Neurobiology of Aging 150 (2025) 109–121

Contents lists available at ScienceDirect

Neurobiology of Aging

journal homepage: www.elsevier.com/locate/neuaging.org

Aging modulates large-scale neural network interactions during speech comprehension

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ARTICLE INFO

Keywords:
Functional connectivity
Speech in noise
Semantic predictability
Functional networks
Domain-general
Aging

ABSTRACT

Speech comprehension in noisy environments constitutes a critical challenge in everyday life and affects people of all ages. This challenging listening situation can be alleviated using semantic context to predict upcoming words (i.e., predictability gain)—a process associated with the domain-specific semantic network. When no such context can be used, speech comprehension in challenging listening conditions relies on cognitive control functions, underpinned by domain-general networks. Most previous studies focused on regional activity of preselected cortical regions or networks in healthy young listeners. Thus, it remains unclear how domain-specific and domain-general networks interact during speech comprehension in noise and how this may change across the lifespan. Here, we used correlational psychophysiological interaction (cPPI) to investigate functional network interactions during sentence comprehension under noisy conditions with varying predictability in healthy young and older listeners. Relative to young listeners, older adults showed increased task-related activity in several domain-general networks but reduced between-network connectivity. Across groups, higher predictability was associated with increased positive coupling between semantic and attention networks and increased negative coupling between semantic and control networks. These results highlight the complex interplay between the semantic network and several domain-general networks underlying the predictability gain. The observed differences in connectivity profiles with age inform the current debate on whether age-related changes in neural activity and functional connectivity reflect compensation or dedifferentiation.

1. Introduction

Extracting speech from a noisy acoustic stream is a fundamental problem that we frequently encounter in our everyday life. One strategy to facilitate comprehension of noisy sentences is to use the semantic context of a sentence to predict upcoming words (i.e., predictability gain). This strategy is most decisive when semantic context is highly predictive and intelligibility is low, but still good enough to understand

Abbreviations: AG, angular gyrus; AIns, anterior insula; ALE, Activation Likelihood Estimation; CO, cingulo-opercular; CPPI, correlational psychophysiological interaction; CRUNCH, Compensation-Related Utilisation of Neural Circuits Hypothesis; DAN, dorasal attention network; DMN, default mode network; FMRI, functional magnetic resonance imaging; FPCN, frontoparietal control network; IC, independent component; ICA, independent component analysis; IFG, inferior frontal gyrus; PCA, principal component analysis; PMTG, posterior middle temporal gyrus pMTG; Pre-SMA, pre-supplementary motor area; SNR, signal-to-noise ratio; SPIN, Speech In Noise; SRT, speech reception threshold; VAN, ventral attention network.

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https://doi.org/10.1016/j.neurobiolaging.2025.02.005
Received 18 September 2024; Received in revised form 22 January 2025; Accepted 19 February 2025
Available online 21 February 2025

some fragments to guide prediction. The predictability gain can be commonly observed in healthy young and older listeners (Guediche et al., 2014; Hartwigsen et al., 2015; Obleser et al., 2007; Obleser and Kotz, 2010; Rysop et al., 2021, 2022).

At the neural level, the predictability gain is associated with increased activity in brain regions that have previously been implicated in semantic processes, including the left angular gyrus (AG), the left posterior middle temporal gyrus (pMTG) and the left inferior frontal gyrus (IFG; Adank, 2012; Jefferies, 2013; Golestani et al., 2013; Obleser and Kotz, 2010; Rysop et al., 2021). In addition, increased activity in regions of the cingulo-opercular (CO) network, including the left and right anterior insula (aIns) and the pre-supplementary motor area (pre-SMA), is frequently observed and has been associated with increased demands when speech signals are compromised (Alavash et al., 2019; Alavash and Obleser, 2024; Rogers and Peelle, 2022; Vaden et al., 2013). In older adults, there is scarce evidence regarding the neural underpinnings of speech processing in difficult listening situations. The ability to decode speech from a noisy signal relies on general cognitive functions, such as working memory and processing speed (Dryden et al., 2017; Rönnberg et al., 2013), which are known to decline with age (Salthouse, 1996; Salthouse et al., 2003). On the other hand, the predictability gain relies on semantic resources, which remain relatively stable or increase with advancing age (Verhaeghen, 2003; Wingfield and Stine-Morrow, 2000). Likewise, age-related changes in neural activity of semantic regions are subtle and tend to occur in combination with altered behavioural performance (Hoffman and Morcom, 2018). Most neuroimaging studies that investigate age-related differences during speech in noise comprehension do not include a manipulation of sentence predictability in their experimental paradigm but focus on general cognitive demands. For instance, Erb and Obleser (2013) found increased levels of activity in the cingulo-opercular network in older adults who performed an overt repetition task with sentences of low predictability. The degree of upregulation predicted comprehension success and was interpreted in terms of the Compensation-Related Utilisation of Neural Circuits Hypothesis (CRUNCH), suggesting that older adults show relatively higher levels of neural activity compared to young adults to achieve similar performance (Reuter-Lorenz and Cappell, 2008). As predictability was not manipulated in this study, it remains unclear how sentence predictability affects neural activity in older adults and if the observed age differences were due to differences in task difficulty. Indeed, when controlling for task difficulty by individualised adjustment of intelligibility levels, older listeners showed strikingly similar task-related activity in regions of the CO network as compared to young listeners (Rysop et al., 2022). It is further a matter of debate whether age-related differences in task-related activity reflect compensation, as claimed by proponents of the CRUNCH theory, or changes in the relative balance from specialized (domain-specific) to less specialized (domain-general) regions, as suggested by the dedifferentiation hypothesis (Li et al., 2001).

At the network level, speech-in-noise processing is thought to be supported by interactions within and between the domain-specific semantic system and the domain-general cingulo-opercular network, although studies targeting network-level effects and age-differences are rare. Using dynamic causal modelling, we have previously shown that high predictability of sentence-final words modulates effective connectivity within the cingulo-opercular network in an inhibitory manner. Importantly, this inhibitory effect was correlated with better behavioural performance in both young and older listeners, indicating a behaviourally relevant change in connectivity (Rysop et al., 2021, 2022). Furthermore, overall connectivity between and within these two networks was stronger in young than older listeners. Another recent study investigated the relationship between successful speech comprehension in noise and resting-state functional connectivity in a group of older adults (Fitzhugh et al., 2021). Resting-state functional connectivity between the frontoparietal control network (FPCN) and the language network was identified as a significant network-level predictor during a sentence-picture matching task. The authors interpreted their finding in line with the theory that increased perceptual or cognitive task demand is supported by increased reliance on cognitive resources, such as processing speed and working memory, putatively provided by domain-general networks, such as the frontoparietal control network. However, it remains unclear whether these results are task-dependent or age-dependent and if the coupling between the FPCN and the language network also contributes to speech comprehension when predictability is manipulated. Although this study suffers from several limitations, such as missing a control group of healthy young adults, it points towards the involvement of domain-general functional networks. Indeed, neuroimaging studies of speech comprehension in challenging listening conditions often focus on selected networks of interest, disregarding the contributions of other large-scale functional networks known to subserve general cognitive functions, such as the control networks, attention networks, or the default mode network. Thus, the contributions of other domain-general functional networks to speech comprehension in challenging listening conditions in young and older adulthood remain unknown.

In the present study, we aimed to overcome these limitations and explore the contributions of domain-general functional networks to speech comprehension under difficult listening conditions in healthy young and elderly listeners. Using a data-driven multivariate approach, we reanalysed previously published fMRI data (Rysop et al., 2021; Rysop et al., 2022). Group-wise spatial independent component analysis (ICA) was used to identify functional networks in younger and older adults. Task-related activity was analysed within these networks and complemented by analyses of between-network functional connectivity via correlational psychophysiological interaction (cPPI).

Going beyond the results reported in Rysop et al. (2021); (2022), we expected to find predictability-dependent effects in semantic and cingulo-opercular network activity, alongside age-related effects in domain-general network activity, consistent with the CRUNCH framework (see Fig. 1D for a schematic visualization of the expected effects). In the exploratory analysis of functional connectivity, we expected to find increased coupling between the semantic network and domain-general networks subserving working memory processes and attentional demands, given the relevance of domain-general cognitive function for speech comprehension in challenging listening conditions and that this increased coupling pattern would be more pronounced in older adults.

