (2) the effect of interbrain coupling on speech understanding after removing the effect of age (denoted as  $b$ ); and (3) the total effect of age on comprehension score (denoted as  $c$ ). The mediation effect of interbrain neural coupling on the age-behavior relationship was assessed by taking the product of coefficient  $a$  and coefficient  $b$  (denoted as  $ab$ , also called "*indirect effect*"). In all three regression models, the backward and forward memory spans of older listeners were included as two covariates. A bootstrapping procedure with 5,000 iterations was used to assess the 95% confidence interval for  $ab$  (51). The indirect (mediation) effect was statistically significant if the confidence interval did not include zero. For the mediation analyses, we examined and reported the collection of brain regions (the top 34) showing the strongest positive correlation with the comprehension score. We also examined other collections and obtained similar results.

## 2.6 Analyses for factors potentially contributing to the aging effect on interbrain coupling

We explored three factors that potentially accounted for the age-related decline in listener-speaker neural couplings, including sustained attention, neural similarity across subjects, and gray matter atrophy. Details for these analyses were provided in the supplementary material.

## 3. Results

### 3.1 Behavioral results

Despite the stories told by the older speaker were more vivid and shorter than those told by the young speaker, whereas the complexity of speech content did not differ between the two, the older listeners still understood the speech less well than the young, as demonstrated in both the self-reports (two-sample  $t_{(47)} = 5.95, p < 10^{-6}$ , Cohen's  $d = 1.73$ ) and comprehension scores (two-sample  $t_{(53)} = 5.80, p < 10^{-6}$ , Cohen's  $d = 1.77$ ). Within the older group, the comprehension score was significantly correlated with the listener's backward memory span ( $r_{(25)} = 0.50, p < 0.01$ , by Spearman's correlation), but not with the forward

memory span ( $r_{(25)} = 0.13, p > 0.5$ ) or hearing level ( $r_{(25)} = -0.12, p > 0.5$ ). After controlling for the individual differences in memory spans, the increasing age of the older listener was associated with a lower comprehension score (Spearman's partial  $r_{(25)} = -0.37$ , one-tailed  $p = 0.035$ ) (Fig.2). These results are consistent with previous reports that the ability to comprehend narrative speech declines with healthy aging.

## 3.2 Neural coupling between the young listener-speaker dyads

Consistent with prior work (16,52), we found widespread neural couplings between the listener and speaker in the young group. On average, the activities in the listener's brain were aligned to the activities in the speaker's brain with some temporal delays. The strongest neural coupling at the whole-brain level occurred at a time lag of 6s (Fig.3a). Notably, the listener's neural alignment with the speaker followed an orderly temporospatial progression: shortly after the speaker's vocalization (0-2s), activities in the lower-order auditory areas (the superior temporal gyrus and sulcus, STG/STS) of the listener's brain exhibited the most significant coupling effects to the activities of the homologous regions in the speaker's brain; 4-6s later, the higher-order semantic/conceptual areas, encompassing bilateral inferior parietal lobule (IPL), inferior and superior frontal gyrus (IFG, SFG), angular, bilateral precuneus and medial prefrontal cortex (mPFC) exhibited the most significant coupling effects (Fig. 3b). For delays longer than 6s, the interbrain coupling declined substantially. When the listener's brain activities were shifted to precede those in the speaker's brain, no significant interbrain correlation was found. Thus, further analyses only focused on the interbrain coupling with a lag from 0s to 6s. Detailed information on those significant regions is provided in the supplementary material (table S2).

## 3.3 Neural coupling between the older listener-speaker dyads

As with the young group, in the older group, the listener's brain activities got aligned with the activities in the speaker's brain with some temporal lags but peaked earlier (at a lag of 2s) and faded quicker (Fig. 3a). In contrast to widespread interbrain couplings of young dyads, the older listener-speaker dyads showed significant neural couplings in only a few cortical regions. At lag 0s, significant couplings were mainly located in the bilateral STG, MTG, SFG and lingual gyrus. At lag 2s, significant couplings were mainly located in the bilateral STG and middle cingulum gyrus. At lag 4s and lag 8s, there was no cortical region exhibiting significant neural couplings that survived the FDR correction for multiple comparisons (Fig.3b). Detailed information on those significant regions is provided in the supplementary material (Table S2).

## **3.4 Listener-speaker neural coupling decreased with advancing age**

The two-sample *t*-test revealed that neural couplings between the young dyads were significantly stronger (threshold: FDR corrected  $p < 0.05$ ) than the older dyads in multiple cortical regions, including the bilateral STG/STS (at lag 2s, 4s and 6s), SFG (at lag 4s and 6s), angular gyrus (at lag 4s and 6s), and precuneus (at lag 4s and 6s). The older dyads showed greater neural couplings than the young dyads only in the left MTG (at lag 2s) and right IFG (at lag 6s) (Fig. 4a). Detailed information about those cortical regions showing significant group differences is provided in the supplementary material (table S3).

Consistent with the results of between-group comparisons, there were significant negative correlations (the largest effect size was  $r_{(26)} = -0.59$ ,  $p = 0.001$ ) between the older listener's age and his/her overall strength of neural alignment with the speaker. This effect was robust to the changes of selected cortical regions showing significant interbrain couplings (Fig. 4b). Since the story played to one half of the older listeners was different from that of the other half, we also performed a partial correlation which took the story identities as two binary covariates. Similar results of negative correlation between age and neural strength were obtained (Fig.S1).

## **3.5 Correlation between neural coupling and speech understanding**

Consistent with previous studies (16,19), the overall strength of listener-speaker neural coupling was positively correlated with listeners' comprehension scores (with memory span controlled) (Fig.5a). This relationship was found in both the young and older groups and was consistent across a wide range of selected cortical regions (Fig.5b). In the young group, it was the 6s-lagged neural coupling (the peaking time) that demonstrated the correlation to speech understanding. In the older group, it was the 2s-lagged (the peaking time) neural coupling that demonstrated the correlation.

## **3.6 Reduced interbrain coupling mediated the negative relationship between age and speech understanding**

In the above analyses, we observed in the older group 1) a negative correlation between age and speech understanding; 2) a negative correlation between age and interbrain coupling; and 3) a positive correlation between interbrain coupling and speech understanding. Based on these findings, it was plausible to assume a mediation role of interbrain coupling in the relationship between age and speech understanding. Indeed, the mediation analysis revealed a significant mediating effect of interbrain coupling on the relationship between age and the comprehension score ( $ab = -0.62$ , 95% confidence interval: [-1.32 to -0.05], obtained from the Bootstrapping test) (Fig. 6). Moreover, after controlling for the effect of neural coupling, the listener's age was no longer a significant predictor for the listener's

comprehension score. These results indicate the advancing age of the older listener was associated with decreased ability to achieve neural alignment with the speaker, which in turn negatively affected their speech understanding.

