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# Hemispheric dissociations in regions supporting auditory sentence comprehension in older adults

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ABSTRACT

We investigated how the aging brain copes with acoustic and syntactic challenges during spoken language comprehension. Thirty-eight healthy adults aged 54 – 80 years ($M$ = 66 years) participated in an fMRI experiment wherein listeners indicated the gender of an agent in short spoken sentences that varied in syntactic complexity (object-relative vs subject-relative center-embedded clause structures) and acoustic richness (high vs low spectral detail, but all intelligible). We found widespread activity throughout a bilateral frontotemporal network during successful sentence comprehension. Consistent with prior reports, bilateral inferior frontal gyrus and left posterior superior temporal gyrus were more active in response to object-relative sentences than to subject-relative sentences. Moreover, several regions were significantly correlated with individual differences in task performance: Activity in right frontoparietal cortex and left cerebellum (Crus I & II) showed a negative correlation with overall comprehension. By contrast, left frontotemporal areas and right cerebellum (Lobule VII) showed a negative correlation with accuracy specifically for syntactically complex sentences. In addition, laterality analyses confirmed a lack of hemispheric lateralization in activity evoked by sentence stimuli in older adults. Importantly, we found different hemispheric roles, with a left-lateralized core language network supporting syntactic operations, and right-hemisphere regions coming into play to aid in general cognitive demands during spoken sentence processing. Together our findings support the view that high levels of language comprehension in older adults are maintained by a close interplay between a core left hemisphere language network and additional neural resources in the contralateral hemisphere.

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## Introduction

Although older adults frequently experience age-related sensory and cognitive declines [1], in many situations their language comprehension is remarkably good [2–4]. Indeed, older adults perform just as well as young adults in a number of tasks involving syntactic [5–7], semantic [8–10], and lexical [11–13] knowledge, all of

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which are key components in language comprehension. Nevertheless, language comprehension in healthy aging may only be stable under limited circumstances; that is, older adults may have difficulty understanding spoken sentences when made more difficult through linguistic or acoustic challenge [14,15]. The neural systems underlying preserved and fragile language processing in healthy aging are still not fully understood.

For neuroimaging studies of language in which young adults show lateralized activity, older adults frequently demonstrate recruitment of additional regions in the contralateral hemisphere [5,16–19] in addition to robust activation in the left perisylvian cortex [5,20–22]. This increase in bilateral activity in older adults relative to young adults is seen in many tasks and is often interpreted in the context of two classic frameworks. In the HAROLD (Hemispheric Asymmetry Reduction in Older Adults) model [23], for example, increased bilateral activity is typically seen as reflecting compensatory activity, i.e., supporting successful behavior. CRUNCH (Compensation-Related Utilization of Neural Circuits Hypothesis; [24] also posits that older adults recruit bilateral neural resources to maintain performance level. However, the involvement of the right hemisphere is only seen when the task demand is low. Critically, from both perspectives, the role of increased bilateral activity is interpreted in the context of behavioral success. By contrast, the dedifferentiation theory views age-related contralateral activity as non-specific activation, responsible for inefficient processes [25,26]. Behavioral performance is therefore key in understanding potential roles of contralateral recruitment.

In language tasks, previous studies in older adults have found both positive and negative associations between right frontal activity and behavioral performance. For example, Hoyau et al. [27] found bilateral frontal activity associated with faster response times during an object naming task, and van Ettinger-Veenstra et al. [28] showed that higher reading test scores were positively associated with the activity in right posterior temporal cortex. By contrast, a negative correlation was found between right frontal activity and performance on tasks related to picture naming [19], semantic fluency [18], or rhythm-judgment [29]. Intriguingly, Geva and colleagues [29] interpreted a negative correlation between right frontal activity and task performance as supporting a compensatory role of the right hemisphere. They based this conclusion on the fact that increased right frontal activity was only observed when error-prone subjects correctly performed the task. That is, recruitment of right frontal cortex was thought to lead to task success specifically for older adults who found the task more challenging.

In addition to the correlational findings within the older adults, group comparisons between young and older adults have indicated greater bilateral activation during various language tasks. For example, older adults activated right frontal cortex more strongly than young adults when they performed the same tasks including object naming [27], semantic categorization [30], and rhyming judgment tasks [29]. Importantly, young and old adult groups were matched in their behavioral task performance, suggesting the importance of the right hemisphere in maintaining task demands.

It is especially difficult to ascertain the functional role of the right frontal cortex in language tasks involving both language-specific (e.g., syntactic) and domain-general (e.g., working memory) processes (see [31]. Behavioral work has established that language-specific and domain-general processes interact [32], and right frontal activity has been associated with both language-specific [33] and domain-general [34] functioning.

In order to isolate the contributions of language-specific and domain-general processes, in the present fMRI study, we adopted the experimental design used in a previous study with young adults [35]. In brief, we presented participants a series of sentences that varied in syntactic complexity depending on the type of center-embedded relative clause (e.g., object-relative vs subject-relative structures). To assess the contributions of domain-general processes, we acoustically degraded these sentences using noise vocoding [36] with 24 channels, thus preserving intelligibility. We draw a distinction between syntactic complexity and general sentence processing. Whereas syntactic complexity specifically taps processing operations related to word order, general sentence processing involves domain-general cognitive operations including sequence monitoring and working memory.

In the present experiment we asked the following questions: first, to what extent do older adults recruit the non-dominant right hemisphere for general sentence processing? For this purpose we directly compare sentence-related activity between older adults (current data) and young adults [35]. In addition, we compute laterality indices from the fMRI data of the two age groups. We hypothesized that older adults would engage additional resources in the right hemisphere compared to the young adults. Secondly, we ask whether the core (i.e., left frontotemporal) language network would show greater activity pertaining to increased syntactic complexity in older than young adults. To this end, we directly compare [objective-relative to subject-relative] contrast between the two age groups. In addition, we perform multiple linear regression to investigate individual differences in both general sentence processing and syntactic complexity within older adults. We hypothesized that right hemisphere activity may reflect individual differences pertaining to task demands, while left hemisphere activity would be specifically sensitive to differences in the syntactic structure of sentences. As was done in Geva et al [29], we focus on correct trials to be related to the fMRI data.

## Materials and methods

### *Materials and behavioral task*

The experimental stimuli were identical to those used in our previous study [35]. In brief, we used 24 base sentences, each containing two characters, one of which was the agent of an action. In each sentence, one of the characters was a male (king, father, uncle, etc.) and the other a female (queen, mother, aunt, etc.), and each of which appeared in two syntactically different structures with gender of the actor being counterbalanced. The syntactic structure was

manipulated by rearranging word order while equating lexical characteristics across sentences with center-embedded clauses containing either a subject-relative structure (e.g., "Brothers that aid sisters are good") or an object-relative structure ("Brothers that sisters aid are good").

In addition, half of the sentences were noise vocoded with 24 channels while the other half were unprocessed, retaining the original acoustic details. The particular sentences presented as unprocessed or noise-vocoded speech were counterbalanced across participants. Our pilot study confirmed that these vocoded sentences were still intelligible to healthy older adults. Together, these manipulations resulted in a $2 \times 2$ factorial design with varying syntactic complexity (subject-relative, object-relative) and acoustic detail (acoustically rich, acoustically less-detailed).

After each sentence was heard, the participant was asked to indicate whether the agent of the action in the sentence was male or female by pressing one of two buttons on an MRI-compatible button pad. For example, for the sentence "Brothers that help sisters are nice", the correct response would be "male". A subset of 24 experimental sentences was vocoded with a single channel to create an unintelligible control condition, for which participants were told to randomly press either the male or female button.