2. Materials and methods

2.1. Participants

Thirty healthy young and thirty healthy middle-aged to older German native speakers took part in the experiment. Inclusion criteria were right-handedness according to the German version of the Edinburgh Handedness Inventory (Oldfield, 1971), no hearing difficulties or disorders, and no history of neurological or psychiatric disorders. Younger adults were included if they had self-reported normal hearing. Older adults were additionally screened for age-normal hearing (pure-tone average $<$ 25 dB HL in the listener's better ear) and cognitive impairment (Mini Mental State Examination score $<$ 27; Folstein et al., 1975). To ensure age-normal hearing, older participants underwent a hearing test (pure-tone audiometry) that was conducted in a sound-proof chamber using an audiometer (Oscilla SM910-B Screening Audiometer). Pure-tone averages were calculated separately for the left and right ear across frequencies from 250 kHz to 8000 kHz. Eight participants were excluded due to excessive head movement during scanning. One additional participant was excluded because of missing field maps, yielding a final sample size of 26 young and 25 older participants (Young adults: age range: 19–29 years; M = 25 years, 15 women; Middle-aged to older adults: age range: 50–77 years, M = 62 years, 19 women).

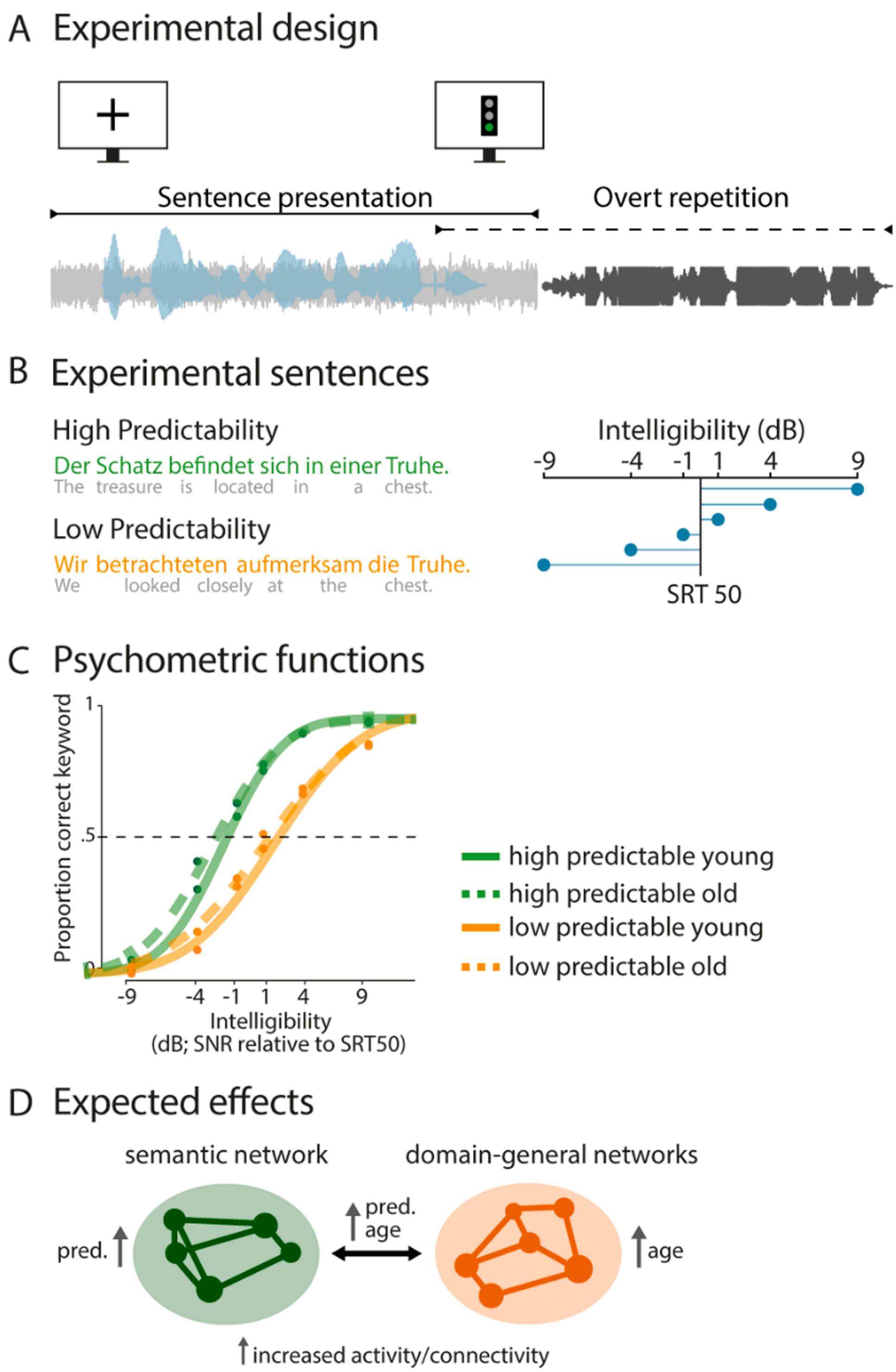

Fig. 1. Experimental design. **A** During the experiment, participants listened to sentences (light blue waveform) that were embedded in speech-shaped noise (grey waveform), while being visually accompanied by a fixation cross. At the onset of the sentence-final word, the fixation cross changed to a green traffic light, indicating the overt repetition phase for the participants. **B** The final word of the sentences was either highly (green) or lowly predictable (orange) from the sentential context. The signal-to-noise ratio of the experimental sentences was centred on individual speech reception thresholds (SRT_{50}) at six intensities. **C** Psychometric curves were fitted to the proportion of correctly repeated final words (solid lines = young listeners, dotted lines = older listeners). Threshold parameters of the psychometric curves (indicated by the black dashed line) were extracted for each predictability condition and age group and used for brain-behaviour correlations. **D** We expected to find increased task-related activity in the semantic network when sentences were highly predictable (pred.), and increased levels of task-related activity in older adults in domain-general networks, consistent with the CRUNCH framework. At the level of functional connectivity, we expected increased coupling between the semantic and several domain-general networks during speech in noise comprehension, and that this pattern would be stronger in older adults. The expected effects are indicated by gray arrows.

The present study constitutes a reanalysis of data that has been published earlier (for further information the reader is referred to Rysop et al., 2021 and Rysop et al., 2022). All participants gave written informed consent in accordance with the declaration of Helsinki and were reimbursed with 10 € per hour. The study was approved by the local ethics committee (University of Leipzig).

2.2. Experimental procedure

All participants took part in one fMRI session. At the beginning of this session, participants performed a one-up-one-down adaptive staircase procedure to determine their speech reception threshold (SRT), i.e., their ability to understand speech in noise. This step was essential, as the intelligibility levels of the experimental sentences were centred on each participant's individual SRT. In the adaptive staircase procedure, participants listened to 20 energetically-masked sentences with highly predictable endings that were not part of the experimental stimulus set. These sentences were presented at an initially high signal-to-noise ratio, which was decreased or increased in subsequent trials, depending on the participant's performance on the preceding trial. Correct repetition yielded a drop in signal-to-noise ratio (i.e., the following trial was more difficult), incorrect answers yielded an increase in signal-to-noise ratio (i.e., the following trial was easier). This procedure was already performed in the MR scanner using the same scanning protocol as in the main experiment to provide a comparable acoustic environment.

In the main experiment, participants listened to sentences that varied in intelligibility (six levels) and predictability (high versus low predictability) and performed an overt sentence repetition task. During the sentence presentation, a fixation cross appeared on the screen. A green traffic light was presented with the keyword to prompt oral repetition. Participants were asked to repeat the sentence, or every word they understood. In case they did not understand anything, they were asked to say so (i.e., say "…"). Sentences were presented via MRI-compatible headphones (MR-Confon, Magdeburg, Germany). Responses were recorded using an MRI-compatible microphone (FOMRI-III, Optoacoustics, Yehuda, Israel). Detailed descriptions of the experimental procedure can be found in Rysop et al., (2021) and Rysop et al., (2022).