## **3.7 Factors potentially contributing to the aging effect on interbrain coupling**

### **3.7.1 Neural coupling between the older dyads decreased over time**

The sliding-window analyses revealed, the older listener-speaker dyads presented extensive neural couplings within the first 2 min of the communication, which gradually decreased thereafter. In comparison, the young dyads exhibited extensive neural couplings across multiple time windows, and the extent of interbrain coupling tended to increase over the course of the communication (Fig.S2). These results indicate that the reduced neural alignment of the older listeners with the speaker was partially accounted for by their deficits in sustained attention.

### **3.7.2 Age-related decline in listener-speaker neural coupling was not an epiphenomenon of age-related reduction in intersubject neural similarity**

Consistent with the previous study (39), we found the listener-listener neural correlations of the young group were greater than that of the older group (Fig.S3). However, after statistically controlling for this variable, the overall interbrain couplings of the young dyads were still stronger than in the older dyads (Fig.S4a). Moreover, the partial correlation analyses which included the listener-listener neural correlation as a covariate still yielded a quite significant negative correlation between neural coupling and the age of older adults (Fig.S4b). These results suggest the age-related decline in listener-speaker neural coupling was not merely an epiphenomenon of age-related decline in intersubject similarity in brain activities.

### **3.7.3 Reduced interbrain coupling was accompanied by gray matter loss**

On those cortical regions of which the listener-speaker neural coupling decreased with age, we also observed a significant negative correlation between the listener's age and the average GMV. This means, the same network showing age-related decline in interbrain coupling also exhibited age-related gray matter loss. Still, this negative relationship between age and GMV was consistent across a wide range of selected cortical regions (Fig.S5). Nevertheless, we did not find a linear correlation for any of the 246 brain regions between the strength of interbrain coupling and the GMV across the participants, indicating a complicated relationship between changes in brain function and brain structure during healthy aging.

## **3.8 Validating the main findings with another brain parcellation scheme**

We repeated the above analyses using the human brain atlas proposed by Craddock *et.al* which partitioned the brain into 200 regions (50). The results of interbrain coupling (Fig.S6), age-coupling correlation (Fig.S7), comprehension-coupling correlation (Fig.S8), and mediation analyses (Fig.S9) were consistent with those using the Human Brainnetome Atlas.

## **4. Discussion**

This study investigated whether listener-speaker neural coupling, an important mechanism underlying information transfer across brains, may change with healthy aging and the association of this change with age-related change in speech understanding. We found, compared to the young listener-speaker dyads, verbal communication between the older dyads was less successful, and at the same time, neural couplings between the older dyads were weaker and faded quicker. Moreover, within the older group, the increasing age of the listener was associated with a decline in listener-speaker neural coupling, which in turn associated with less well speech understanding. The implications of those findings are discussed below.

### **4.1 Age-related reduction in listener-speaker neural coupling**

Consistent with previous reports (16,17), we observed widespread neural couplings between the young listener-speaker dyads during the communication, covering the bilateral STG/STS, MTG, the bilateral IPL, the IFG, the angular gyrus, the precuneus, and mPFC. However, applying similar experimental protocol and analytical methods, we found much less extensive neural couplings between the older listener-speaker dyads, which occurred mainly in the bilateral STG, lingual gyrus and PCG. Compared to the young dyads, the older dyads exhibited reduced neural couplings in both frontal-temporal language areas and a set of extra-linguistic areas, including the angular gyrus, the precuneus and medial prefrontal cortex. Moreover, the overall strength of interbrain coupling was negatively correlated with the age of the older listener. The two folds of results provide reliable evidence for the age-related decline in interbrain coupling during verbal communication.

Among those cortical regions showing significant between-group differences in interbrain coupling, the STG/STS, MTG, and IFG are critical for the phonological, semantic, and syntactic processing of language (53). The angular gyrus, precuneus and mPFC are involved in social cognition critical for interpersonal communication, including mentalizing, simulation, and making inferences for other's emotions and intentions (54). The reduced neural couplings in those regions indicate the older listener-speaker dyads achieved less alignment on both linguistic and extra-linguistic representations (such as the situation model) than did the young dyads. The aging effect in interbrain coupling also implies that, as we get

older, our brains become less able to resonate with and be shaped by other brains during social interactions.

Previous studies have investigated the age-related neurofunctional changes at multiples levels of language processing within individual brains. It has been repeatedly shown that activations in core language areas (such as the left STG/STS and IFG) were maintained or reduced in older adults compared to the young, while activations in those extra-linguistic regions (such as the precuneus and prefrontal cortex) were increased (4,6,8,55). Interestingly, most of those cortical regions showing age-related changes in brain activations were detected by this study, exhibiting reduced interbrain couplings. This overlap raises the possibility that the deficits of older adults in interbrain couplings might originate from the changes in neural processing in single brains. Future studies should measure both within-brain activations and interbrain couplings, and examine whether the two neural indices change in parallel or independently with healthy aging. Exploring this issue will provide a more complete picture of the aging brain and deepen our understanding of the anatomo-functional basis of interpersonal neural coupling.

## **4.2 Possible causes for age-related decline in interbrain coupling**

The reduced neural coupling between the older listener-speaker dyads may arise from age-related declines in peripheral hearing, high-level cognitive functions, as well as regional brain atrophy. It has been suggested that the brain-to-brain neural couplings are built on the brain-to-stimuli couplings (26,56). Given that healthy aging is accompanied by reductions in neural entrainments to the temporal structure of speech (57), it is possible that reduced couplings to the stimuli in the listener's brain partially lead to the reduced neural couplings to the speaker. Another possible cause is the decreased ability of older listeners to keep attention to the external speech. Indeed, the sliding window analyses revealed the extent of neural coupling between the older listener-speaker dyads tended to decrease over the course of communication, while that between the young dyads tended to increase. Finally, age-related brain structural changes may play a role in the reduced interbrain coupling. We found the same network showing age-related decline in interbrain coupling also exhibited age-related reduction in GMV. Nevertheless, we did not find a significant linear relationship between the GMV and interbrain coupling, possibly because there exist complicated nonlinear interactions between brain function and structure during the aging process.

## **4.3 How reduced neural alignment relates to poorer speech understanding**

In both the young and older groups, stronger neural alignment of the listener with the speaker was associated with better speech understanding. Currently, despite that brain-to-brain couplings have been frequently reported, how this interbrain effect contributes to interpersonal communication remains

elusive. Notably, prior studies have revealed that greater neural similarity between the encoding and retrieval of an event was associated with better memory for the event (58,59). In addition, it has been demonstrated that neural patterns observed as participants watched a movie were significantly correlated with the neural patterns of naïve participants listening to the spoken description of the movie, and greater viewing-listening pattern similarity was associated with listener's better memory for the speech (60). Considering that the interbrain neural alignment reflects the degree of neural similarity (in the temporal space), an intriguing possibility is that resembling the neural activities in the speaker's brain can help the listener to store the fleeting speech information into memory. In this study, the deficit in neural alignments with the speaker may reduce the efficiency of the older listeners to store the currently decoded information into memory, which may lead to less successful online comprehension and subsequently poorer recall for the speech contents.

