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Neurophysiological signatures underlying preserved lexical-semantic proficiency in healthy aging

Pietari Nurmi [a,*], Heidi Ala-Salomäki [a,b], Hanna Renvall [a,b], Mia Liljeström [a,b,c]

[a] Department of Neuroscience and Biomedical Engineering, Aalto University, Espoo, 02150, Finland
[b] BioMag Laboratory, HUS Diagnostic Center, Aalto University, Helsinki University and Helsinki University Hospital, Helsinki, 00290, Finland
[c] Aalto Neuroimaging, Aalto University, Espoo, 02150, Finland

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ABSTRACT

Although semantic cognition remains behaviorally stable with age, neuroimaging studies report age-related alterations in response to semantic context. To address these inconsistent findings, we combined behavioral and magnetoencephalography (MEG) measures and examined the neural mechanisms underlying lexical-semantic processing in healthy aging. Forty-six Finnish-speaking adults across younger (22 – 32 years) and older (62 – 69 years) cohorts performed a semantic congruency judgment task on word pairs. Both age groups performed the task with high accuracy, with older adults responding faster than younger. While task performance was retained in older adults, MEG revealed a shift in the neural activation patterns with advancing age. Younger participants exhibited the canonical N400 effect in the left temporal cortex 300 – 400 ms post-stimulus, followed by a late semantic effect, whereas older adults showed less pronounced congruency effects, and the activation distribution was shifted toward frontal and bilateral regions. Despite the absence of the canonical N400 effect in older participants, multivariate time-resolved decoding demonstrated that the congruency effect was decodable from the MEG activation patterns in both groups from ~300 ms post-stimulus, indicating preserved sensitivity to congruency with age. Decoding performance further correlated with response times, suggesting that greater neural separation between semantic concepts, indicated by higher decodability, is associated with rapid decision-making. Critically, age groups were distinguishable based on their neural responses 300 – 800 ms post-stimulus, indicating a functional reorganization of semantic processing in older adults. Overall, our findings suggest that healthy aging involves a reconfiguration of neural systems associated with preserved semantic proficiency, despite broader age-related cognitive changes.

1. Introduction

Unlike most cognitive domains, semantic cognition endures relatively well into older age (Burke and MacKay, 1997; Park et al., 2002). Healthy older individuals typically maintain performance on tests assessing general knowledge, word associations, and vocabulary (Burke and Peters, 1986; Nyberg et al., 1996; Salthouse, 2004; Verhaeghen, 2003). Similarly, knowledge assessed implicitly through priming techniques exhibits constancy with age (Laver and Burke, 1993). Priming tasks reliably reveal the semantic congruency effect, where the preceding linguistic context (prime) facilitates the processing of target words that are semantically expected or related (congruent), in contrast to incongruent targets which are associated with longer reaction times. This effect remains stable across age, indicating integrity of implicit semantic processing (Laver and Burke, 1993).

Despite the well-established findings in behavioral psycholinguistics showing stable semantic cognition across age, functional neuroimaging studies have identified age-dependent changes in the neural basis of semantic processing. In electroencephalography (EEG) or magnetoencephalography (MEG) recordings, processing of meaningful stimuli is reflected in the N400 response, occurring between 200 and 600 ms after stimulus onset. The N400 is associated with a well-documented congruency effect, characterized by weaker amplitude for semantically congruent than incongruent stimuli (Kutas and Federmeier, 2011; Kutas and Hillyard, 1980). Notably, EEG studies have consistently reported a reduced N400 congruency effect in healthy aging (Federmeier and

* Corresponding author.
E-mail addresses: pietari.nurmi@aalto.fi (P. Nurmi), heidi.ala-salomaki@hus.fi (H. Ala-Salomäki), hanna.renvall@hus.fi (H. Renvall), mia.liljestrom@aalto.fi (M. Liljeström).

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Kutas, 2005; Kemmotsu et al., 2012; Kutas and Iragui, 1998; Wlotko and Federmeier, 2012), suggesting that older adults may rely on contextual cues less than younger individuals when accessing semantic information. However, this interpretation contradicts psycholinguistic evidence.