2.3. Stimulus material

Experimental sentences consisted of sentence pairs with identical sentence-final words but differing sentence frames providing either high or low semantic context for the final word. Consequently, sentence-final words had either a high or low cloze probability (i.e., expectancy of a word given the preceding context; Taylor, 1953). High cloze probability was generated by several pointer words that were highly associated with the sentence-final word ("She made the bed with new sheets"). Low cloze probability was provided using less associated words ("We are very pleased with the new sheets"). We used 216 sentences (108 sentence pairs) from the German adaptation of the speech in noise (SPIN) corpus (Kalikow et al., 1977; Erb et al., 2012). Keywords from highly predictable sentences had a mean cloze probability of 0.85 (SD = 0.14). Keywords from lowly predictable sentences had a mean cloze probability of 0.1 (SD = 0.02). We further manipulated the intelligibility of the sentences using speech-shaped noise as an energetic masking signal at six different intensities. Speech-shaped noise was generated by filtering white noise with the long-term average spectrum of the 216 experimental sentences (Nilsson et al., 1994). Importantly, intelligibility levels were centred on the individual SRT and comprised three levels that were less intelligible (-1 dB SNR, −4 dB SNR, −9 dB SNR relative to SRT) and three levels that were more intelligible (+1 dB SNR, +4 dB SNR, +9 dB SNR relative to SRT).

2.4. MRI acquisition

Functional images were acquired with a 3-Tesla Siemens Prisma scanner equipped with a 32-channel head coil. We used a dual gradient-echo planar imaging multiband sequence (Feinberg et al., 2010) with the following parameters: TR = 2000 ms; TE_1 = 12 ms, TE_2 = 33 ms; flip angle = 90°; voxel size = 2.5 × 2.5 × 2.5 mm with an interslice gap of 0.25 mm; FOV = 204 mm; multiband acceleration factor = 2. 1500 volumes with 60 slices were acquired in interleaved order in axial direction for each participant. To increase coverage of the anterior temporal lobe regions, we tilted the slices by 10° off the AC-PC line. Additionally, field maps were acquired with the following parameters: TR = 620 ms; TE = 4 ms, 6.46 ms. Field maps were used for distortion correction in the preprocessing pipeline. Structural T1-weighted images were obtained from the in-house database or acquired at the end of the fMRI session using an MPRAGE sequence and the following parameters: TR = 1300 ms; TE = 2.98 ms, voxel size = 1×1 x 1 mm, matrix size = 256 x 240 mm, flip angle = 9°.

2.5. Behavioural data analysis

As the analysis of behavioural performance in the sentence repetition task was not the focus of the present study, the interested reader is referred to Rysop et al., 2022 for a detailed description and report. In brief, psychometric curves were fitted to repetition accuracies of the sentence-final keywords for highly and lowly predictable sentences across all intelligibility levels using the Psignifit toolbox (Fründ et al., 2011). Specifically, we used cumulative Gaussian sigmoid functions to model speech comprehension as a function of predictability and intelligibility. Psychometric curves can be described by a combination of the following parameters: threshold, slope, width, guess rate and lapse rate. In the present analysis, we were only interested in the threshold parameter that denotes the intelligibility level corresponding to a probability of 50 % for a correct repetition. In our previous study, we found a significant difference between sentences of high versus low predictability. Keywords from highly predictable contexts were understood correctly already at lower levels of intelligibility, compared to keywords from lowly predictable contexts (i.e., predictability gain). There was no difference between age groups, rather the psychometric curves from both age groups were strikingly similar (Rysop et al., 2022). For the present study, the threshold parameter estimates of the psychometric curves were extracted for highly and lowly predictable sentences of both age groups and used for correlation analyses between behavioural performance and task-related network activity and functional connectivity (see Fig. 1B for an illustration of the psychometric curves and the threshold parameter).

2.6. Functional imaging

2.6.1. Preprocessing

FMRI data were preprocessed using SPM12 (version 7219, Wellcome Department of Imaging Neuroscience, London, UK) and MATLAB (version R2020b). Only data from the second echo time were used, therefore the first five timepoints were excluded from preprocessing and further analyses, as they were used for echo alignment. Data were realigned, distortion corrected and segmented. Functional images were co-registered to the individual anatomical T1 scan and normalised to the template by the Montreal Neurological Institute (MNI). Original voxel size was kept throughout this process. Finally, a two-dimensional in-slice Gaussian smoothing kernel of 5 mm^2 was applied. Motion parameters obtained from the realignment procedure were used as nuisance regressors. Additionally, framewise displacement was calculated as suggested in Power et al., (2012) and each frame that exceeded a framewise displacement of 0.9 mm was assigned a temporal censor as a nuisance regressor (Siegel et al., 2014).

2.6.2. Independent component analysis

As the overt repetition of speech in the experiment introduced motion artefacts, we applied a dual-ICA approach to obtain denoised group-level independent components (ICs) using the Group ICA of fMRI toolbox (GIFT; version GroupICATv4.0b (GIFTv3.0b); Calhoun et al., 2001). That is, the entire group-wise spatial ICA procedure was implemented once as a denoising step and a second time to identify and characterise network components for further spatial and temporal analysis. ICA included several steps. First, time series were intensity-normalised. Then, data dimensions were reduced in a two-step principal component analysis (PCA) procedure. An initial PCA performed at the participant-level reduced the full 1470 timepoint session length to 62 per session, as determined using minimum description length criteria. An ensuing PCA on concatenated group data reduced the full data to 62. After data reduction, ICA was applied using the Infomax algorithm, and Icasso repeated ICA 50 times to determine the components with the most stability (Himberg and Hyvärinen, 2003). The first implementation of ICA separated the fMRI signal into 62 maximally independent group-level sources containing cortical signal, noise, or a mixture of both. Through visual inspection, we identified 40 noise-only components dominated by scanner artefacts, physiological noise, or subject motion (Griffanti et al., 2017). These components were subsequently removed using the *remove components* utility in GIFT, resulting in reconstructed session-level datasets. The second ICA was run on the reconstructed dataset, pre-setting the number of components to be extracted to 30 (no minimum description length criteria applied) as previous resting-state network studies have reported a reduction to 20 and 40 dimensions as optimal for network identification (Wang and Li, 2015). The resulting 30 components were used for further analyses, and each component was back-reconstructed to each session using the GICA3 method in GIFT and then scaled to Z-scores within each component.

2.6.3. *Network identification*

Visual inspection of independent components determined which components reflected physiological noise or other artefacts, and those were removed from further analysis. Out of the 30 components, 17 maps comprised signal generated by wide-spread regions across the cortex, representing large-scale neural networks active during the task. This set of ICs, or networks, were further narrowed down by excluding primary sensory networks (except for the primary auditory network) alongside subcortical and cerebellar components. The final set of selected networks consisted of 13 cortical networks. To classify and label the 13 components of interest, we compared the spatial map of each component with templates of relevant functional networks described in the literature. These network templates comprised resting-state networks from the 17-network parcellation by Yeo and colleagues (2011), resting-state ICA networks from Smith and colleagues (2009), Activation Likelihood Estimation (ALE)-derived networks for general semantic cognition, auditory semantic cognition and semantic control (Jackson, 2021), and the task-based template of the multiple-demand network (Fedorenko et al., 2013). The resting-state, ALE-derived, and task-based network maps were thresholded to a minimum of 20 % of the map's maximum value and binarized. Next, we quantified the overlap between each component and template using the Jaccard similarity index (Jaccard, 1912). The Jaccard similarity index computes an overlap index between two binarized images, ranging from 0 (no overlap) to 1 (full overlap) and has been used for this purpose before (Jackson et al., 2019; Martin et al., 2022). The components were labelled according to their maximum Jaccard index with these networks. In case of several competing networks, the decision was guided by visual inspection of the spatial distribution of the respective component. Some components did not span the entire template but rather formed topologically separate subnetworks. In these cases, the assigned network label contains topological specifications in addition to the network name (e.g., for the *anterior default mode network (DMN)*, the DMN had the highest Jaccard index, but only anterior DMN regions were involved).