## 4.4 Limitations

In order to construct an ecological setting of natural communication and to ensure the participants' intention to communicate, the current study employed the task of storytelling based on personal experience. This design limited this study in at least two aspects. First, we failed to exert strict control over the properties (such as semantic content, linguistic complexity, prosodies) of the stories played to the young and older adults. Thus, in addition to age, variations in speech properties may also play a role in the between-group differences in listener-speaker neural coupling. Second, only one speaker was exposed to a group of listeners, limiting the generalizability of our findings. It remains to be seen whether the aging effect in interbrain coupling persists regardless of the speaker. To test this, future studies should recruit a range of speakers and randomize the exposure between speakers and listeners. A related question deserving further investigation is whether different speakers (such as a young versus an older adult) have different abilities to induce resonance in the listener's brain.

## 4.5 Conclusions and outlook

In summary, this study revealed for the first time that the listener-speaker neural coupling during naturalistic verbal communication declined with the increasing age of the listener, which in turn was linked to the poorer performance of listener in comprehending and memorizing the speech contents. These findings provide novel insights into the neural basis underlying age-related decline in speech understanding, and suggest the between-brain neural coupling can potentially be used as a biomarker for quantifying the degree to which an individual understands other people via speech. Future studies should combine the analyses of between-brain interactions and within-brain activities to obtain a more complete picture of the neural mechanism underlying speech comprehension and the effect of age on this function. Besides, it would be interesting for future studies to examine the neural coupling between children, together with our findings on the young and older adults, to uncover the developmental trajectory of interbrain interactions.

## **Declarations**

### **Funding:**

This work is supported by grants from the National Natural Science Foundation of China (NSFC: 3190082, 31971036), China Postdoctoral Science Foundation (2019M653248), and the Open Research Fund of the State Key Laboratory of Cognitive Neuroscience and Learning (CNLYB1803).

### **Conflicts of interest:**

No conflict of interest is declared.

### **Ethics approval:**

This study is approved by the Reviewer Board of Southwest University.

### **Consent to participate:**

Written informed consent was obtained from all participants.

### **Consent for publication:**

Written informed consent was obtained from all participants.

### **Availability of data and material:**

The data and material used in this study are available from the corresponding author upon reasonable request.

### **Code availability:**

The data and material used in this study are available from the corresponding author upon reasonable request.

### **Authors' contributions:**

Guosheng Ding: Conceptualization, Writing-Review & Editing, Supervision; Lanfang Liu: Conceptualization, Formal analysis, Writing-Original Draft, Project administration; Xiaowei Ding: Writing -

Review & Editing; Hehui Li: Writing-Review & Editing; Qi Zhou: Project administration; Dingguo Gao: Writing-Review & Editing; Chunming Lu: Conceptualization, Writing - Review & Editing.

## References

1. Zacks, J. M., Speer, N. K., Vettel, J. M., & Jacoby, L. L. (2006). Event understanding and memory in healthy aging and dementia of the Alzheimer type. *Psychology and Aging, 21*(3), 466-482. doi:10.1037/0882-7974.21.3.466
2. DeDe, G., & Flax, J. K. (2016). Language comprehension in aging. In *Cognition, language and aging*. (pp. 107-133). Amsterdam, Netherlands: John Benjamins Publishing Company.
3. Schneider, B. A., Daneman, M., & Pichora-Fuller, M. K. (2002). Listening in aging adults: From discourse comprehension to psychoacoustics. *Canadian Journal of Experimental Psychology/Revue canadienne de psychologie expérimentale, 56*(3), 139-152. doi:10.1037/h0087392
4. Shafto, M. A., & Tyler, L. K. (2014). Language in the aging brain: the network dynamics of cognitive decline and preservation. *Science, 346*(6209), 583-587.
5. Tyler, L. K., Shafto, M. A., Randall, B., Wright, P., Marslen-Wilson, W. D., & Stamatakis, E. A. (2010). Preserving syntactic processing across the adult life span: the modulation of the frontotemporal language system in the context of age-related atrophy. *Cerebral Cortex, 20*(2), 352-364. doi:10.1093/cercor/bhp105
6. Du, Y., Buchsbaum, B. R., Grady, C. L., & Alain, C. (2016). Increased activity in frontal motor cortex compensates impaired speech perception in older adults. *Nature Communication, 7*, 12241. doi:10.1038/ncomms12241
7. Anderson, S., Parbery-Clark, A., White-Schwoch, T., & Kraus, N. (2012). Aging Affects Neural Precision of Speech Encoding. *Journal of Neuroscience, 32*(41), 14156-14164. doi:10.1523/JNEUROSCI.2176-12.2012
8. Wong, P. C., Jin, J. X., Gunasekera, G. M., Abel, R., Lee, E. R., & Dhar, S. (2009). Aging and cortical mechanisms of speech perception in noise. *Neuropsychologia, 47*(3), 693-703.
9. Pickering, M. J., & Garrod, S. (2004). Toward a mechanistic psychology of dialogue. *Behavioral and Brain Sciences, 27*(2), 169-190.
10. Stolk, A., Verhagen, L., & Toni, I. (2016). Conceptual Alignment: How Brains Achieve Mutual Understanding. *Trends in Cognitive Science, 20*(3), 180-191. doi:10.1016/j.tics.2015.11.007
11. Wheatley, T., Kang, O., Parkinson, C., & Looser, C. E. (2012). From mind perception to mental connection: Synchrony as a mechanism for social understanding. *Social and Personality Psychology Compass, 6*(8), 589-606.
12. D'Ausilio, A., Pulvermüller, F., Salmas, P., Bufalari, I., Begliomini, C., & Fadiga, L. (2009). The motor somatotopy of speech perception. *Current Biology, 19*(5), 381-385.
13. Menenti, L., Gierhan, S. M., Segaert, K., & Hagoort, P. (2011). Shared language: overlap and segregation of the neuronal infrastructure for speaking and listening revealed by functional MRI.

*Psychological Science*, 22(9), 1173-1182.