*Pilot study*

To determine the optimal range of noise vocoding, we conducted a behavioral pilot study. We presented sentences at levels of vocoding that ranged from unprocessed (clear) speech and 8, 16, 24, and 32 channel vocoded speech. Vocoding with <8 channels resulted in extremely poor signal quality as illustrated in the spectrograms in Fig. 1A. We tested 40 adults aged 62–88 years. All participants provided written informed consent according to a protocol approved by the Brandeis University Institutional Review Board.

Sentences were identical to those used in the main study. After hearing each sentence, participants were instructed to press a key, as quickly and accurately as possible, to indicate the gender of the character performing the action. The accuracy of responses as a function of acoustic clarity is shown in Fig. 1B. When <16 channels were used in noise vocoding, accuracy drastically decreased. These results indicated that noise vocoding down to 16 channels would be sufficient to ensure relatively high levels of accuracy for all conditions in the fMRI study for all participants, regardless of age. Because the pilot study was conducted in a quiet room with minimum levels of background noise, we chose 24-channel noise vocoded speech as a conservative manipulation of acoustic challenge for the noisy MR scanning environment.

*fMRI study*

*Participants*

The fMRI experiment included 46 participants. All participants reported themselves to be right-handed, in good health, having no known neurological disorders, being native speakers of English, and having normal hearing. Among the 46 participants, eight individuals' data were later discarded due to a chance-level performance in any of the 4 functional runs ($N = 6$), excessive head motion (translation > 10 mm) ($N = 1$), and missing working memory scores ($N = 1$). This resulted in a total of 38 usable subjects (54–80 years of age; $M = 66$ years, $SD = 6.7$; 24 females; education $M = 16$ years, $SD = 2.4$; Mini-Mental Status Examination $M = 29$, $SD = 0.8$). All participants submitted written consent and the study was approved by the Institutional Review Board at the University of Pennsylvania.

Prior to the fMRI experiment, we measured hearing acuity and verbal working memory performance. For hearing acuity, we used standard pure-tone audiometry in which pure tones were presented at octave intervals between 250 and 8000 Hz, with each participant's pure tone threshold reflecting the softest tone they could reliably hear (Fig. 2A). We then averaged thresholds over 1000, 2000, and 4000 Hz for a pure-tone average (PTA). We used each participant's better-ear PTA as a parsimonious summary of their hearing ability.

To measure verbal working memory, we used a reading span task [37]. In this test, participants were given a set of written sentences, for each of which they were required to make a true/false judgment. Upon completion of all sentences in a set, participants were asked to recall the last words of each sentence. Participants proceeded with the next set in which the number of sentences was increased. The task was finished either when the participants correctly remembered the last word of each sentence or when they could not correctly give more than three target words.

*Experimental procedure.* Prior to entering the scanner, participants received instructions and performed a practice session to ensure they understood the task. Once inside the scanner, but prior to scanning, the volume of auditory stimuli was determined by asking participants to repeat each of four recorded sentences (two unprocessed and two 24-channel vocoded sentences). An optimal volume level was determined upon perfect repetition of all sentences. These sentences were not included in the main stimuli set. Once set, the volume remained constant for that participant.

Following the volume determination, the participant conducted the sentence comprehension task across four fMRI runs. On each trial, either an intelligible (both clear and 24-channel vocoded speech) or unintelligible noise (1-channel vocoded speech) was presented to the participant using E-Prime 2.0 (Psychology Software Tools, Inc., Pittsburgh, PA). These sentence stimuli were presented binaurally using MRI-compatible high-fidelity insert earphones (Sensimetrics Model S14).

For each trial participants were told to indicate the gender of the individual who performed the action in the sentence via a button press. These button responses were later analyzed to assess sentence comprehension. For the 1-channel vocoded speech participants were instructed to randomly press either the male or female button. Together, each run consisted of 36 trials with 24 intelligible sentences (6 sentences $\times$ 2 syntactic constructions $\times$ 2 acoustic manipulations), 6 unintelligible speech (1-channel vocoded), and 6 trials of silence. The trials were randomized within runs and 96 trials were presented only once across four functional runs.

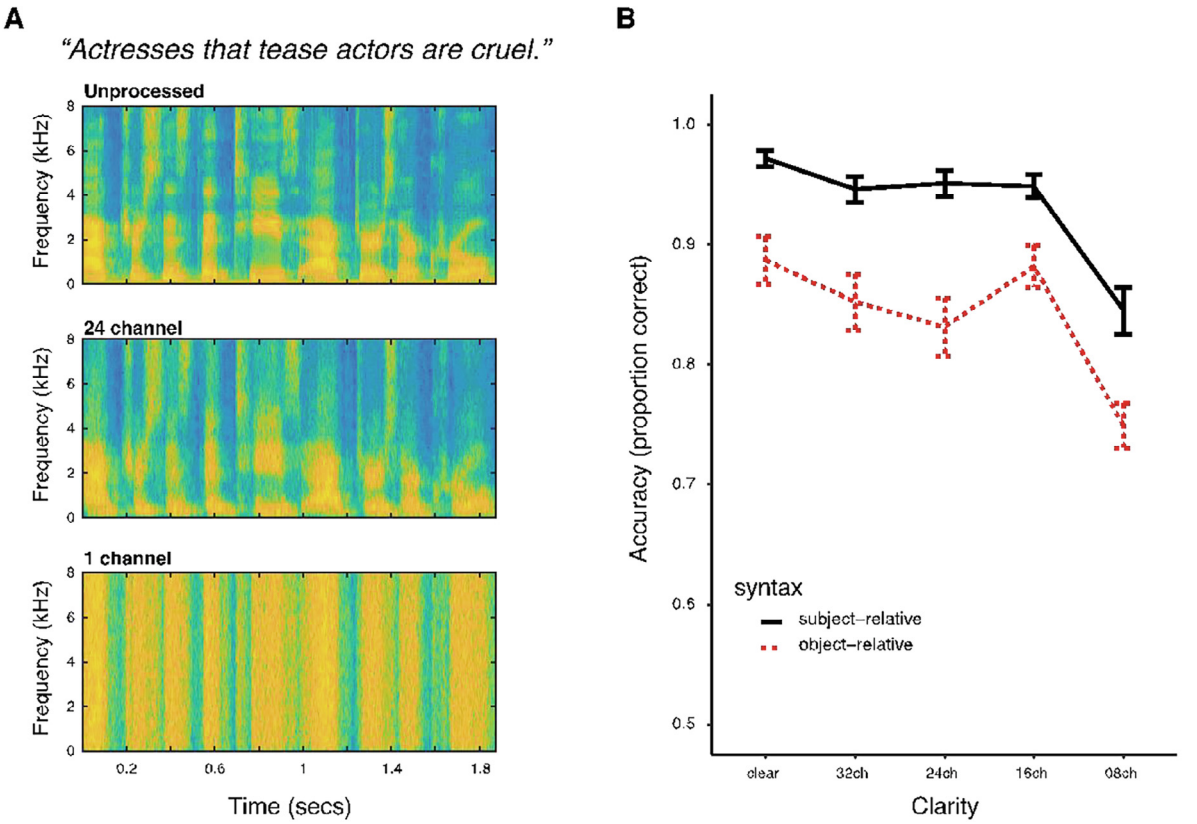


**Fig. 1.** A. Spectrograms of unprocessed speech, 24-channel noise vocoded speech, and 1-channel noise vocoded speech. B. Accuracy from a pilot study examining performance as a function of acoustic clarity in 40 older adults. Error bars show one standard error.