2.6.4. *Task-related activity*

At the participant level, we created a design matrix in SPM modelling sentence onsets and durations of the high and low predictability condition, yielding two task regressors (i.e., *unmodulated regressors*). Intelligibility levels entered the model as parametric modulators of both task regressors, yielding two additional regressors (i.e., *parametrically modulated regressors*). The parametric regressors were orthogonalized with respect to the unmodulated regressors. Hence, the unmodulated regressors can be interpreted as the average activity across all levels of intelligibility and the parametrically modulated regressors encode the intelligibility-dependent effect of predictability on the fMRI signal (Mumford et al., 2015). As we were interested in the interactive effect of predictability and intelligibility, only the parametric (i.e., intelligibility-dependent) regressors were used in the present analyses. Several nuisance regressors were added to model the response onsets and durations of participants‘ overt responses and to capture movement-related signal (six motion parameters obtained from the realignment step, additional regressors for volumes that exceeded the framewise displacement threshold).

We were interested in age- and predictability-dependent differences in activity within each network. Thus, we conducted a multiple temporal regression analysis on the timeseries of the 13 ICA-derived networks applying the *temporal sorting* function of *GIFT* using the parametrically modulated experimental regressors for high and low predictability (as described above) to investigate the intelligibility-dependent effect of predictability. Time and dispersion derivatives were included to account for interindividual variability in the haemodynamic response function (Friston et al., 1998). This analysis yields estimates of task-related activity for each network and each experimental condition. To investigate the involvement of the functional networks in the experimental task, the resulting beta weights were extracted and submitted to 2×2 factorial ANOVAs in R (R Core Team, 2021), with the within-participant factor *predictability* (high/low + parametrically modulated intelligibility) and between-participant factor *age* (younger/older adults). Finally, beta weights from those networks that showed a significant statistical effect in the ANOVAs were correlated with the threshold parameter extracted from the psychometric curves to assess the behavioural relevance of activation differences. The correlations between activity and behavioural parameter estimates were tested using Spearman's rank correlations and Bonferroni-corrected for multiple comparisons.

2.6.5. *Functional connectivity*

To estimate task-related network connectivity between the ICA-derived networks, we used the correlational psychophysiological interaction (cPPI) approach (Fornito et al., 2012; Williams et al., 2022). In brief, this method generates PPI terms for each pair of networks by multiplying a task regressor with each network's deconvolved time course and convolving the resulting term with a canonical hemodynamic response function again. In contrast to the traditional PPI approach (Friston et al., 1997; Gitelman et al., 2003), cPPI computes pair-wise partial correlations between two networks, which control for confounds and the activity of the remaining networks, resulting in non-directed estimations of network pair interactions. Confounds include task-based regressors of no interest, such as the time windows in which participants repeated what they heard, noise parameters, including motion parameters, and average signal from white matter and cerebrospinal fluid, as obtained using masks derived from tissue probability maps output during preprocessing. At the single-participant level, we generated separate cPPIs for highly predictable sentences with parametrically modulated intelligibility, and for lowly predictable sentences with parametrically modulated intelligibility. This procedure was applied for all network pairs, resulting in a 13 x 13 symmetrical partial correlation matrix for each participant. Finally, the correlation coefficients were Fisher–z-transformed.

For second-level analyses, the participant-level connectivity matrices were submitted to one-sided t-tests to assess the effect of predictability and two-sample t-tests to assess the effect of age. These analyses were performed using the *Network-Based Statistics* toolbox (NBS; Zalesky et al., 2010). NBS uses permutation testing to for multiple comparisons. The initial cluster-forming threshold was set to $p < 0.01$ and the FWE-corrected significance threshold was set to $p < 0.05$ with 10,000 permutations. Framewise displacement was included as a covariate of no interest to control for motion-related effects. Results of the cPPI analyses were exported to R and visualised using the package *circlize* (Gu et al., 2014).

To investigate the behavioural relevance of differences in functional connectivity, we performed a set of Spearman's rank correlations between the respective connectivity parameter estimate and the threshold parameter of the psychometric curves. Results were corrected for multiple comparisons using Bonferroni correction. Correlation analyses were conducted in R (R Core Team, 2021) and visualised using the package *ggplot2* (Wickham, 2016).

3. Results

3.1. Domain-specific and domain-general functional networks identified via ICA

Using spatial ICA, we identified 13 cortical components of interest corresponding to established domain-general and domain-specific functional networks (Fig. 2). We classified the components according to their overlap with network templates of common resting-state networks (Smith et al., 2009; Yeo et al., 2011), semantic cognition networks (Jackson, 2021) and the multiple demand network (Fedorenko et al., 2013) using the Jaccard similarity index (Supplementary Table 1). IC02 showed highest spatial similarity with SomatoMotor B network (Yeo et al., 2011), originally described to include the auditory cortex. Because the second and third highest spatial similarities were with the auditory network (Smith et al., 2009) and auditory cognition (Jackson, 2021), and the largest clusters fell within left and right Heschl's gyri (Supplementary Table 2), we refer to IC02 as the temporal auditory network. IC06 and IC16 most closely resembled Smith's frontoparietal control network (FPCN) and split into the right (IC06) and left hemisphere (IC16).

We found three independent components (IC07, IC15 and IC30) that

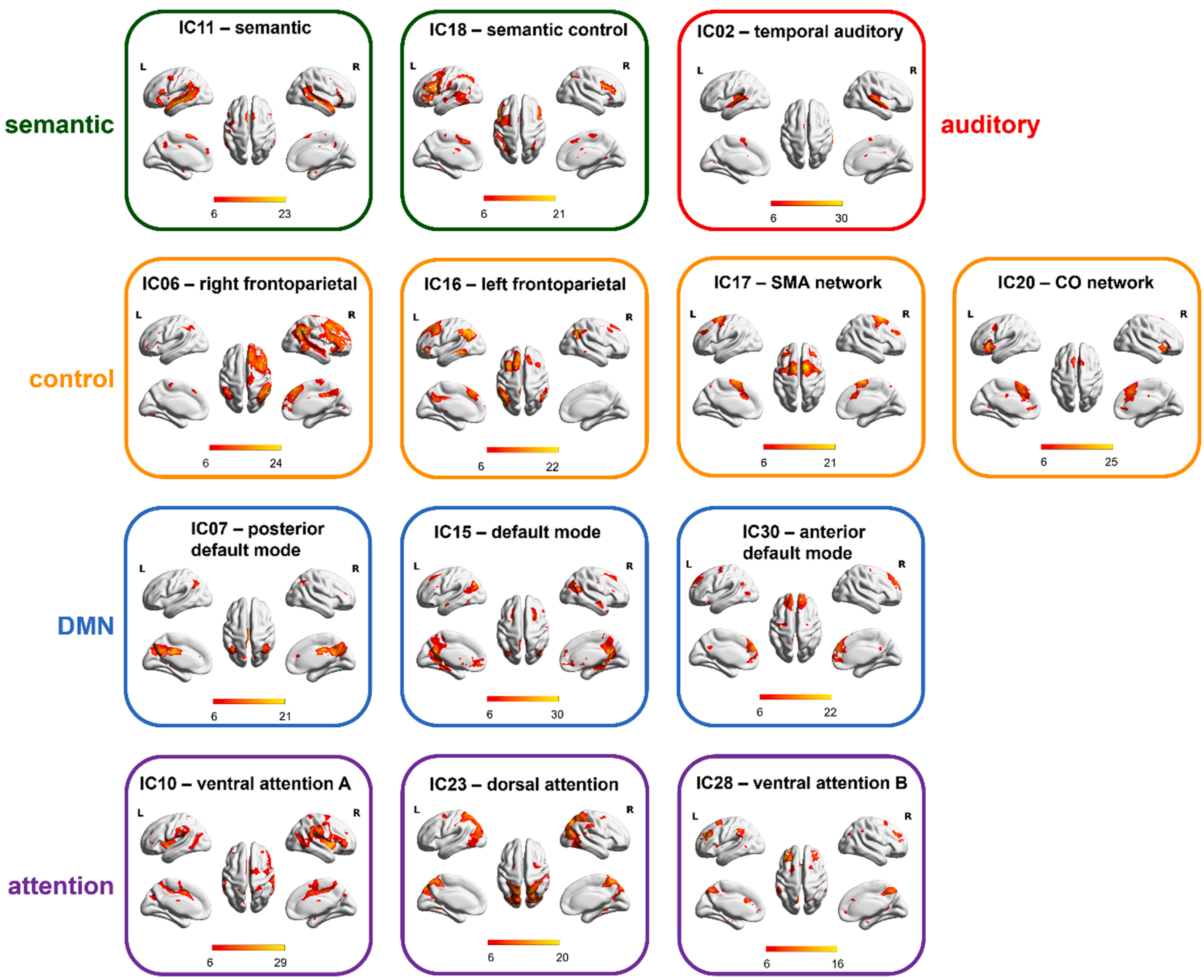

Fig. 2. ICA results. Spatial maps of ICA-derived networks with their original component number and the most probable cognitive network label according to the Jaccard index. Displayed maps show t-scores from one-sided t-tests (peak-level, FWE-corrected at $p < 0.05$, cluster size > 10 voxels). Networks are categorised according to their putative sensory or cognitive function.