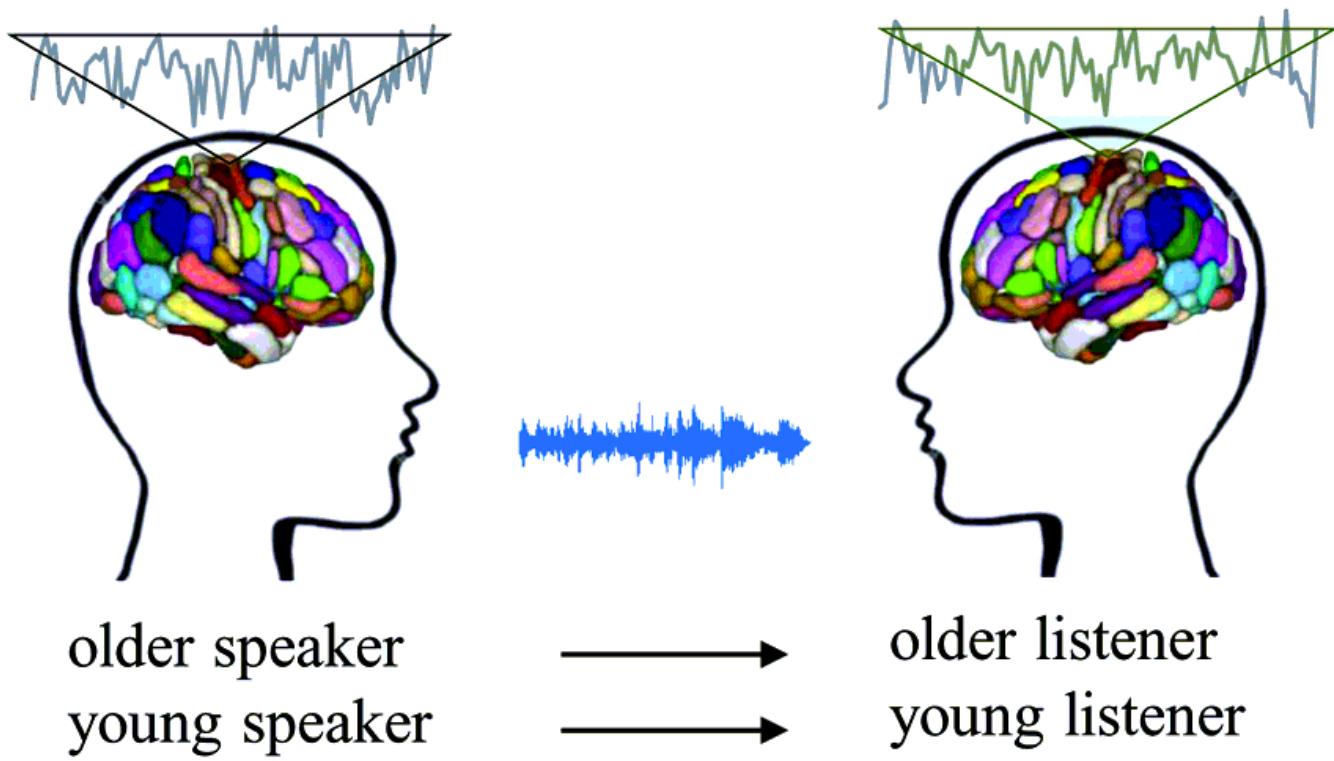
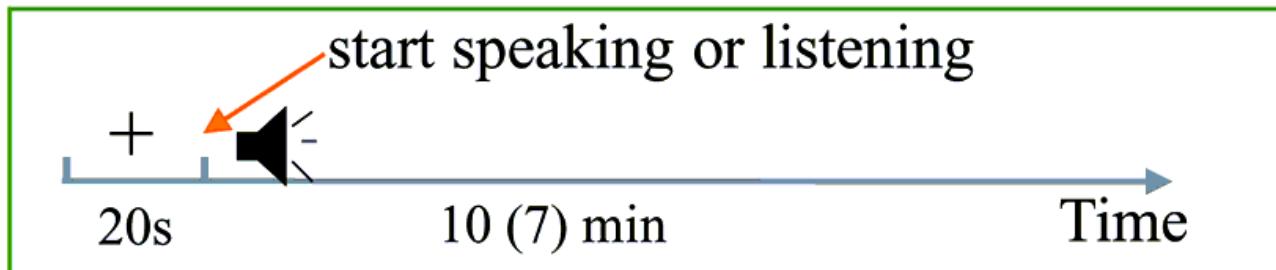
14. Segaert, K., Menenti, L., Weber, K., Petersson, K. M., & Hagoort, P. (2012). Shared syntax in language production and language comprehension—an fMRI study. *Cerebral Cortex*, 22(7), 1662-1670.
15. Menenti, L., Garrod, S., & Pickering, M. (2012). Toward a neural basis of interactive alignment in conversation. *Frontiers in Human Neuroscience*, 6(185). doi:10.3389/fnhum.2012.00185
16. Stephens, G. J., Silbert, L. J., & Hasson, U. (2010). Speaker–listener neural coupling underlies successful communication. *Proceedings of the National Academy of Sciences*, 107(32), 14425-14430. doi:<https://doi.org/10.1073/pnas.1323812111>
17. Silbert, L. J., Honey, C. J., Simony, E., Poeppel, D., & Hasson, U. (2014). Coupled neural systems underlie the production and comprehension of naturalistic narrative speech. *Proceedings of the National Academy of Sciences*, 111(43), E4687-E4696.  
doi:<https://doi.org/10.1073/pnas.1323812111>
18. Dikker, S., Silbert, L. J., Hasson, U., & Zevin, J. D. (2014). On the Same Wavelength: Predictable Language Enhances Speaker–Listener Brain-to-Brain Synchrony in Posterior Superior Temporal Gyrus. *The Journal of Neuroscience*, 34(18), 6267-6272.
19. Liu, L., Zhang, Y., Zhou, Q., Garrett, D. D., Lu, C., Chen, A., . . . Ding, G. (2020). Auditory–Articulatory Neural Alignment between Listener and Speaker during Verbal Communication. *Cerebral Cortex*, 30(3), 942-951. doi:<https://doi.org/10.1093/cercor/bhz138>
20. Liu, W., Branigan, H. P., Zheng, L., Long, Y., Bai, X., Li, K., . . . Lu, C. (2019). Shared neural representations of syntax during online dyadic communication. *NeuroImage*, 198, 63-72.  
doi:10.1016/j.neuroimage.2019.05.035
21. Dai, B., Chen, C., Long, Y., Zheng, L., Zhao, H., Bai, X., . . . Lu, C. (2018). Neural mechanisms for selectively tuning in to the target speaker in a naturalistic noisy situation. *Nature Communication*, 9(1), 2405. doi:10.1038/s41467-018-04819-z
22. Hu, Y., Hu, Y., Li, X., Pan, Y., & Cheng, X. (2017). Brain-to-brain synchronization across two persons predicts mutual prosociality. *Social Cognitive and Affective Neuroscience*, 12(12), 1835-1844.  
doi:10.1093/scan/nsx118
23. Hirsch, J., Adam Noah, J., Zhang, X., Dravida, S., & Ono, Y. (2018). A cross-brain neural mechanism for human-to-human verbal communication. *Social Cognitive and Affective Neuroscience*, 13(9), 907-920. doi:10.1093/scan/nsy070
24. Liu, Y., Piazza, E. A., Simony, E., Shewokis, P. A., Onaral, B., Hasson, U., & Ayaz, H. (2017). Measuring speaker-listener neural coupling with functional near infrared spectroscopy. *Scientific Reports*, 7, 43293. doi:10.1038/srep43293
25. Kuhlen, A. K., Allefeld, C., & Haynes, J.-D. (2012). Content-specific coordination of listeners' to speakers' EEG during communication. *Frontiers in Human Neuroscience*, 6, 266. doi:<https://doi.org/10.3389/fnhum.2012.00266>
26. Perez, A., Carreiras, M., & Dunabeitia, J. A. (2017). Brain-to-brain entrainment: EEG interbrain synchronization while speaking and listening. *Scientific Reports*, 7(1), 4190. doi:10.1038/s41598-