Functional magnetic resonance imaging (fMRI) has similarly identified age-related changes in the neural organization of semantic cognition. In younger adults, semantic language processing engages a predominantly left-lateralized network, including medial temporal, posterior inferior parietal, and inferior prefrontal brain regions (Binder et al., 2009). In older adults, fMRI studies have reported reduced activation in semantic-specific regions in the left hemisphere, accompanied by increased activation in the right frontal and parietal regions, particularly in the inferior prefrontal cortex (Hoffman and Morcom, 2018). This pattern of frontal and bilateral hyperactivation in older adults has been interpreted as a compensatory mechanism supporting task performance despite age-related neuronal decline (Cabeza et al., 1997).

Discrepancies between behavioral and neuroimaging findings may partly reflect methodological differences, as each approach captures different perceptual and cognitive processing stages (Payne and Silcox, 2019). Electrophysiological studies on aging often focus on the processing stage related to the N400 response. Late semantic responses, occurring after 500 ms, may reflect more controlled, deliberate aspects of semantic processing, including semantic integration, conflict resolution, decision-making and strategic use of context, in contrast to the relatively automatic context-driven semantic access reflected in the N400 response (Brouwer et al., 2012; Hoshino and Thierry, 2012; Kim and Osterhout, 2005; Kutas and Federmeier, 2011; van de Meerendonk et al., 2009; Yang et al., 2019). Converging neuroimaging and neurocognitive accounts suggest these more controlled semantic operations to be associated with left frontal brain regions, particularly the left inferior frontal cortex (Badre and Wagner, 2007; Lau et al., 2008; Thompson-Schill et al., 1997; Wagner et al., 2001). Findings on the effects of aging on the late semantic response have been mixed, with older adults showing either reduced (Federmeier et al., 2010) or an increased (Xu et al., 2017) late semantic congruency effects. These inconsistent findings may reflect sensitivity to task-related modulations or larger individual variability in later processing stages with age.

The exact impact of aging on context processing in semantic tasks thus remains a subject of ongoing debate across disciplines (Payne and Silcox, 2019). While psycholinguistic research suggests stability in context-dependent congruency effects, imaging evidence indicates changes with age. One potential way to reconcile the relative stability of behavioral performance with these neural changes is offered by broader theories of cognitive aging. These suggest that older adults increasingly rely on well-established world knowledge, schemas and gist-like representations to support performance, while other systems (e.g. episodic memory and processing speed) decline (Park and Reuter-Lorenz, 2009; Spreng and Turner, 2019; Umanath and Marsh, 2014). For example, older adults depend more on plausibility and prior knowledge during sentence and discourse comprehension, sometimes at the cost of memory for specific perceptual or contextual details (Radvansky and Dijkstra, 2007; Umanath and Marsh, 2014), and they tend to perform better in memory tasks where they can make strategic use of their accumulated semantic knowledge and schematic expectations (McGillivray and Castel, 2017). This reliance on acquired knowledge to compensate for declines in other cognitive domains is sometimes referred to as the "semanticization of cognition" (Spreng and Turner, 2019). Taken together, these accounts suggest that aging introduces substantial changes in how semantic information is neurally and cognitively processed, while leaving overt semantic performance largely preserved.

The present study addresses this issue by combining electrophysiological and behavioral measures to investigate the neural dynamics of lexical-semantic processing and context-driven decision-making in younger (22 – 32 years) and older (62 – 69 years) adults. For this purpose, we adopt an MEG judgment task using semantically related and unrelated word pairs to probe the congruency effect. In addition to traditional univariate analysis, we apply multivariate time-resolved decoding to characterize the temporal dynamics of lexical-semantic processing in healthy aging. The decoding approach allows for analyzing the overall activation patterns, thus increasing sensitivity (Grootswagers et al., 2017; Haynes and Rees, 2006) and revealing differences in neural patterns that may not be localized to a single brain region. Increased decodability of semantic relatedness from neural response patterns is considered to indicate greater neural separation between semantic concepts. This can provide more detailed insights into age-related differences underlying semantic congruency evaluations (Contini et al., 2017; King and Dehaene, 2014), thereby advancing our knowledge of neural reorganization in older adults.