matched templates of the default mode network. IC07 shows a considerable overlap with Smith's DMN and is therefore referred to as default mode network. IC15 shows a similarly high Jaccard coefficient for Smith's DMN, but key nodes are predominantly located in anterior regions, therefore we refer to IC15 as anterior subnetwork of the DMN (aDMN). Likewise, IC30 matches Yeo's Default A and Default B networks, but encompasses mostly posterior regions, such as the precuneus and posterior cingulate cortex and is therefore referred to as posterior subnetwork of the DMN (pDMN). The components IC10 and IC28 were classified as Yeo's ventral attention network A (VAN A, IC10) and ventral attention network B (VAN B, IC28). IC11 showed greatest similarity with Jackson's general semantic cognition map and is thereafter referred to as semantic network. IC17 showed no clear similarity to any of the templates. It most closely matched the template of the multiple demand network (only overlapping with anterior regions of the multiple demand network) and for the ventral attention network B, however the Jaccard coefficients are low ($J = 0.12$). As it mostly covers the medial anterior regions, such as the pre-SMA, SMA (identified via the Human Motor Area Template, Mayka et al., 2006), as well as the superior and middle frontal gyri, we refer to this component as the SMA network. With respect to IC18, additional analyses were necessary as the Jaccard similarity coefficient was the same for the Jackson's semantic control network and for the multiple demand network. A weighted correlation was conducted using AFNI's 3dMatch function (Taylor and Saad, 2013) and showed greater similarity between IC18 and Jackson's semantic control network. Considering this result as well as the spatial topography, IC18 was referred to as semantic control network. In a similar manner, IC20 showed spatial similarity with the semantic control,

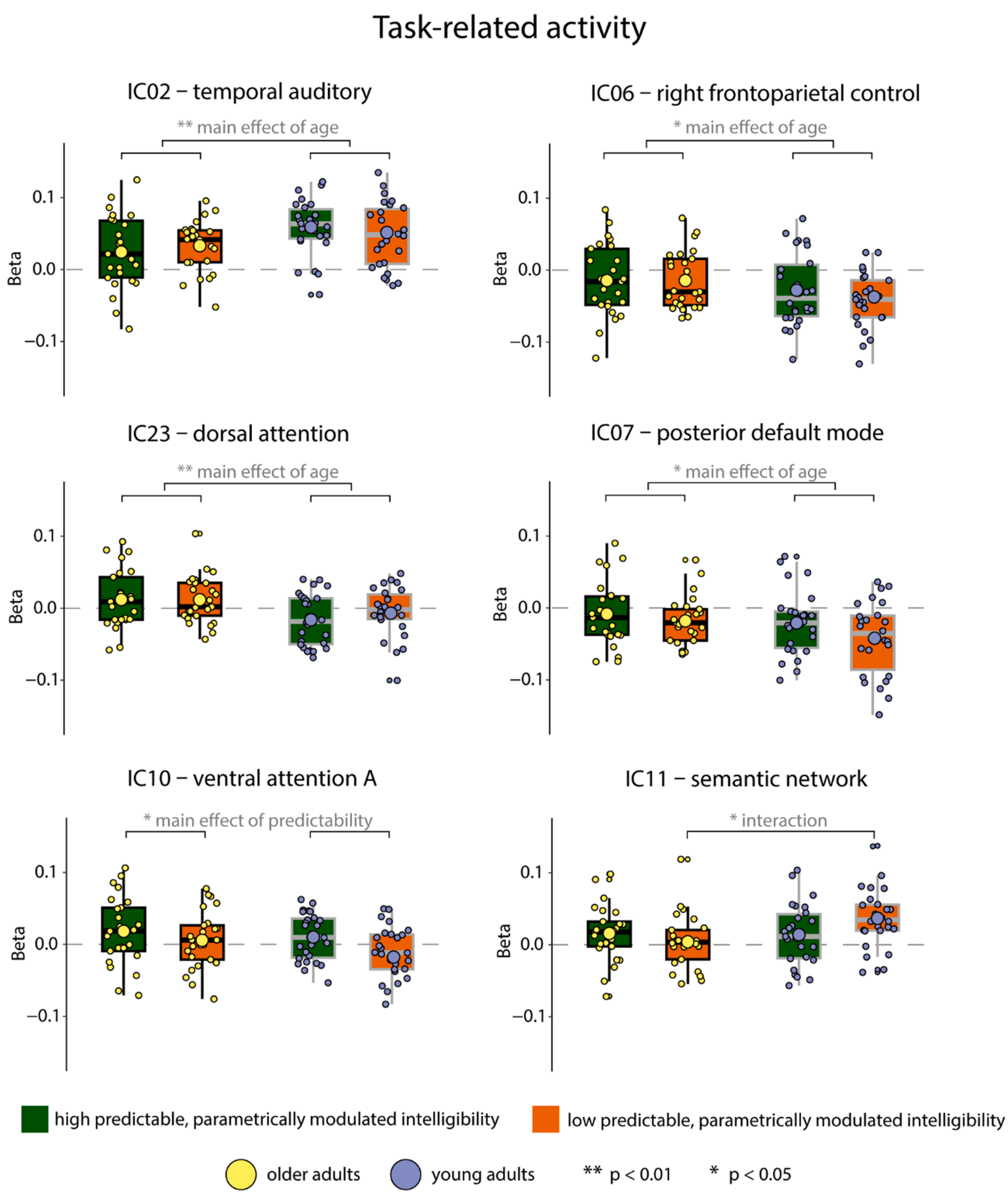

Fig. 3. Results task-related activity. Dots represent parameter estimates from the multiple regression analysis of task-related activity in the ICA-derived networks. Asterisks denote significant effects of predictability, age or the interaction of predictability and age. Large dots represent the mean.

Smith's executive control network and Yeo's salience/ventral attention B network. The spatial topography of IC20 spans across left and right insula as well as the anterior cingulate cortex, regions that are classically associated with the cingulo-opercular network (Dosenbach et al., 2008; Dosenbach et al., 2025). Throughout the literature, there is generally a vast heterogeneity in the practice of network labelling, with most diverse labels for the cingulo-opercular network, which is often referred to as salience network or part of the multiple-demand network (Menon and Uddin, 2010; Uddin et al., 2019). However, in the speech in noise literature, the cingulo-opercular network, encompassing bilateral anterior insulae and the dorsal anterior cingulate cortex, is one of the most frequently reported networks (Rogers and Peelle, 2022). Hence, to maintain consistency within the field, we refer to IC20 as cingulo-opercular network. Finally, IC23 showed a high overlap with the dorsal attention network A and is therefore referred to as DAN. All ICs and corresponding networks are visualized in Fig. 2 and their spatial topography can be found in Supplementary Table 2.