*MRI scanning.* We collected MRI data on a 3 T Siemens Trio scanner (Siemens Medical System, Erlangen, Germany) using an 8-channel head coil. The field of view was angled approximately 30° away from the AC-PC line. First, a T1-weighted structural volume was acquired using a magnetization prepared rapid acquisition gradient echo (MPRAGE) protocol [axial orientation, repetition time (TR) = 1620 ms, echo time (TE) = 3 ms, flip angle = 15°, field of view (FOV) = 250 × 188 mm, matrix = 256 × 192 mm, 160 slices, voxel resolution = 0.98 × 0.98 × 1 mm]. Next, four runs of blood oxygenation level-dependent (BOLD) functional MRI scanning were conducted [TR = 2000 ms, TE = 30 ms, flip angle = 78°, FOV = 192 × 192 mm, matrix = 64 × 64 mm, 32 slices, voxel resolution = 3 × 3 × 3 mm with 0.75 mm gap] using an interleaved silent steady state (ISSS) protocol [38], in which five consecutive volumes were acquired in between four seconds of silence. Each trial consisted of four seconds of relative quiet period and a subsequent 10 s (5 volumes) of data collection period. Before completion of the fMRI experiment, we acquired a B0 field mapping sequence [TR = 1050 ms, TE = 4 ms, flip angle = 60°, FOV = 240 × 240 mm, matrix = 64 × 64 mm, 44 slices, slice thickness = 4 mm, voxel resolution = 3.8 × 3.8 × 4 mm].

*fMRI data analysis.* Preprocessing was performed via SPM12 (version 6906; Wellcome Trust Centre for Human Neuroimaging) after raw images were unwarped in the *prelude* and *flirt* routines from FSL version 5.0.5 (FMRIB Software Library, University of Oxford). First, all time-series were realigned to the first image in the first session. Next, the structural image was coregistered to the functional images before being normalized to the standard MNI T1 template using a unified segmentation approach [39]. The same transformation was then applied to normalizing all functional images to MNI space with the original voxel size preserved. Preprocessing was completed by smoothing with a Gaussian kernel of nine mm full-width half maximum (FWHM).

To model the ISSS data, we fit the functional data using a finite impulse response (FIR) function, wherein five time points were separately estimated per trial (Peelle, 2014). We also separately estimated sentences associated with correct and incorrect responses. For those conditions with no errors (i.e., 100 % accuracy), the last TR was modeled as a dummy event in order to avoid a regressor of empty vector. Although we applied high-pass filtering with a 128 *sec* cutoff, temporal autocorrelation was disabled due to the temporal discontinuity of our data sets. Together, there were 20 regressors per correct and incorrect sentence conditions, 5 regressors of 1 channel vocoded speech, and 6 motion parameters, totaling 51 estimates per run. There were additional 4 run regressors in the design matrix.

After estimating the GLM, we calculated the summed positive area (SPA) using the 5 beta estimates for each condition [35]. More specifically, we integrated the area of the estimated response above zero and used this as a metric

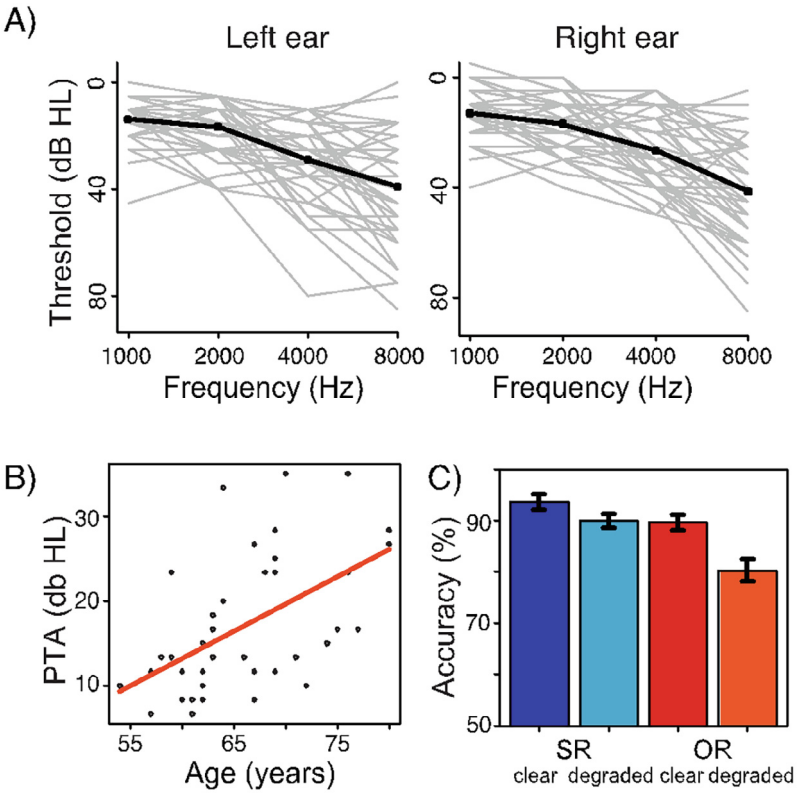


**Fig. 2.** A. Hearing acuity in left and right ear of 38 participants. Light gray lines indicate individual participants, black line the group average. B. Relationship between age and better-ear PTA. Age is positively associated with hearing decline [Pearson r = 0.53; p < 0.001].; C. Behavioral accuracy during the fMRI experiment. There are significant effects of syntactic complexity and acoustic detail.

for further analyses. These SPA maps were then submitted to a series of 2nd level random effects analyses including one-sample t-tests and multiple regressions. All results were obtained using a voxel-wise threshold of $p < 0.001$ (uncorrected) in combination with cluster-wise threshold of $p < 0.05$ corrected using gaussian random field theory [40,41]. Results were displayed using SPM or MRIcron [42]. Unthresholded statistical maps are available at https://neurovault.org/collections/9592/ [43].

The degree of lateralization was determined on group maps using the LI toolbox (version 1.3.2) [44]. In brief, the LI (lateralization index) was calculated by subtracting the sum of voxel values above the cut-off threshold (i.e., T = 3) of the right hemisphere from the left hemisphere, which was subsequently normalized by the total sum of voxel values of both hemispheres. The LI ranges between +1 and −l with positive value being left lateralization. We obtained the LI separately in frontal, parietal, temporal, subcortical regions (thalamus + basal ganglia), and cerebellum. In each of these regions, only voxels located >11 mm from to the midline were considered.

## Results

### *Behavioral results*

As seen in Fig. 2C, overall, participants exhibited relatively good accuracy on the comprehension task during scanning ($M = 88.4$ percent correct; $SD = 7.9$). We set up a linear mixed effects model using *lmerTest* package [45] in R (version 4.1.1) to predict task performance in logit-transformed accuracy with a set of fixed effects including PTA, age, working memory, and PTA-by-working memory for between-group variables as well as syntax, acoustic clarity, and syntax-by-acoustic clarity as within-group variables. Participants were included as a random effect. Results are shown in Table 1. The model yielded significant main effects of syntax [$F_{(1,114)} = 43.75$, $p < 0.001$, $\eta^2 = 0.28$ ] and acoustic clarity [$F_{(1,114)} = 44{,}07$, $p < 0.001$, $\eta^2 = 0.28$]; consistent with the behavioral pilot, accuracy of comprehension was poorer for object-relative sentences compared to subject-relative sentences, and accuracy of comprehension decreased in the presence of degraded rather than clear speech. Age, hearing acuity, and working memory had no significant impact on the task performance.

In addition, we compared the behavioral performance between the current older adults and the young adults (N = 26) who performed the same task in our previous study [35]. An independent samples *t*-test using logit-transformed accuracy revealed that older adults performed significantly worse than young adults [$t_{(62)} = 3.68$, $p < 0.001$, *Cohen's d* = 0.93]. We also compared syntactic performance between older and young adults. For the comparison, we used a metric of [% accuracy of subject – object-relative sentences], in which larger positive values indicate greater vulnerability to the syntactic complexity.