27. Schoot, L., Hagoort, P., & Segaert, K. (2016). What can we learn from a two-brain approach to verbal interaction? *Neuroscience & Biobehavioral Reviews*, 68, 454-459.  
doi:<http://dx.doi.org/10.1016/j.neubiorev.2016.06.009>
28. Walton, J. P. (2010). Timing is everything: temporal processing deficits in the aged auditory brainstem. *Hearing Research*, 264(1-2), 63-69. doi:10.1016/j.heares.2010.03.002
29. Di Paolo, E., & De Jaegher, H. (2012). The interactive brain hypothesis. *Frontiers in Human Neuroscience*, 6, 163. doi:10.3389/fnhum.2012.00163
30. Bortfeld, H., Leon, S. D., Bloom, J. E., Schober, M. F., & Brennan, S. E. (2001). Disfluency rates in conversation: Effects of age, relationship, topic, role, and gender. *Language and Speech*, 44(2), 123-147.
31. Juncos-Rabadán, O., Pereiro, A. X., & Rodríguez, M. S. (2005). Narrative speech in aging: Quantity, information content, and cohesion. *Brain and Language*, 95(3), 423-434.  
doi:<https://doi.org/10.1016/j.bandl.2005.04.001>
32. Meltzer, C. C., Becker, J. T., Price, J. C., & Moses-Kolko, E. (2003). Positron emission tomography imaging of the aging brain. *Neuroimaging Clinics of North America*, 13(4), 759-767.  
doi:[https://doi.org/10.1016/S1052-5149\(03\)00108-4](https://doi.org/10.1016/S1052-5149(03)00108-4)
33. Takada, H., Nagata, K., Hirata, Y., Satoh, Y., Watahiki, Y., Sugawara, J., . . . Kanno, I. (1992). Age-related decline of cerebral oxygen metabolism in normal population detected with positron emission tomography. *Neurological Research*, 14(2), 128-131. doi:10.1080/01616412.1992.11740031
34. D'Esposito, M., Deouell, L. Y., & Gazzaley, A. (2003). Alterations in the BOLD fMRI signal with ageing and disease: a challenge for neuroimaging. *Nature Reviews Neuroscience*, 4(11), 863-872.  
doi:10.1038/nrn1246
35. DeDe, G., Caplan, D., Kemtes, K., & Waters, G. (2004). The Relationship Between Age, Verbal Working Memory, and Language Comprehension. *Psychology and Aging*, 19(4), 601-616. doi:10.1037/0882-7974.19.4.601
36. Caplan, D., & Waters, G. (2005). The relationship between age, processing speed, working memory capacity, and language comprehension. *Memory*, 13(3-4), 403-413.
37. McAvinue, L. P., Habekost, T., Johnson, K. A., Kyllingsbæk, S., Vangkilde, S., Bundesen, C., & Robertson, I. H. (2012). Sustained attention, attentional selectivity, and attentional capacity across the lifespan. *Attention, Perception, & Psychophysics*, 74(8), 1570-1582. doi:10.3758/s13414-012-0352-6
38. Staub, B., Doignon-Camus, N., Bacon, E., & Bonnefond, A. (2014). Investigating sustained attention ability in the elderly by using two different approaches: Inhibiting ongoing behavior versus responding on rare occasions. *Acta Psychologica*, 146, 51-57.  
doi:<https://doi.org/10.1016/j.actpsy.2013.12.003>
39. Campbell, K. L., Shafto, M. A., Wright, P., Tsvetanov, K. A., Geerligs, L., Cusack, R., . . . Tyler, L. K. (2015). Idiosyncratic responding during movie-watching predicted by age differences in attentional

- control. *Neurobiology of Aging*, 36(11), 3045-3055.  
doi:<https://doi.org/10.1016/j.neurobiolaging.2015.07.028>
40. Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1), 97-113.
41. Turner, C. W., & Cummings, K. J. (1999). Speech audibility for listeners with high-frequency hearing loss. *American Journal of Audiology*, 8(1), 47-56.
42. Peelle, J. E., & Wingfield, A. (2016). The Neural Consequences of Age-Related Hearing Loss. *Trends in Neurosciences*, 39(7), 486-497. doi:<https://doi.org/10.1016/j.tins.2016.05.001>
43. Yan, C.-G., Wang, X.-D., Zuo, X.-N., & Zang, Y.-F. (2016). DPABI: Data Processing & Analysis for (Resting-State) Brain Imaging. *Neuroinformatics*, 14(3), 339-351. doi:10.1007/s12021-016-9299-4
44. Behzadi, Y., Restom, K., Liau, J., & Liu, T. T. (2007). A component based noise correction method (CompCor) for BOLD and perfusion based fMRI. *NeuroImage*, 37(1), 90-101.  
doi:<https://doi.org/10.1016/j.neuroimage.2007.04.042>
45. Friston, K. J., Williams, S., Howard, R., Frackowiak, R. S. J., & Turner, R. (1996). Movement-Related effects in fMRI time-series. *Magnetic Resonance in Medicine*, 35(3), 346-355.  
doi:10.1002/mrm.1910350312
46. Kannurpatti, S. S., Motes, M. A., Rypma, B., & Biswal, B. B. (2010). Neural and vascular variability and the fMRI-BOLD response in normal aging. *Magnetic Resonance Imaging*, 28(4), 466-476.  
doi:<https://doi.org/10.1016/j.mri.2009.12.007>
47. Raz, N., Ghisletta, P., Rodriguez, K. M., Kennedy, K. M., & Lindenberger, U. (2010). Trajectories of brain aging in middle-aged and older adults: Regional and individual differences. *NeuroImage*, 51(2), 501-511. doi:<https://doi.org/10.1016/j.neuroimage.2010.03.020>
48. Geerligs, L., Tsvetanov, K. A., Cam, C., & Henson, R. N. (2017). Challenges in measuring individual differences in functional connectivity using fMRI: The case of healthy aging. *Human Brain Mapping*, 38(8), 4125-4156. doi:10.1002/hbm.23653
49. Fan, L., Li, H., Zhuo, J., Zhang, Y., Wang, J., Chen, L., . . . Jiang, T. (2016). The Human Brainnetome Atlas: A New Brain Atlas Based on Connectional Architecture. *Cerebral Cortex*, 26(8), 3508-3526.  
doi:10.1093/cercor/bhw157
50. Craddock, R. C., James, G. A., Holtzheimer III, P. E., Hu, X. P., & Mayberg, H. S. (2012). A whole brain fMRI atlas generated via spatially constrained spectral clustering. *Human Brain Mapping*, 33(8), 1914-1928. doi:10.1002/hbm.21333
51. Hayes, A. F., & Scharkow, M. (2013). The Relative Trustworthiness of Inferential Tests of the Indirect Effect in Statistical Mediation Analysis: Does Method Really Matter? *Psychological Science*, 24(10), 1918-1927. doi:10.1177/0956797613480187
52. Stolk, A., Noordzij, M. L., Verhagen, L., Volman, I., Schoffelen, J.-M., Oostenveld, R., . . . Toni, I. (2014). Cerebral coherence between communicators marks the emergence of meaning. *Proceedings of the National Academy of Sciences*, 111(51), 18183-18188.  
doi:<https://doi.org/10.1073/pnas.1414886111>