3.2. Older adults show higher activity in domain-general networks during speech comprehension in noise

To identify age- and task-related differences in network activity, we conducted a multiple regression analysis using the *temporal sort* utility of the GIFT package. As we were interested in age-related differences in the interactive effect of predictability and intelligibility, we extracted beta weights using those regressors that captured the intelligibility-modulated effect of predictability. We found differences in activity patterns in six networks (Fig. 3; see Supplementary Table 3 for all statistical results and Supplementary Fig. 1 for a visualisation of task-related activity in the remaining networks).

Older participants showed reduced activity relative to young participants in the auditory network in both intelligibility-modulated predictability conditions. In comparison with young listeners, older adults showed increased activity in the right FPCN, DAN and pDMN. Further, there was a main effect of predictability in the VAN A network, with higher activity for highly predictable sentences of increasing intelligibility in both groups. Finally, we found a significant interaction of age and intelligibility-modulated predictability in the semantic network. Here, young listeners showed higher levels of activity for lowly predictable sentences. The opposite pattern emerged for older listeners: Task-related activity was higher for highly predictable sentences at increasing intelligibility (Fig. 3).

Next, we were interested in the behavioural relevance of task-related activity. Therefore, we correlated the threshold parameter of the psychometric curves with estimates of network activity that showed a significant effect in the multiple regression analysis. Four significant brain-behaviour correlations emerged (see Supplementary Table 3). Increased activity in the auditory network was associated with a higher threshold for highly predictable sentences in young, but not older listeners (rho 0.52, $p = 0.007$). Activity in the right FPCN was correlated with performance for highly predictable sentences in young and older listeners. In young listeners, the relationship was positive, that is, higher levels of activity were associated with worse behavioural performance ($rho = 0.38$, $p = 0.055$). In older listeners, increased levels of activity were associated with better behavioural performance ($rho = -0.43$, $p = 0.032$). Lastly, the threshold of lowly predictable sentences was associated with activity in the semantic network, but only in older adults ($rho = 0.5$, $p = 0.013$). Those older listeners who showed higher levels of activity in the semantic network for lowly predictable sentences showed worse behavioural performance. However, none of these brain-behaviour correlations survived the Bonferroni correction for multiple comparisons, thus we refrain from overinterpreting these correlational results.

3.3. Functional connectivity between semantic and domain-general networks during high predictability

Finally, we were interested in the influence of predictability on the connectivity between functional networks and whether connectivity patterns would differ depending on age. First, we assessed functional connectivity differences between highly and lowly predictable sentences across all participants (predictability-dependent effect, Fig. 4A). Again, the parametrically modulated regressors were used for analysis. Several significant connections emerged that were stronger for highly predictable sentences than for lowly predictable sentences.

The semantic network showed increased coupling with domain-general cingulo-opercular, SMA, DAN and VAN A networks. Further, the semantic control network showed increased coupling with the domain-general DMN and the rFPCN. In addition to the semantic network, the cingulo-opercular network was also coupled with the DAN and DMN. Most coupling parameters were positive, except for the following three network pairs: semantic network and cingulo-opercular network, semantic network and SMA network, cingulo-opercular network and DAN. The reverse contrast of lowly > highly predictable sentences yielded no significant connections. To investigate the relationship between functional connectivity and behaviour, we correlated individual task performance (threshold of psychometric curves) with individual connection weights of those connections that were found to be significant (Fig. 4B).

Only one significant connectivity-behaviour relationship emerged: Functional connectivity between the semantic network and the cingulo-opercular network was negatively correlated with the threshold of the psychometric function for lowly predictable sentences ($rho = -0.3$, $p = 0.03$; Fig. 4B). Thus, those participants with a lower threshold (i.e., better comprehension) showed higher connectivity between the semantic and the cingulo-opercular network when predictability was low, indicating a beneficial effect of increased functional connectivity between these networks when semantic context cannot be used to facilitate comprehension. However, this significant association vanished after correcting for multiple comparisons, and must therefore be interpreted with caution. All other connectivity-behaviour correlations were not significant (see Supplementary Table 6).

3.4. Younger adults show higher overall between-network connectivity than older adults

Next, we investigated the effect of age on between-network connectivity during speech processing in challenging listening conditions, irrespective of predictability. Younger adults showed numerous significant connections between functional networks that were overall stronger compared to older adults (Fig. 4C). All coupling parameters were positive, except for the connection between the auditory network and aDMN. In contrast, older adults had no greater functional connectivity between any of the networks than young adults.

Further, we examined the relationship between connectivity and behaviour. Three significant connectivity-behaviour associations emerged (Fig. 4D). For young listeners, the connection weight between VAN A and DAN was negatively correlated with the threshold of the psychometric curves ($rho = -0.277$, $p = 0.046$). That is, the stronger the connection between these two attention networks, the lower the intelligibility threshold, thus indicating better hearing performance. Older adults showed significant brain-behaviour correlations between the SMA network and the anterior and posterior DMN. Specifically, the connection between SMA and pDMN was negatively associated with the behavioural threshold ($rho = -0.304$, $p = 0.032$). This negative correlation indicates better hearing performance when these two networks show stronger coupling. In contrast, the connection between aDMN and the SMA network was positively associated with the threshold ($rho = 0.286$, $p = 0.044$). Thus, stronger connectivity between the two networks is associated with a higher threshold, indicating worse hearing