**Table 1**
Behavioral results on the sentence comprehension task.

| Variable | Estimate | Std. Error | t value | P value |
|---|---|---|---|---|
| syntax (SR) | 0.58 | 0.14 | 4.27 | **4.10E-05** |
| acoustic clarity (degraded) | −0.71 | 0.14 | −5.1 | ***1.35E-06*** |
| age | −0.02 | 0.02 | −0.9 | 0.37 |
| working memory | 0.21 | 0.570 | 0.37 | 0.71 |
| hearing acuity (pta) | −0.01 | 0.04 | −0.29 | 0.78 |
| syntax-by-acoustic | 0.11 | 0.2 | 0.58 | 0.56 |
| working memory-by-pta | 0.004 | 0.03 | 0.13 | 0.9 |

These metrics — after confirming normal distribution using Shapiro-Wilk normality test ($p > 0.05$) —were submitted to the independent samples *t*-test. We found that older adults indeed performed significantly worse than younger adults as the syntactic structure becomes more complex [$t_{(62)} = 2.97$, $p < 0.001$, *Cohen's d* = 0.66].

### *fMRI results*

We first examined the activity pertaining to general sentence processing (i.e., between all sentences versus noise) using group-level random effects. As expected, widespread activity was seen bilaterally throughout both cortical and subcortical areas (Fig. 3A; Table 2). To further examine this bilateral pattern of activation, we compared the resulting map to the same group-level result obtained from young adults [35] via independent samples *t*-test. We found four significant clusters exclusively in the right hemisphere that were more active in the older than young adults; those include the insula, pre-supplementary motor area (SMA), and two cerebellar loci in VII and crus II (Fig. 4; Table 3). To further explore the bilateral activation in the current data, we computed LIs in 5 atlas-based regions of interest (ROIs): frontal, parietal, temporal, subcortical, cerebellum. These LIs were then compared to those obtained from the study with young adults [35]. Because only one LI score was drawn from each of the two group-level T maps, no statistical comparison was made. As summarized in Table 4, frontal, parietal, temporal, and subcortical areas displayed increased bilateralization in older compared to young adults. In addition the cerebellum showed weaker right lateralization in the older adults.

Next, we examined the fMRI activity more specifically related to differences in syntactic structure by comparing the difference between object-relative and subject-relative sentences. We found significant clusters predominantly in the left hemisphere including IFG (both pars triangularis and pars opercularis), posterior aspect of STG/MTG, SMA, precentral gyrus, and thalamus. In addition, bilateral clusters were seen within the insula, putamen, and cerebellum (Fig. 3B; Table 5).

As was done for the general sentence processing map, we directly compared the group map of the [object-relative > subject-relative] contrast between the young and older adult groups via independent samples *t*-test, which did not yield any significant clusters in either [older > young] or [young > old] even at a relaxed threshold ($P < 0.01$ voxel-wise uncorrected and extent cluster-size = 20). Nevertheless, the LI index revealed that frontal, parietal, and temporal areas were more left-lateralized in the young than older adults (Table 4).

Next, we performed a series of multiple regressions to investigate the individual differences in the degree of activations pertaining to their behavioral performance within older adults. As an independent variable, we used percent accuracy from the sentence comprehension task. As covariates, we included age, PTA, working memory, and the interaction term of PTA-by-working memory, with mean-centering in the model. We found 6 significant clusters that were negatively correlated with the task accuracy. These clusters were mostly located in the right hemisphere, including IFG/insula, frontal pole, SMA, angular gyrus/-supramarginal gyrus — all of which were parts of general sentence processing network described in the group level *t*-test result above. In addition, two large clusters emerged in the bilateral cerebellum (Fig. 5; Table 6).

We performed another multiple regression to identify areas that would be sensitive to individual differences in behavioral performance for syntactically more complex sentences. To this end, we used a score that reflected differences in task performance between subject-relative accuracy and object-relative condition (i.e., subject-relative minus object-relative accuracy). As such, smaller scores indicate comparable performance between the two syntactic conditions and higher scores reflect worse performance in the object-relative condition. This score was then regressed against the syntactic contrast map (object-relative > subject-relative). The same covariates as above were also included. We found that left insula, pre-SMA, precentral gyrus, and right cerebellum showed positive correlations with performance, indicating participants who struggled more with syntactic complexity tended to upregulate these areas during successful syntactic operation (Fig. 6, Table 7).[2]

To further confirm these results solely derived from correct trials, we performed the same multiple regression exclusively on error trials. Because participants overall committed relatively few errors in each condition, we constructed a new model in which the error trials were col-

[2] At the suggestion of a reviewer, we repeated this analysis by replacing negative scores for [subject-relative minus object-relative accuracy] with zeros, the logic being that it is difficult to interpret scores if listeners perform worse on the easier sentences. This modified analysis yielded results that were largely comparable, but slightly weaker: the left dorsolateral frontal cluster was no longer significant (see Supplementary Material for a side-by-side comparison). In addition, we replaced the [object-relative vs subject-relative] contrast with [all sentences vs 1 ch. noise] contrast to be regressed against the original score of [subject-relative minus object-relative accuracy]. This did not yield any significant clusters.

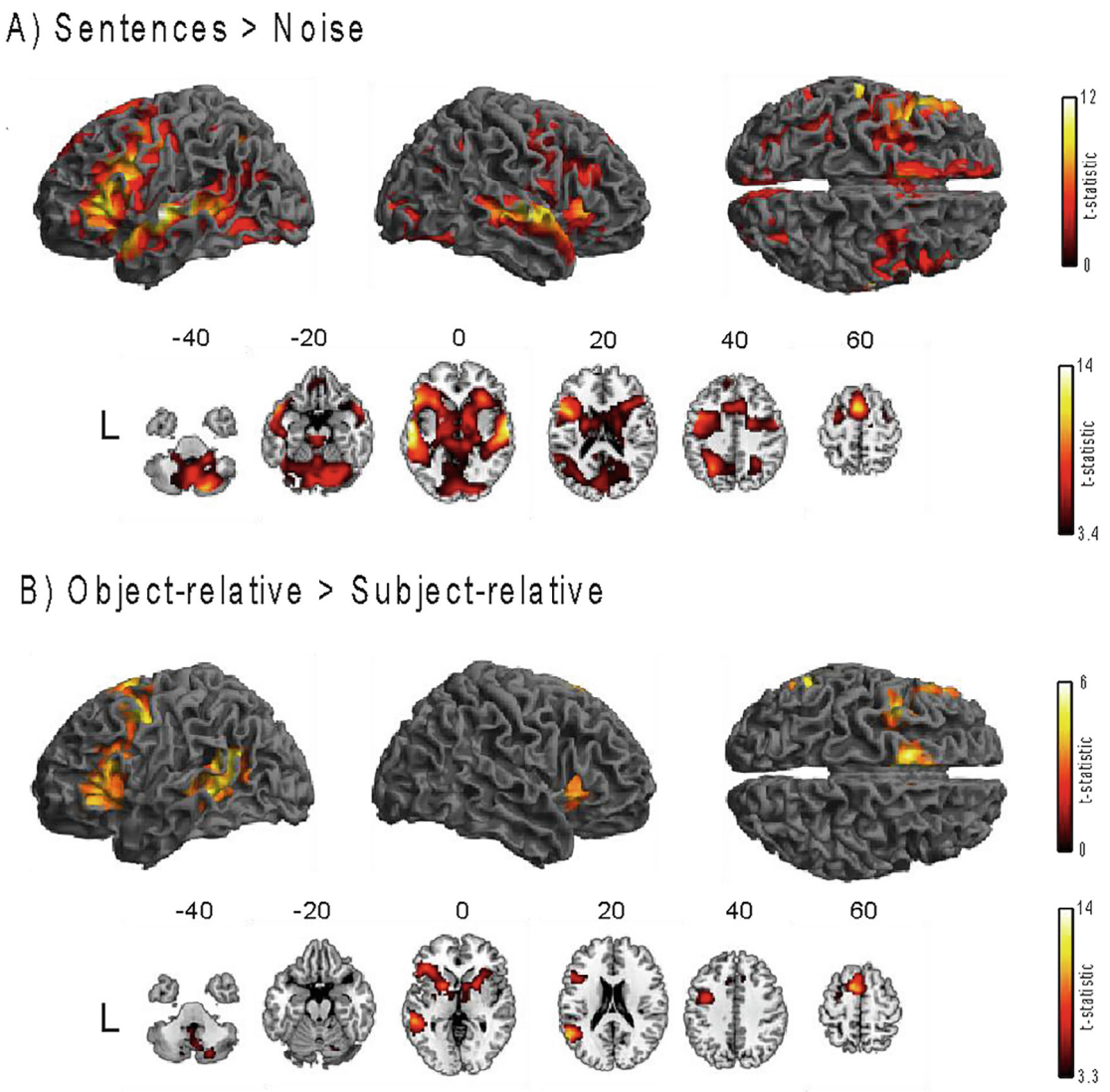


**Fig. 3.** A) Group-level results of sentence processing [all sentences > 1 channel vocoded speech] B) Group-level results of the main effect of syntactic complexity [Object-relative > Subject-relative]; L = Left hemisphere.

lapsed across all sentence conditions. In addition, for this model, functional runs with no errors were removed per participant in the first level analysis. The results revealed no significant voxels.