53. Price, C. J. (2010). The anatomy of language: a review of 100 fMRI studies published in 2009. *Annals of the New York Academy of Sciences*, 1191, 62-88. doi:10.1111/j.1749-6632.2010.05444.x
54. Spreng, R. N., & Grady, C. L. (2009). Patterns of Brain Activity Supporting Autobiographical Memory, Prospection, and Theory of Mind, and Their Relationship to the Default Mode Network. *Journal of Cognitive Neuroscience*, 22(6), 1112-1123. doi:10.1162/jocn.2009.21282
55. Manan, H. A., Franz, E. A., Yusoff, A. N., & Mukari, S. Z.-M. S. (2015). The effects of aging on the brain activation pattern during a speech perception task: an fMRI study. *Aging Clinical and Experimental Research*, 27(1), 27-36. doi:10.1007/s40520-014-0240-0
56. Hasson, U., Ghazanfar, A. A., Galantucci, B., Garrod, S., & Keysers, C. (2012). Brain-to-brain coupling: a mechanism for creating and sharing a social world. *Trends in Cognitive Science*, 16(2), 114-121. doi:10.1016/j.tics.2011.12.007
57. Henry, M. J., Herrmann, B., Kunke, D., & Obleser, J. (2017). Aging affects the balance of neural entrainment and top-down neural modulation in the listening brain. *Nature communications*, 8(1), 1-11.
58. Ritchey, M., Wing, E. A., LaBar, K. S., & Cabeza, R. (2013). Neural similarity between encoding and retrieval is related to memory via hippocampal interactions. *Cerebral cortex*, 23(12), 2818-2828.
59. Xue, G., Dong, Q., Chen, C., Lu, Z., Mumford, J. A., & Poldrack, R. A. J. S. (2010). Greater neural pattern similarity across repetitions is associated with better memory. *Science*, 330(6000), 97-101.
60. Zadbood, A., Chen, J., Leong, Y. C., Norman, K. A., & Hasson, U. (2017). How We Transmit Memories to Other Brains: Constructing Shared Neural Representations Via Communication. *Cerebral Cortex*, 1-13. doi:10.1093/cercor/bhx202

## Figures



**Figure 1**

Experimental and analytical protocols. We scanned with fMRI a young and an older speaker telling real-life stories, and then played the recordings to groups of young and older listeners, respectively. In the experiment, a fixation cross lasting for 20s and then an icon of a horn lasting until the end of the scanning were presented to all participants. To assess interbrain coupling, the brain of each participant was first partitioned into 246 regions based on the Brainnetome Atlas, and Pearson's correlations were calculated between the mean signals of each cortical region in the speaker's brain and those of the homologous region in each listener's brain.

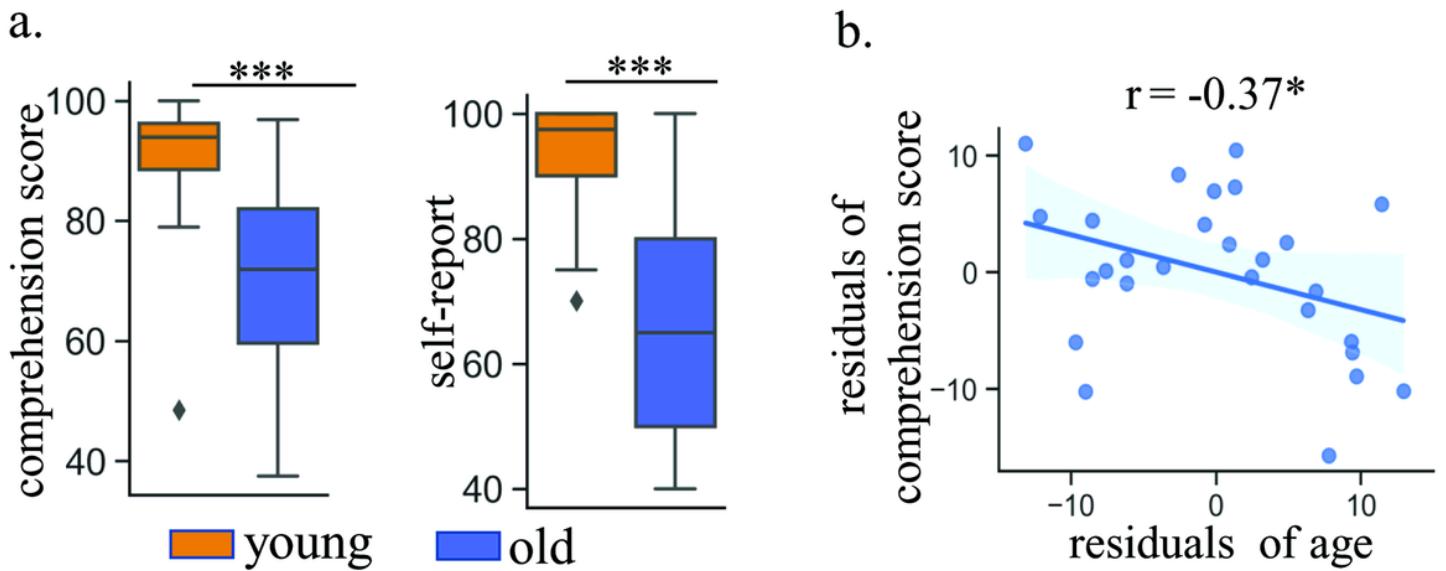
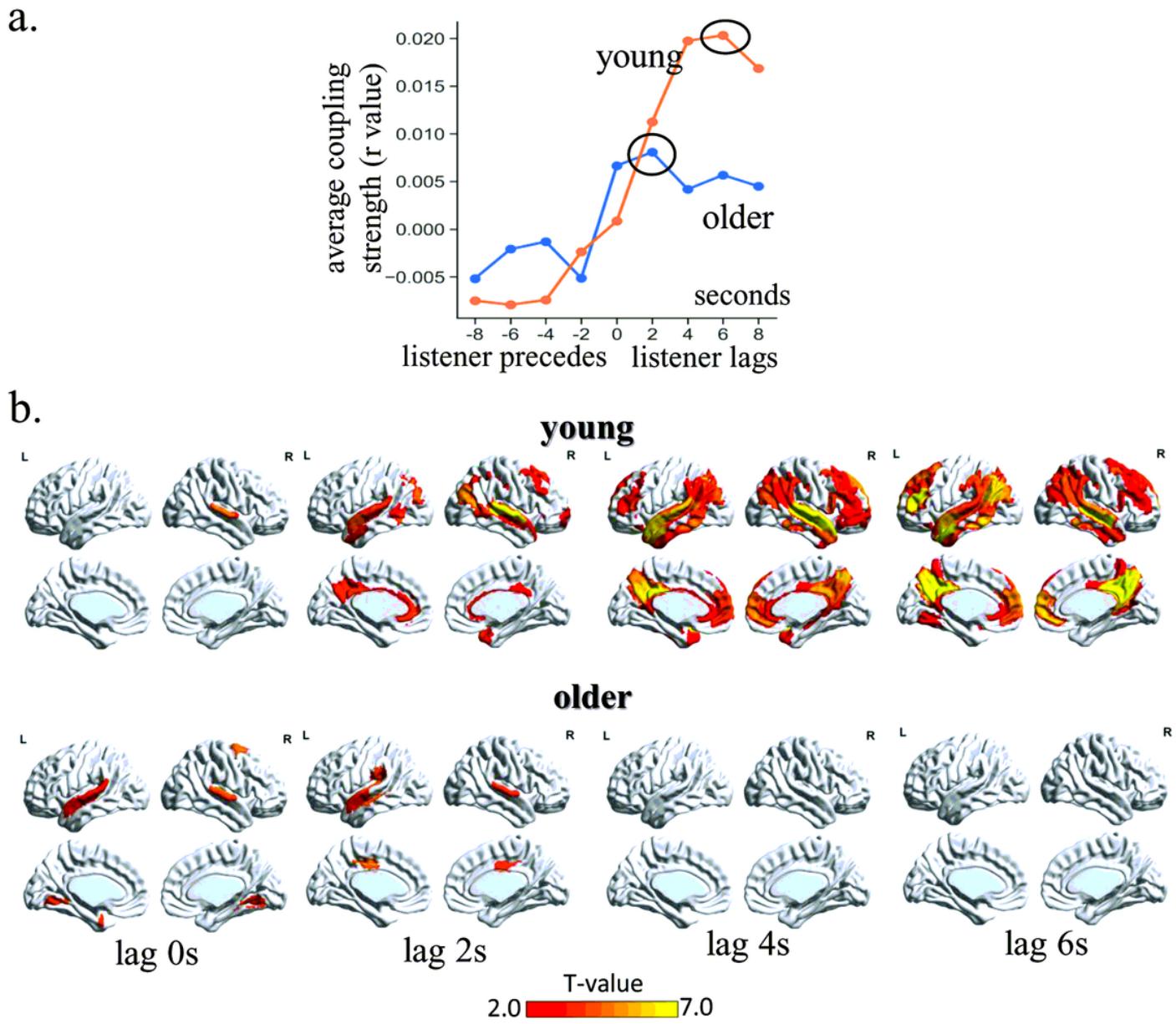