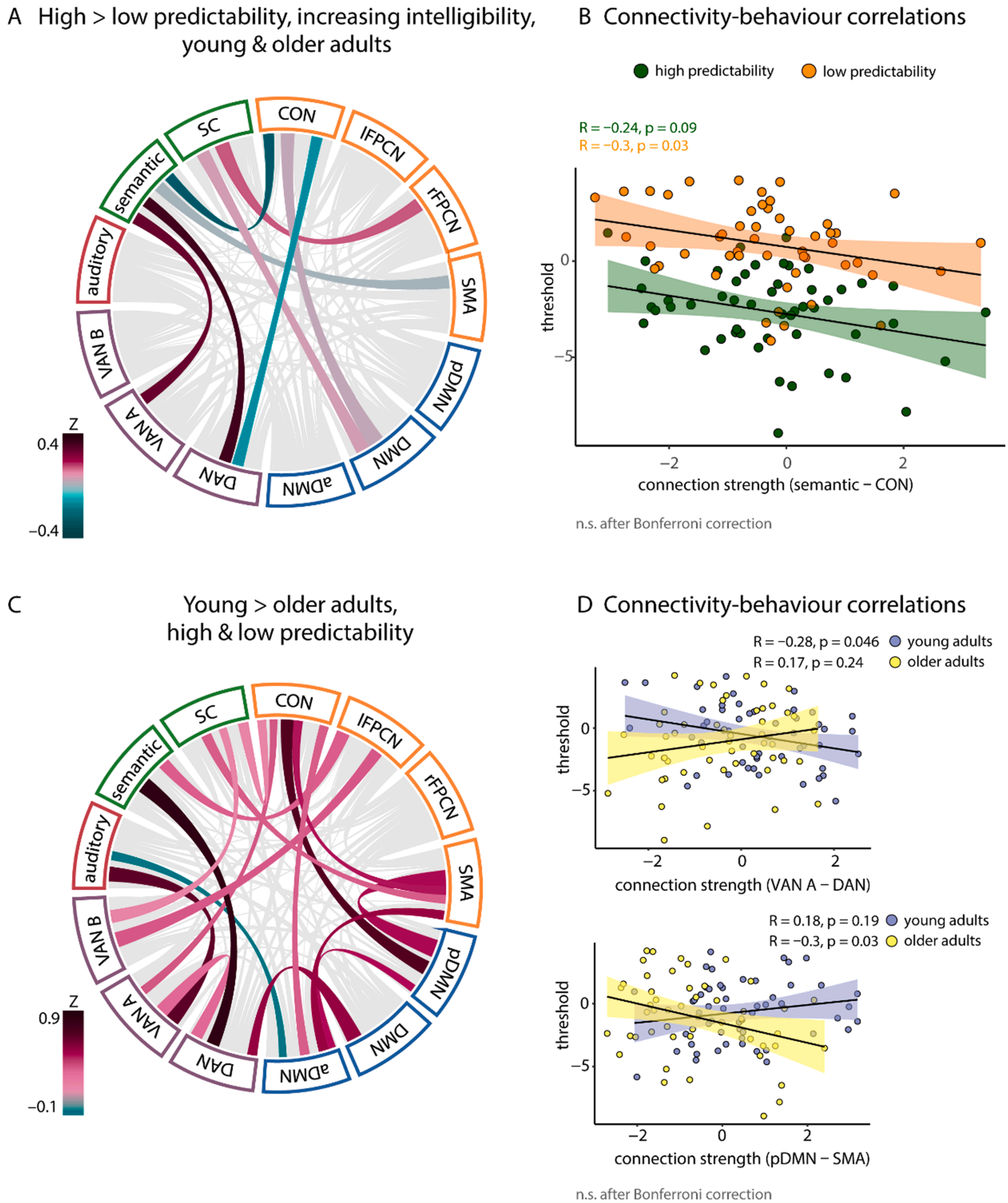

Fig. 4. cPPI Results. **A** Circle plot displays the connections that showed increased coupling for highly predictable sentences compared to lowly predictable sentences across both age groups. **B** Connectivity-behaviour correlation. The scatter plot displays how the connection between the semantic and the cingulo-opercular network is associated with behavioural performance measured as threshold of the psychometric curves. More positive connectivity between these networks is associated with better performance when predictability is low (significance vanishes after Bonferroni correction) and shows a trend towards significance when predictability is high. **C** Circle plot shows between-network connections that were more pronounced in young than older listeners across both predictability levels. **D** Connectivity-behaviour correlation. The scatterplots show relationships between performance (both predictability levels) and the connection between VAN A and DAN in young adults (upper scatterplot) and between performance and the connection between pDMN and SMA in older adults (lower scatterplots). The significance vanishes after Bonferroni correction. In the circle plots, significant connections are colour-coded according to the corresponding Z-value. All remaining connections are shown in light grey. Network colours in the circle plots correspond to the categories of networks established in Fig. 2. SC = semantic control, CON = cingulo-opercular network, lFPCN = left frontoparietal control network, rFPCN = right frontoparietal control network, SMA = supplementary motor area, pDMN/DMN/aDMN = posterior / anterior default mode network; DAN = dorsal attention network, VAN A/B = ventral attention network A/B.

performance in noise. No other connectivity-behaviour correlation was significant and none of the significant correlations remained after correcting for multiple comparisons (see Supplementary Table 5). Therefore, all connectivity-behaviour associations must be interpreted with caution.

4. Discussion

In the present study, we investigated the effect of predictability in challenging listening conditions on semantic and domain-general network activity and on interactions between functional networks in healthy younger and older listeners. Specifically, we probed the effect of age and predictability on sentences that were embedded in speech-shaped noise and tailored to individual hearing abilities in noise to keep task difficulty at a comparable level. The following main findings emerged. First, older adults showed higher task-related activity in several domain-general networks and reduced activity in the auditory network when compared to younger adults. Second, functional connectivity between networks was largely increased for young listeners during speech comprehension in challenging listening conditions. Finally, high predictability increased the coupling of the semantic network with attention networks and decreased the coupling of the semantic network with control networks across both age groups. Key findings of our study on between-network connectivity are summarized in Fig. 5. Our results demonstrate that functional connectivity underlying the predictability gain extends from the classically associated networks to several other domain-general networks but overall decreases with advancing age.

4.1. Network activity in several domain-general networks is modulated by age and predictability

Older adults showed higher task-related activity than younger adults in several domain-general networks, including the right FPCN, DAN and pDMN. This finding is generally in line with neurocognitive accounts of aging, according to which older adults show increased levels of domain-general activity already at lower task demand (Cabeza, 2002; Grady, 2012; Li et al., 2001; Reuter-Lorenz and Cappell, 2008). In particular, the CRUNCH hypothesis suggests that this pattern may be related to compensatory processes, i.e., that increased activity in regions of domain-general networks supports the maintenance of behavioural performance (Reuter-Lorenz and Cappell, 2008). Indeed, we did not observe age-related differences in task performance in the present dataset (see Rysop et al., 2022 for details of the behavioural results). Nonetheless, unlike previous work (Erb and Obleser, 2013) our results do not provide evidence for the compensation account, as we did not find significant brain-behaviour associations between the upregulated domain-general networks and task performance. Thus, the pattern of increased task-related activity in domain-general networks possibly reflects an age-related shift towards less specialized, more domain-general neural circuits, as postulated by the dedifferentiation account (Li et al., 2001). In sum, the present results cannot fully resolve whether the observed upregulations reflect compensatory processes or age-related processes of dedifferentiation.

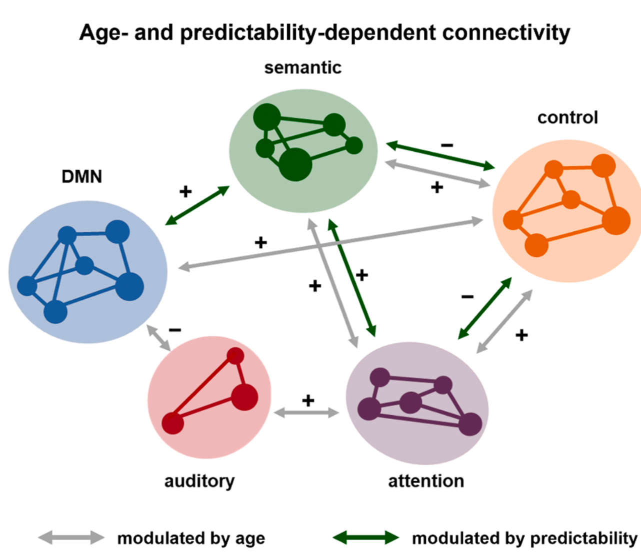

Fig. 5. Schematic of the functional connectivity results. Predictability and age modulate functional connectivity between a variety of functional networks, including the previously implicated semantic and cingulo-opercular networks, and extending to other networks, including control, attention, default mode and auditory network. Connections between regions or networks are indicated with arrows. Green arrows illustrate predictability-dependent modulations (greater for high predictability), grey arrows illustrate age-dependent modulations (greater for younger adults). + /- indicate a positive coupling (i.e., correlation) or negative coupling (i.e., anticorrelation).

Another finding was a main effect of predictability in the VAN A. Here, task-related activity was higher for highly predictable sentences. This finding can be explained by the involvement of the ventral attention network in verbal short-term memory, specifically in the retrieval phase of previously encoded verbal stimuli (Majerus et al., 2012). In our experiment, the overt repetition task loaded on the verbal short-term memory in several aspects. First, the task required participants to hold the heard sentence (or sentence fragments) in short-term memory until the repetition phase. Second, due to the acoustic degradation, sentence fragments of less intelligible sentences had to be held in short-term memory, for further (controlled) operations, such as validation, updating, refinement or reanalysis. As the behavioural performance was overall better for highly predictable sentences (due to the predictability gain), the observed main effect of predictability in the ventral attention network might be a consequence of the larger number of successfully repeated highly predictable sentences and thus a task-dependent effect. Future studies are needed to disentangle task-dependent from task-independent effects.

In the semantic network, we found a significant interaction in task-related activity, driven by higher activity for lowly predictable sentences in younger adults and higher activity for highly predictable sentences in older adults. This finding is striking, as we expected higher levels of activity in the semantic network in both age groups when predictability was high. One explanation for this might be that age groups differ in terms of their strategy during speech comprehension in noise. Younger adults might rely relatively more on bottom-up decoding of the degraded auditory input, whereas older listeners might rely relatively more on top-down semantic information to facilitate speech comprehension. This interpretation is supported by a line of "false hearing" studies, that found a semantic bias when older adults were asked to identify words that were embedded in noise and preceded by either facilitative, misleading, or neutral context (Rogers, 2017; Rogers and Wingfield, 2015). This semantic bias has been explained by a transition in hearing strategies across the lifespan, as age-related hearing loss leads to increasingly degraded auditory input in daily life, shifting the focus towards contextual cues (Pichora-Fuller, 2008; Rogers, 2017; Spreng and Turner, 2019). An alternative explanation could be related to the topographical composition of the independent component, labelled as semantic network. This independent component has been referred to as semantic network due to its high degree of overlap with Jackson's general semantic cognition network template (Jackson, 2021). This template includes both semantic representation and semantic control regions such as the left posterior middle temporal gyrus and inferior frontal gyrus, the latter being also recruited by demanding semantic tasks (Chiou et al., 2018; Lambon Ralph et al., 2017; Whitney et al., 2011). Moreover, this template overlaps with the multiple demand network (Fedorenko et al., 2013), which is associated with domain-general cognitive control. Thus, this component likely captures task-related responses to both high and lowly predictable sentences.