Lastly, we evaluated the [clear > 24 ch vocoded] contrast by collapsing object-relative and subject-relative conditions and syntax-by-acoustic interactions, none of which yielded significant differences.

## Discussion

In the present study, we investigated the neural underpinnings of successful sentence comprehension in healthy older adults. We found widespread activity throughout cortical and subcortical areas *bilaterally* while participants performed an auditory sentence comprehension task. Given the current study adopted the identical experimental design, sentence materials, and behavioral task used in our previous study [35], we were able to make some direct comparisons to the previous study, which confirmed the appearance of significant clusters exclusively within the right hemisphere that were more active in the older adults than previously shown in the young adults.

As noted in the introduction, for tasks in which young adults show strongly lateralized activity, bilateral activity in older adults has been ascribed to either compensation or dedifferentiation, depending on the relationship with behavioral performance. That is, from a compensatory perspective, the contralateral hemisphere is recruited in older adults to maintain the level of behavioral performance that is supported solely by the dominant hemisphere in young adults. By contrast, a dedifferentiation perspective suggests that increased bilateral activity in older adults relative to young adults reflects non-specific and inefficient processing, hampering task performance. Indeed, when

**Table 2**
Significant regions in the [sentence > noise] group-level comparison.

| | MNI Coordinates | | | | |
|---|---|---|---|---|---|
| Region name | x | y | z | *z*-value | volume of cluster (μl) |
| L anterior STG/STS | −57 | −10 | −1 | >7.61 | 532,008 |
| R anterior STG/STS | 63 | −13 | −1 | >7.61 | |
| L MTG | −57 | −25 | −1 | >7.61 | |
| L MTG | −60 | −28 | 2 | >7.61 | |
| L SMA | −3 | 5 | 62 | 7.61 | |
| L IFG (Operculum) | −42 | 8 | 23 | 7.49 | |
| L Orbitofrontal Cortex | −51 | 23 | −4 | 7.43 | |
| R anterior STG/STS | 60 | −1 | −4 | 7.41 | |
| R middle STG/STS | 54 | −22 | 2 | 7.33 | |
| L IFG (Triangularis) | −51 | 26 | 8 | 7.22 | |
| L Superior temporal pole | −54 | 8 | −10 | 7.11 | |
| Cerebellum (Crus2) | 18 | −79 | −40 | 7.05 | |
| L Superior temporal pole | −48 | 14 | −22 | 7.02 | |
| L Insula | −33 | 26 | 8 | 7.01 | |
| R Cerebellum VIII | 30 | −64 | −52 | 6.9 | |

STG: Superior Temporal Gyrus; STS: Superior Temporal Sulcus
MTG: Middle Temporal Gyrus; SMA: Supplementary Motor Area
IFG: Inferior Frontal Gyrus; R:Right; L: Left

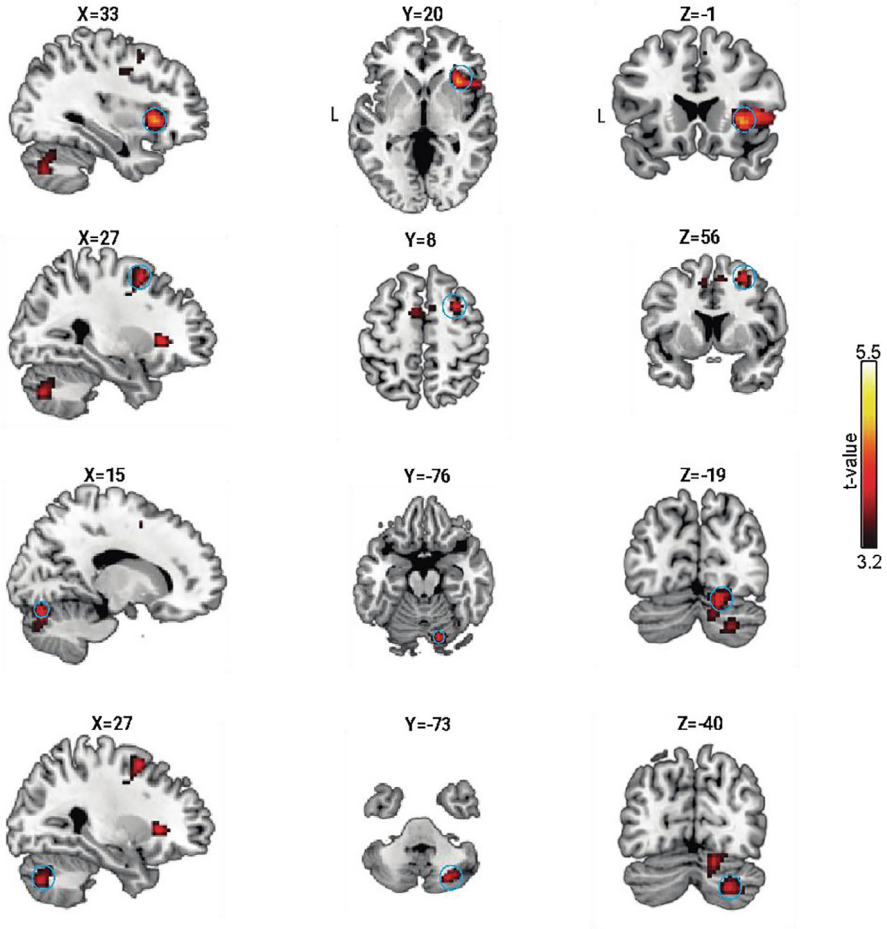


**Fig. 4.** Areas that were more active in the older adults than young adults during general sentence processing. These clusters were exclusively located within the right hemisphere, further confirming the bilateral activation in older adults.