Figure 2

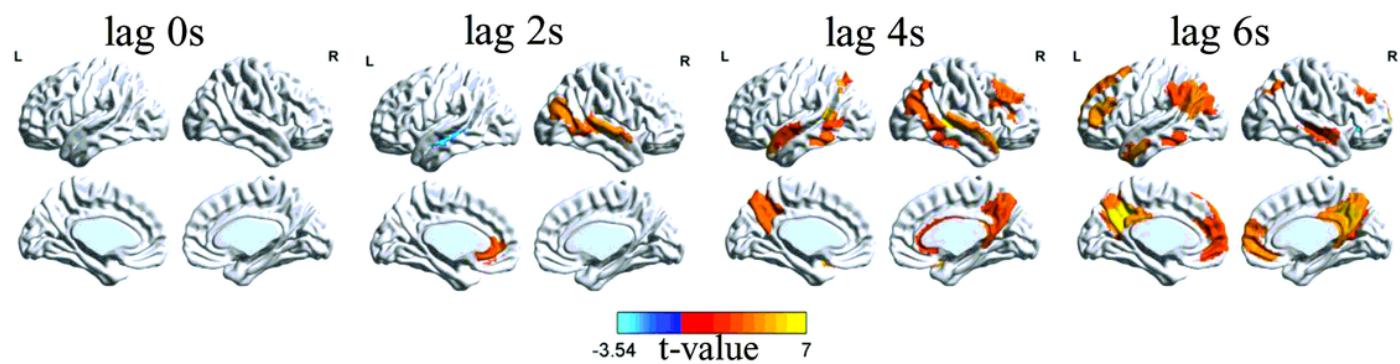
Behavioral results. (a). Older adults understood the narratives less well than did the young, as demonstrated by both self-reports and comprehension scores. (b). The age of the older listener was negatively correlated with the comprehension score (with memory spans controlled). \*:  $p < 0.05$ ; \*\*\*:  $p < 0.0005$ .



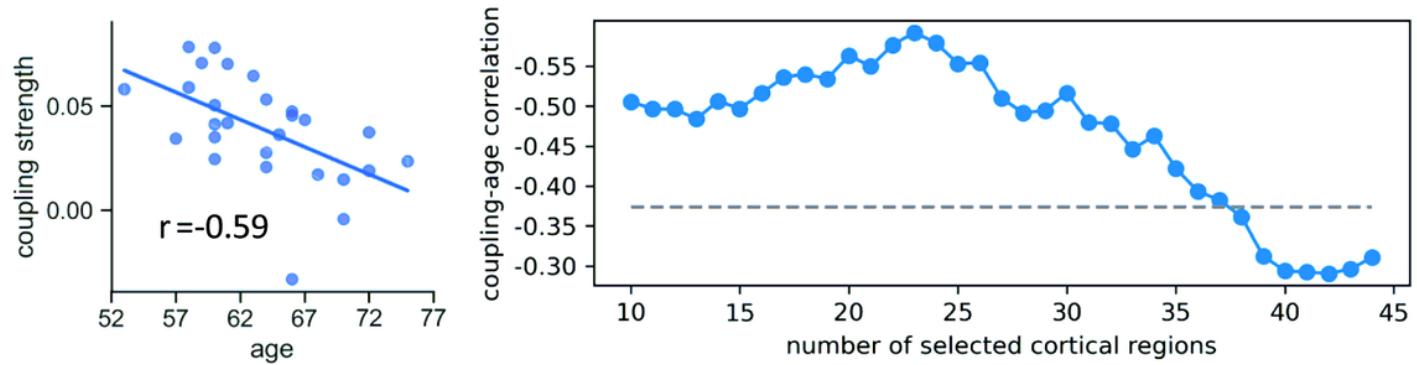
**Figure 3**

The temporospatial pattern of listener-speaker neural coupling. (a) The coupling strength averaged across the whole brain and across all subjects. (b) The t-statistic maps thresholded with FDR corrected  $p < 0.05$ . In both groups, the listener's brain activities got aligned with the speaker's brain activities with some temporal lags. Compared to the young listener-speaker dyads, neural couplings between the older dyads were less extensive and peaked earlier (6s versus 2s).