Lastly, older adults showed less task-related activity in the auditory network than younger adults. This finding is in line with previous studies on age-related differences in speech comprehension in noise, reporting an age-related reduction of activity in auditory brain regions (Hwang et al., 2007; Manan et al., 2017; Rogers et al., 2020; Wong et al., 2009), and supports the dedifferentiation account, according to which aging reduces domain-specific and increases domain-general activity.

4.2. Predictability modulates functional connectivity during speech comprehension in challenging listening conditions

At the level of functional connectivity, we were interested in differences in functional coupling between networks as a function of sentence predictability. For highly predictable sentences compared to less predictable sentences, increased coupling was found between the semantic network and domain-general attention (VAN A and DAN) and control networks (CO and SMA). Importantly, the semantic network showed negative coupling (i.e., anticorrelation) with both control networks and positive coupling (i.e., correlation) with both attention networks. While this may sound counterintuitive at first, as one would expect more attention to be required when less context is available to predict the sentence, one would rather expect increased coupling between domain-general networks, but not with the semantic network. This finding aligns well with our previous effective connectivity analysis, showing that inhibitory connectivity between regions of the semantic network and the cingulo-opercular network increased when sentence predictability was high (Rysop et al., 2021; Rysop et al., 2022). Also, this finding points towards the notion that the SMA network and the CO network might have shared functions or perform similar computations in the context of speech in noise comprehension. Indeed, cingulo-opercular regions as well as the pre-SMA/middle cingulate cortex are functionally described as organizational hubs in the framework of an extended multiple demand network (Camilleri et al., 2018; Martin et al., 2023) or associated with a hub for adaptive control that monitors and flexibly coordinates cognitive control resources depending on external demands (Eckert et al., 2016).

Further, the semantic network showed increased coupling with the attention networks VAN A and DAN. These two networks are described as two systems for attentional control (Vossel et al., 2014), with the VAN being associated rather with bottom-up detection of unexpected or unattended signals and DAN with top-down goal directed attention (Vossel et al., 2014). Also, both networks are implicated in verbal short term memory (Majerus et al., 2012). With respect to the number of significant connections, the semantic network had the highest number of significant connections, coupling with the cingulo-opercular network, VAN A, DAN and the SMA network. The cingulo-opercular network showed increased positive coupling with the DMN and increased negative coupling with the DAN in high versus low predictability. Thus, during highly predictable sentences, the semantic network and the DAN seem to work in concert, while being both anticorrelated with the CO. A similar anticorrelation of CO and DAN was found in a study that investigated between-network functional connectivity across three different task domains, including lexical semantics, attention and social cognition (Williams et al., 2022). Interestingly, the anticorrelation of CO and DAN was found across all three tasks, indicating that it might reflect a more general cognitive process.

4.3. Younger listeners show richer between-network connectivity during speech comprehension in challenging listening conditions

Finally, we investigated the effect of age on functional connectivity during the comprehension of challenging, but increasingly intelligible sentences, irrespective of predictability. Compared to older listeners, younger listeners had higher overall connectivity between most categories of functional networks. At first glance, this finding is surprising and contrasts with the literature which often reports higher levels of between-network connectivity as a hallmark of aging. However, these studies usually rely on measures of segregation, calculated as the ratio of within-network to between-network connectivity obtained from graph theoretical approaches (Chan et al., 2014; Geerligs et al., 2015), which could not be calculated in the present study, as we only focused on between-network connectivity. Moreover, most of these studies are based on task-free resting-state functional connectivity. However, studies that analysed age-related differences in task-based functional connectivity tend to provide a more mixed pattern of results, with various decreases and increases in between-network connectivity (Ferré et al., 2020; Varangis et al., 2019; Zhang et al., 2021). Finally, the finding of higher overall between-network connectivity in younger adults mirrors the results of our previous effective connectivity analysis of the same dataset, where we also found that coupling between the CO and the semantic network was stronger in younger adults (Rysop et al., 2022).

All coupling parameters were positive, except for the connection between the auditory network and the aDMN. The control networks (CO, SMA network and left and right FPCN) showed the highest number of significant connections and showed increased coupling with all network categories, except for the auditory network. This finding points towards a complex interaction of domain-specific networks (i.e., auditory network, semantic network, semantic control network) and domain-general networks (i.e., control networks, attention networks, DMN) during speech-in-noise comprehension and lends support to the notion that general cognitive functions are involved in speech comprehension under challenging listening conditions.

5. Limitations

In this exploratory study, we used a data-driven approach to identify functional networks and investigated differences between these functional networks. To the best of our knowledge, this study represents the first investigation of large-scale functional brain network interactions underlying speech-in-noise comprehension, extending the view from the classically associated networks (language network or semantic network and cingulo-opercular network) to other established functional networks and, importantly, their between-network associations.

One disadvantage resulting from this approach is the rather coarse (i.e., network-level) granularity of the results. We investigated connectivity between whole functional networks, ignoring the possibly heterogeneous nature of some networks, with different subregions supporting different computations. Further research is needed to address predictability- and age-related differences in speech-in-noise processing in a fine-grained manner. Likewise, the classification procedure of independent components to relevant functional networks using the Jaccard similarity index has some drawbacks. The templates differ in several aspects, such as their origin (resting-state functional connectivity vs. ALE analyses), differences in the granularity of their parcellation schemes, and the final network labels highly depend on the selected network templates. Moreover, there is an ongoing debate in the field of network neuroscience about the use of heuristic network labels leading to a multitude of different network names for similar underlying regions, rendering it difficult to compare studies across disciplines (Uddin et al., 2019). It is important to keep these drawbacks in mind when interpreting the results. Despite its exploratory nature and the limitations presented above, this study provides a first characterization of age- and predictability-dependent effects on functional connectivity between large-scale networks.

6. Conclusion

The present study provides insight into age- and predictability-dependent interactions between functional networks during speech comprehension in difficult listening conditions. We show that the known predictability gain is underpinned by increased positive coupling of the domain-specific semantic network with domain-general attention networks and increased negative coupling with domain-general control networks. Further, older adults showed relatively higher task-related activity in domain-general networks than younger adults, alongside decreased between-network connectivity. These findings shed new light on age-related differences in network activity and functional connectivity during speech comprehension in difficult listening conditions. Our findings emphasize that changes in activity and connectivity do not necessarily point into the same direction and highlight the complementary insight gained from task-related connectivity analyses.

CRediT authorship contribution statement

Rysop Anna Uta: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Williams Kathleen Anne:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Schmitt Lea-Maria:** Writing – review & editing, Data curation, Conceptualization. **Meinzer Marcus:** Writing – review & editing, Supervision. **Obleser Jonas:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Hartwigsen Gesa:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Conflict of interest

None of the authors has a conflict of interest to declare.

Acknowledgements

We would like to thank Isabel Gebhardt and Rebekka Luckner for assistance in data acquisition and transcription. We also wish to thank Anke Kummer, Sylvie Neubert and Manuela Hofmann for acquiring participants and assistance during the fMRI measurements. We are grateful to Julia Erb for providing the stimulus materials and to the University of Minnesota Center for Magnetic Resonance Imaging for providing the fMRI multiband sequence software. This work was supported by the German Research Foundation (DFG: Research Unit 5429/1 (467143400); project grants HA 6314/10-1, ME 3161/3-1, ME 3161/5-1; HA 6314/4–1, HA 6314/4–2; OB 352/2–1, OB 352/2–2), European Research Council (ERC-CoG-2014; grant number 646696 to JO; ERC-CoG-2021; grant number 101043747 to GH) and Lise Meitner Excellence Funding to GH.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neurobiolaging.2025.02.005.

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