**Table 3**
Areas that were more activated in the older than young adults for general sentence processing.

| | MNI Coordinates | | | | |
|---|---|---|---|---|---|
| Region name | x | y | z | *z*-value | volume of cluster (μl) |
| R Insula | 33 | 20 | −1 | 4.29 | 177 |
| | 45 | 20 | 5 | 4.07 | |
| | 54 | 17 | 2 | 3.74 | |
| R Cerebellum VI | 15 | −76 | −19 | 3.86 | 107 |
| | 12 | −79 | −31 | 3.56 | |
| R PreSMA | 27 | 8 | 56 | 3.82 | 178 |
| | 21 | 2 | 50 | 3.69 | |
| | −9 | 5 | 53 | 3.57 | |
| R Cerebellum Crus II | 27 | −73 | −40 | 3.72 | 166 |
| | 39 | −61 | −28 | 3.66 | |
| | 36 | −67 | −43 | 3.59 | |

PreSMA: Pre-Supplementary Motor Area

**Table 4**
Lateralization indices of old vs young adults data.

| | Frontal | | Parietal | | Temporal | | BG + Thalamus | | Cerebellum | |
|---|---|---|---|---|---|---|---|---|---|---|
| | old | young | old | young | old | young | old | young | old | young |
| sentence > noise | 0.18 | 0.63 | 0.17 | 0.31 | 0.15 | 0.29 | 0.01 | 0.39 | −0.38 | −0.86 |
| OR > SR | 0.56 | 0.79 | 0.93 | N.A | 0.77 | 0.95 | 0.13 | 0.06 | −0.8 | N.A |

"+": left-lateralized; "−": right-lateralized; young adults' LI are from data in Lee et al. [35].
N.A: Not Available; analyses were failed to yield an LI
BG: Basal Ganglia

**Table 5**
Significant regions in the [OR > SR] group-level comparison.

| | MNI Coordinates | | | | |
|---|---|---|---|---|---|
| Region name | x | y | z | *z*-value | *volume of cluster (μl)* |
| R putamen | 21 | 8 | −7 | 5.56 | 61,749 |
| L SMA | −9 | 5 | 62 | 5.51 | |
| R caudate | 15 | 5 | 11 | 5.47 | |
| L putamen | −18 | 5 | 8 | 5.29 | |
| L precentral gyrus | −39 | 2 | 50 | 5.16 | |
| L putamen | −18 | 8 | −4 | 5.07 | |
| L IFG (pars triangularis) | −36 | 29 | 5 | 4.78 | |
| L IFG (orbitofrontal cortex) | −42 | 29 | −4 | 4.74 | |
| L thalamus | −12 | −4 | 11 | 4.61 | |
| L IFG (pars opercularis) | −51 | 17 | 14 | 4.35 | |
| L IFG (pars triangularis) | −54 | 23 | 8 | 4.22 | |
| R insula | 33 | 17 | −7 | 4.09 | |
| L insula | −27 | 17 | −4 | 3.97 | |
| R insula | 30 | 26 | 2 | 3.72 | |
| L cerebellum VIIII | −3 | −49 | −37 | 4.24 | 15,633 |
| R cerebellum VI | 18 | −67 | −31 | 4.17 | |
| cerebellum (vermis) | 0 | −61 | −34 | 4.12 | |
| R cerebellum VI | 30 | −61 | −28 | 4.05 | |
| L cerebellum VIII | −12 | −64 | −31 | 3.98 | |
| R cerebellum (crus II) | 21 | −79 | −40 | 3.93 | |
| R cerebellum (crus I) | 45 | −64 | −31 | 3.86 | |
| R cerebellum VIII | 6 | −67 | −46 | 3.76 | |
| R cerebellum VIII | 9 | −70 | −43 | 3.68 | |
| R cerebellum (crus II) | −15 | −79 | −40 | 3.25 | |
| R cerebellum V | 15 | −46 | −19 | 3.23 | |
| L MTG | −54 | −52 | 20 | 5.49 | 15,363 |
| L MTG | −57 | −37 | 2 | 5.16 | |
| L MTG | −51 | −43 | 11 | 4.92 | |

behavioral performance on the same auditory comprehension task was compared between the two age groups, older adults performed significantly worse than young adults in the current data.

To better understand the role of the bilateral activity in older adults, we performed multiple regression analyses within older adults. Although we only included correct trials in our main imaging analyses, participants varied in

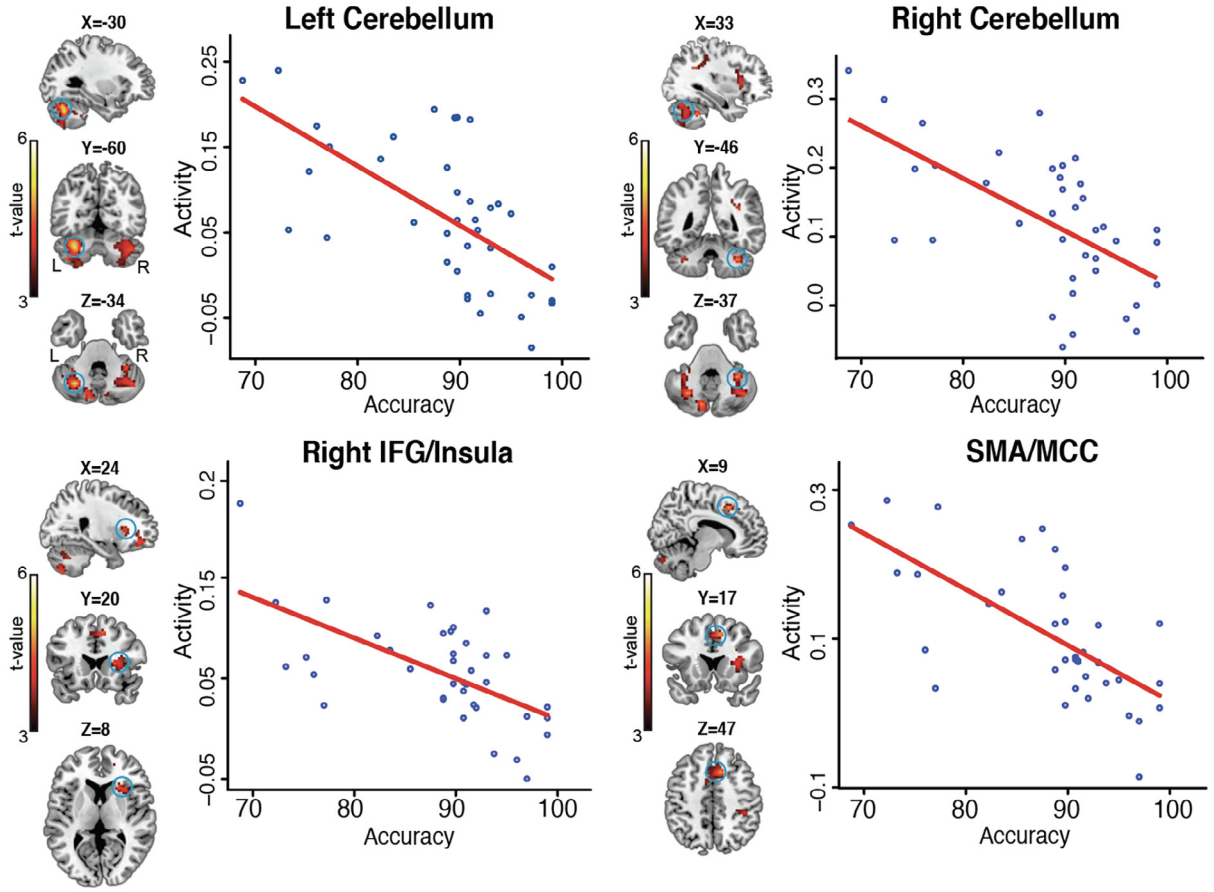


**Fig. 5.** Areas in which activity negatively correlates with individual differences in overall task performance. These areas are situated contralateral to the conventional language network, suggesting that compensatory neural resources support sentence comprehension. The correlation plot is for visualization purposes on significant clusters found by the whole-brain multiple regression using [sentences > 1ch. vocoded speech], in which activity was averaged across voxels within a significant cluster.