### a. young versus older

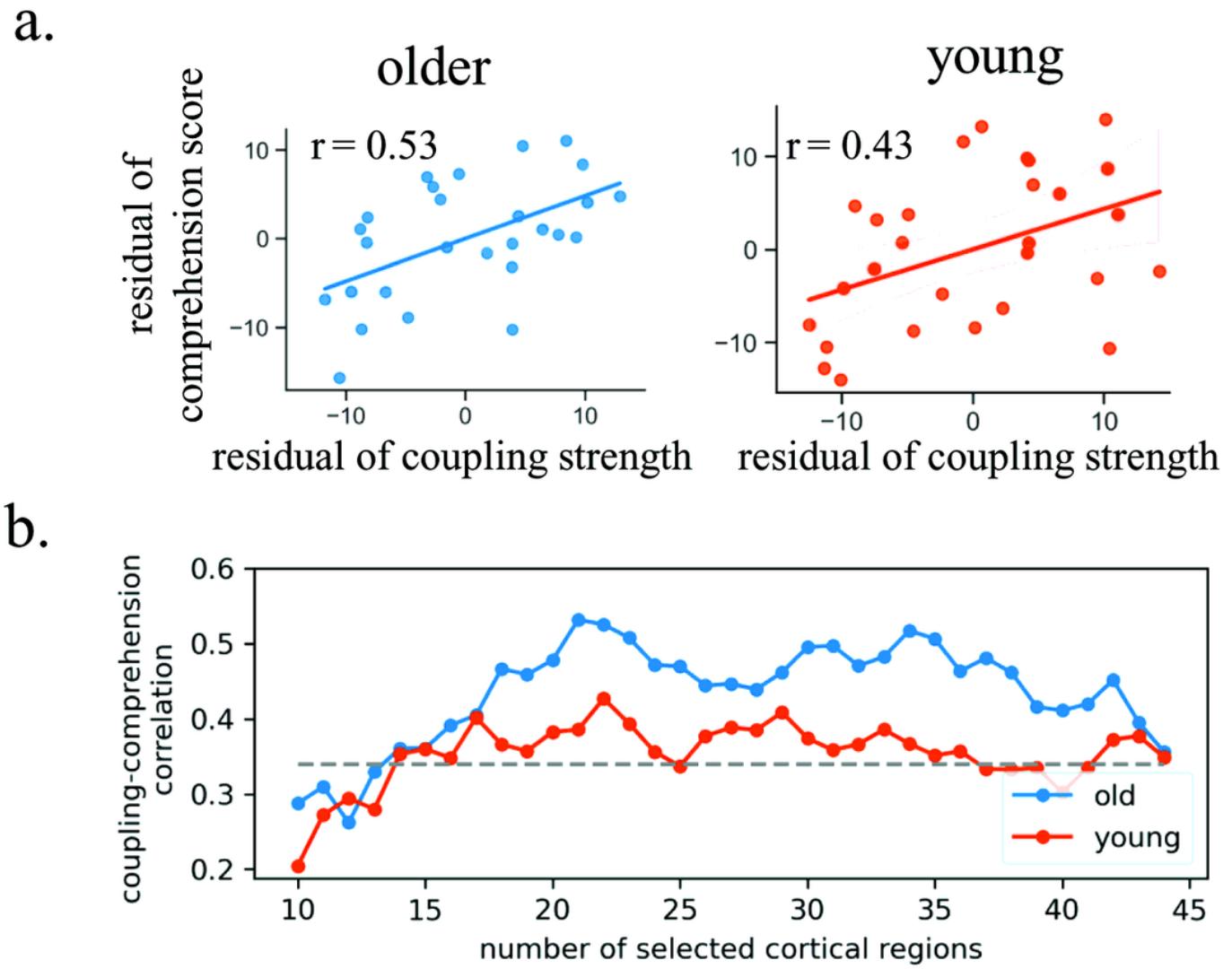


### b. within older group



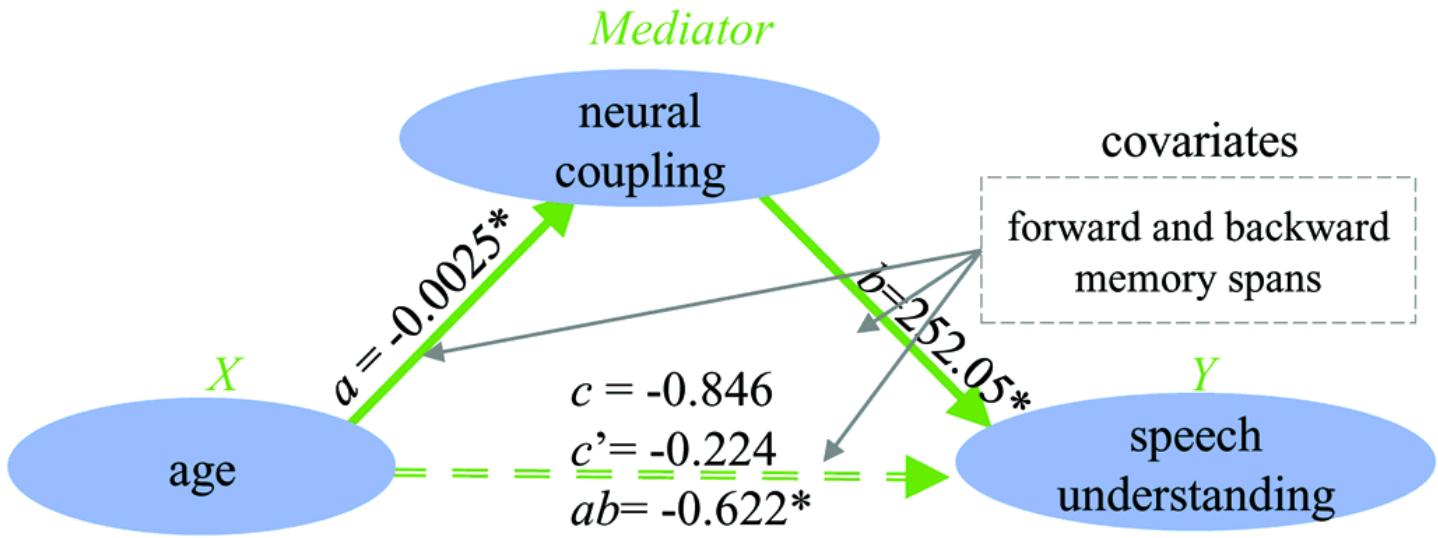
**Figure 4**

Reduced listener-speaker neural couplings with aging. (a). Direct contrast between the young and the older group. Orange: young > older; Blue: older > young. Threshold: FDR corrected  $p < 0.05$ . (b). The overall strength of interbrain coupling declined as a function of the older listener's age. Left: a scatter plot showing the negative correlation between the older listener's age and the overall strength of listener-speaker neural coupling. Right: The negative correlation was consistent across a wide range of selected cortical regions. The horizontal line indicates the  $r$  value corresponding to  $p = 0.05$ .



**Figure 5**

Stronger listener-speaker neural coupling was associated with better speech understanding in both the young and older groups. (a). A scatter plot showing a significant positive correlation between the overall strength of listener-speaker neural coupling and the listener's comprehension score (with the effect of memory spans controlled). (b). This positive correlation was consistent across a wide range of selected cortical regions. The horizontal line indicates the  $r$  value corresponding to  $p = 0.05$ .



**Figure 6**

Reduced interbrain coupling mediated the negative relationship between age and speech understanding. The  $a$  denotes the negative effect of older listener's age on listener-speaker neural coupling. The  $b$  denotes the positive effect of neural coupling on speech understanding after controlling for the effect of age. The  $c$  denotes the total effect of age on speech understanding. The  $c'$  denotes the direct effect of age on speech understanding. The  $ab$  denotes the indirect effect of age on speech understanding through interbrain coupling.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Supplementarymaterial2020227.docx](#)