**Table 6**
Significant regions in the multiple regression on [sentence > noise] contrast.

| | MNI Coordinates | | | | |
|---|---|---|---|---|---|
| Region name | x | y | z | *z*-value | volume of cluster (μl) |
| L Cerebellum (Crus I) | −30 | −64 | −34 | 4.35 | 14,634 |
| L Cerebellum (Crus II) | −9 | −76 | −40 | 4.32 | |
| L Cerebellum (Crus I) | −36 | −67 | −46 | 4.02 | |
| R vmPFC | 21 | 47 | −10 | 4.31 | 2241 |
| R vmPFC | 18 | 50 | 2 | 4.04 | |
| R vmPFC | 27 | 41 | −1 | 3.62 | |
| R SMA/preSMA | 9 | 17 | 47 | 4.11 | 4590 |
| L SMA/preSMA | −15 | 2 | 53 | 3.97 | |
| L SMA/preSMA | −9 | −19 | 62 | 3.61 | |
| R Cerebellum (Crus I) | 33 | −46 | −37 | 4.06 | 8235 |
| R Cerebellum (Crus I) | 30 | −70 | −22 | 3.89 | |
| R Cerebellum (Crus I) | 24 | −70 | −55 | 3.87 | |
| R Supramarginal gyrus | 36 | −49 | 29 | 3.86 | 2187 |
| R Postcentral gyrus | 39 | −34 | 47 | 3.53 | |
| R Supramarginal gyrus | 36 | −37 | 35 | 3.43 | |
| R Insular cortex | 24 | 20 | 8 | 3.86 | 2376 |
| R Insular cortex | 36 | 17 | 14 | 3.63 | |
| R Frontal operculum | 30 | 14 | 23 | 3.32 | |

vmPFC: ventromedial prefrontal cortex; SMA: suppelmentary motor cortex
L: Left; R: Right

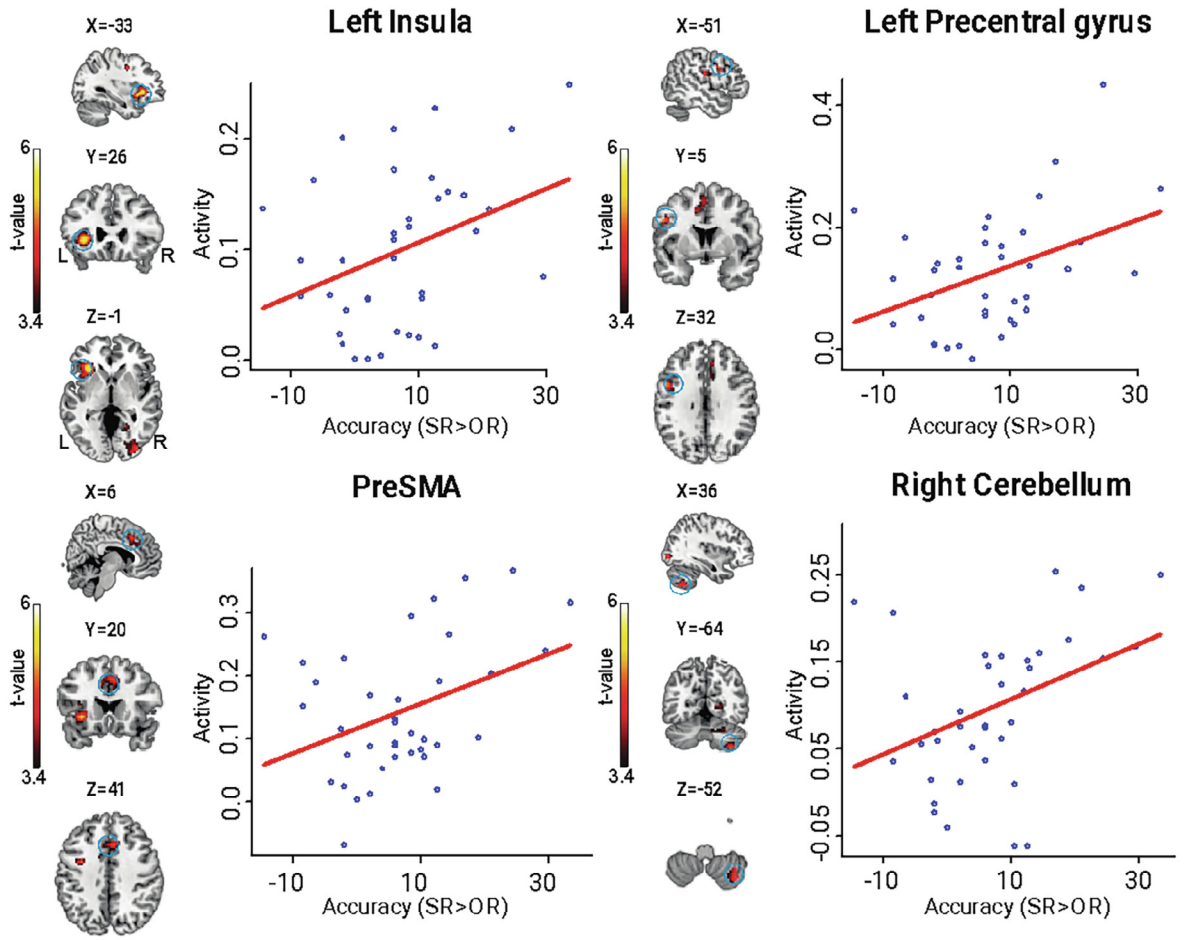


**Fig. 6.** Areas in which activity positively correlates with the difference in syntactic performance, i.e., SR (subject-relative) vs OR (object-relative). These areas are situated in the left-lateralized frontal network and right cerebellum. The correlation plot is for visualization of the significant clusters found by the whole-brain multiple regression, in which activity was averaged across voxels within a significant cluster.

**Table 7**
Significant regions in the multiple regression on [OR > SR] contrast.

| | MNI Coordinates | | | | |
|---|---|---|---|---|---|
| Region name | x | y | z | *z*-value | volume of cluster (μl) |
| L Insula | −33 | 26 | −1 | 4.64 | 4590 |
| L Precentral Gyrus | −51 | 5 | 32 | 4.22 | 3024 |
| L Middle Frontal Gyrus | −33 | −1 | 41 | 4.13 | |
| L Postcentral Gyrus | −51 | −16 | 23 | 3.96 | |
| R Lateral Occipital Cortex | 36 | −85 | −1 | 4.1 | 4617 |
| R Intracalcarine Cortex | 18 | −76 | 14 | 3.73 | |
| R Intracalcarine Cortex | 33 | −76 | 2 | 3.66 | |
| R preSMA | 6 | 20 | 41 | 4.06 | 5427 |
| L preSMA | −9 | 11 | 47 | 3.94 | |
| L preSMA | −3 | 8 | 53 | 3.79 | |
| R Cerebellum VIIb | 36 | −64 | −52 | 4.01 | 5211 |
| R Cerebellum VI | 27 | −52 | −31 | 3.89 | |
| R Cerebellum VI | 15 | −55 | −28 | 3.75 | |

SMA: Supplementaryt Motor Area

their overall performance, which allowed us to relate task accuracy to neural activity pertaining to general sentence processing using whole-brain multiple regressions. We indeed found a set of right cortical areas (mostly in frontal cortex) that showed greater activity in participants with poorer performance. Similar to the present finding, Wier-

enga et al. [19] reported a negative correlation between right frontal activity and picture naming accuracy. Meinzer et al. [18] also found the same relationship between right frontal activity and semantic fluency.

Such a negative correlation may, at first glance, suggest that the right frontal activity is non-beneficial or even harmful to language processing. However, it is important to consider that we found the negative association in the correct trials only, ruling out a potential contribution of the stronger right activity toward failure. Similarly, Geva and colleagues [29] found a negative correlation between right frontal activity associated with correct trials and behavioral performance on a rhyme-judgment task in healthy older adults. Although further research is warranted, our data suggest that the right prefrontal cortex may aid in language performance of older adults who experience more difficulty in the task than others.

What compensatory roles do these right cortical areas play during sentence comprehension? Frontoparietal regions (typically in the left hemisphere) are often implicated in various processes intrinsic to sentence processing, as briefly described below. First, the ventromedial portion of prefrontal cortex is thought to monitor upcoming events from the ongoing action sequences [46]. As such, upregulation of this prefrontal region might help facilitate successive word analyses while listening to speech. The insula, especially the anterior portion, has been implicated in studies examining degraded speech perception [47]. For example, Erb et al [48] reported greater activity of the right insula in degraded (i.e., 4 channel vocoded sentences) than clear speech. They also showed that the right insula's activity was negatively associated with older adults' hearing acuity.

In contrast to Erb et al. [48], we did not find a significant correlation between the right insula and hearing acuity. This may be due to our use of 24 channel vocoded speech, which was intended to present a minimal acoustic challenge. Moreover, sound intensity was calibrated for each participant prior to MRI scanning, which could have further obscured differences in acoustic sensitivity among the older adults. Instead, we found that bilateral insula showed a significant negative correlation with sentence comprehension accuracy. The SMA/pre-SMA may be recruited for procedural and predictive coding which is important for syntactic construction [49–51]. In addition, the pre-SMA plays a role in semantic and lexical processing during language comprehension, as evidenced by studies reporting increased activity during semantic priming [52] and semantic/lexical decision tasks [53].

Outside of the prefrontal cortex, we also observed activity in the right supramarginal gyrus (SMG), presumably due to its role in phonological processing. Activity in SMG has been reported in studies that required explicit phonological or rhyme judgment tasks [54,55]. In support of this notion, an inhibitory TMS (transcranial magnetic stimulation) resulted in slower responses in phonological, but not semantic processing [56]. Together, these right frontoparietal regions may begin to play a compensatory role in linguistic or speech processes and are more leveraged by older adults who are more prone to age-related declines in language operations.

Alternatively, however, right frontoparietal activity may also reflect domain-general processing, not language-specific processing *per se* [57]. Previous studies have suggested that requiring listeners to perform an explicit task resulted in a lateralization shift from left to right, whereas task-free sentence comprehension evoked activities only in the left-lateralized frontotemporal system [17,58]. In the present study, we used a gender judgment task on every sentence except occasional unintelligible stimuli (i.e., 1 channel vocoded speech), for which participants were allowed to press the male or female button at their discretion. As such, trials with sentence stimuli were presumably more demanding than trials with unintelligible noise stimuli, indicating that the right hemisphere may play an important role in keeping up with general task demands.

In stark contrast to the right-lateralized activity associated with general sentence processing (sentences vs noise), robust left-lateralization was found to be sensitive to the syntactic complexity (object-relative vs subject-relative) in older adults as is typically found in young adults. For example, consistent with extant literature [59–63], we observed the left dorsolateral prefrontal cortex and the posterior aspect of superior temporal gyrus that evoked stronger activity in response to object-relative than subject-relative sentences. Hence, the conventional language system in the left frontotemporal network is still robustly sensitive to the syntactic structure of sentences, independent of aging. However, it is worth noting that the correlation of the [object-relative > Subject-relative] with the behavioral scores of [subject-relative minus object-relative] did not implicate the core syntactic regions including pars triangularis, pars opercularis in the left IFG, or posterior STG/MTG. Instead, the analysis yielded areas outside of the core language network [64–66]. Indeed, these frontal clusters (left insula, precentral gyrus, and pre-SMA) are parts of the multiple demand network [67], which are active across different cognitive domains. As such, it appears that those older adults who experience greater difficulty in syntactically complex sentences (i.e., object-relative sentences) leverage domain-general constructs such as verbal working memory [68–73]. Future research using systematic manipulation of the syntactic structure [74,75] is warranted to better understand the compensatory role of these domain-general regions on syntactic analysis.

In the present study, when the same group map of [object-relative > subject-relative] was compared between older and young adults, the degree of activation was comparable between the two groups. Importantly, however, upregulation of the left frontotemporal language system was observed in older adults who were more vulnerable to the syntactic complexity. Indeed, object-relative sentences are known to be more demanding than subject-relative sentences, as evident here by lower behavioral scores (see also [14,15]). Despite the differences in task demands, syntactic comparisons — in both group-level *t*-test and multiple regression — yielded activity mostly in the left hemisphere, in contrast to the results regarding general sentence processing. This finding is in line with the notion that the core language function is stable across

lifespan, and that it continues to rely on the left-lateralized frontotemporal system [3,5,10,20].

Stable language function in healthy aging has been supported by previous neuroimaging work showing that the left frontotemporal system is consistently activated during language comprehension across a large cohort of young and older participants, and with no intrinsic functional connectivity difference in syntactic processing between young and older adults [20]. Relatedly, decreased resting-state functional connectivity within the left frontotemporal system in older adults is associated with agrammatism in early stage of primary progressive aphasia (i.e., non-fluent/agrammatic variant PPA or naPPA) even before atrophy becomes noticeable [76]. In a clinical-pathological study of naPPA, non-fluent speech errors and grammatical simplifications were associated with increased burden of tau pathology in left mid-frontal cortex [77] and associated frontal white matter regions [78]. Contrary to these findings, a recent study using transcranial Direct Current Stimulation (tDCS) study reported that increase of language score was associated with decrease of functional connectivity between left IFG and posterior MTG [79]. Future research is required to provide more insights into the relationship between functional connectivity and grammar processing in both healthy older adults and those with naPPA. For example, it needs to be determined whether or not an effective behavioral therapy for agrammatistim [80] can be achieved by re-stablizing the aberrant funtional connectivity in patients with naPPA [81,82].

Although we found robust activation in the left frontotemporal network associated with syntactic processing in our healthy older adults, the laterality index pertaining to the syntactic manipulation indicated less left-lateralization in the older adults compared to young adults. Such bilateral activations in cortical areas are paralleled by bilateral activation in the cerebellum which typically shows contralateral activity (i.e., more robust right-lateralized) during language processing. Although the cerebellum has been traditionally viewed as a motoric processor, there is a growing body of evidence that the cerebellum plays a key role in language comprehension [83,84], especially syntactic processing [85–88]. Typically, right cerebellar activity is seen along with left-lateralized frontotemporal network activity during language comprehension [89]. Early case reports with right cerebellar lesions revealed that both expressive and receptive syntactic operations were impaired [90,91]. Schwartze and Kotz [92] theorized that the cerebellum mediates, in concert with basal ganglia, analyses of temporal structures (e.g., boundaries across words and phrases) during speech comprehension. In particular, lobule VII in the right cerebellum is thought to play a key role in syntactic analysis with its robust connection to the prefrontal cortex [93].

In the present study, we found a large expanse of the right cerebellum spanning across lobule V to VIII that responded to syntactically complex speech. Moreover, lobule VII from the right cerebellar cluster was found to be associated with age-group difference (i.e., stronger in older adults) for general sentence processing as well as individual differences within older adults in syntactic perfromance. Although less common, both bilateral and left-lateralized cerebellum activities have been reported in studies involving language perception and production tasks [88,93]. Indeed, the left cerebellum, along with the right frontoparietal areas, was most robustly (in both cluster-size and *t*-statistic) associated with individual differences in general sentence processing. Together, we found different hemispheric roles in the cerebellum that correspond to the opposite hemisphere of the core language network.

In summary, in the present study we investigated the neural underpinnings of successful sentence comprehension in healthy older adults. Our main findings within older adults suggest distinct functional roles in supporting spoken sentence processing: whereas the right frontal cortex and the left cerebellum were newly recruited to maintain general sentence processing [17], the left frontal cortex and the right cerebellum — the conventional language network — continued to play a key role in core syntactic function despite aging (see also [20]). Furthermore, these regions were leveraged to a greater extent by worse performers. In addition, we found that, compared to young adults, older adults recruited a much wider brain network that included the traditional left sylvian cortex as well as right frontoparietal and cerebellar regions. We note that the direct comparison between the two age groups was made in a post-hoc and supplementary manner, which posed some issues including unbalanced sample sizes. Future study should employ larger and matched sample size as well as more planned statistical analyses in delineating neuroanatomical differences between young and older adults in sentence processing. Together, our findings are broadly compatible with a neural compensation perspective and the observed resilience of the core language system in healthy aging.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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