2. Materials and methods

2.1. Participants

We studied 46 healthy right-handed (one ambidextrous, assessed using the Edinburgh Handedness Inventory) native Finnish speakers from two age groups: younger adults (22 – 32 years, mean 26 years, SD 2.6) and older adults (62 – 69 years, mean 65 years, SD 1.6). All participants (25 in the younger group [12 females], 21 in the older group [13 females]) were screened for pre-existing neurological disorders, learning disabilities, language disorders and cognitive impairment (Montreal Cognitive Assessment score 26 or above), had normal or corrected-to-normal vision and were not considered part of Covid-19 risk groups due to the pandemic situation at the time of the recordings. They signed an informed consent before participating and were compensated for lost working hours. The ethical statement for the study was obtained from the Aalto University Research Ethics Committee.

2.2. Neuropsychological assessments

A series of neuropsychological tests were employed to examine potential age-related variances in participants' verbal and non-verbal abilities. From the fourth edition of the Wechsler Adult Intelligence Scale, WAIS-IV (Wechsler, 2008), four subtests were applied: Block Design (visuoconstructive reasoning), Similarities (abstract verbal reasoning, semantic knowledge), Vocabulary (word knowledge, verbal concept formation), and Digit-Symbol-Coding (perceptive-motor processing speed, working memory). In addition, we used the Trail Making Test (TMT) A (attention, processing speed) and B (attention, set-shifting, cognitive flexibility) (Reitan, 1958). To address verbal skills, two verbal fluency tests were incorporated, where participants were to produce as many words as possible within 60 s for a given category. A semantic (animals) and a phonemic (words beginning with letter s) test were included (Benton, 1968). Raw scores were converted to a common scale using sample-based Z-scores. In addition, age-adjusted standardized Z-scores were derived based on Finnish normative data. Differences in raw and standardized neuropsychological test scores between age groups were assessed with two-tailed independent-samples *t*-tests.

2.3. Experimental design

We recorded MEG data from participants while they were performing a lexical-semantic judgment task. During the task, written Finnish word pairs were projected onto a screen placed at 120-cm distance in front of the participants using the Presentation software (version 22.0; Neurobehavioral Systems Inc.). The words were presented one at a time. The word pairs consisted of a prime and a target word, and the participants were asked to indicate whether the words were semantically related/congruent (e.g., banana – orange) or unrelated/incongruent (e.g., banana – police) by responding either with their right index or middle finger. The prime and target words were presented sequentially, such that each word was shown for 300 ms, with a 700 ms interval between

the words. The participants were given 2500 ms time to respond, during which time a blank screen was presented, and an additional 1000 ms (500 ms fixation cross + 500 ms blank screen) to prepare for the next word pair. The total inter-stimulus interval between the pairs was then 3500 ms. A fixed inter-trial interval was used to maintain stable task pacing across participants. Although fixed trial timing may introduce anticipatory preparation, potentially to different degrees in younger and older adults, the use of evoked contrast responses should attenuate activity common to both conditions, including general effects of temporal predictability. The responses were registered using an optical device, and response fingers and corresponding stimulus conditions were counterbalanced between the participants within each age group. A short practice task was introduced before the recordings. In total, 108 congruent and 108 incongruent word pairs were presented to the participants in a random order. Structural magnetic resonance (MR) images were obtained in a separate session after the MEG measurement.

2.3.1. Stimuli

For the prime words, 216 common Finnish nouns were selected (mean word length [len] = 5.78 letters, mean word frequency per million [wpm] = 49 015 [The Finnish Internet Parsebank, Kanerva et al., 2014]). Each prime word was assigned both a semantically congruent and a semantically incongruent target word (len = 5.86, wpm = 42 056). Semantic congruency between the prime and target words was assessed using a distributional model of the semantic system, word2vec, trained with a lemmatized 126 617 892 -word Finnish Internet Parsebank (Kanerva et al., 2014). Word2vec is a computational method for extracting distributional vector space representations of a lexicon which can be used to derive semantic similarities between words using cosine similarity (Mikolov et al., 2013). The average cosine similarity for congruent pairs was.6675 (SD =.1702), while for incongruent pairs, it was.0398 (SD =.06612).

Two stimulus sets, A and B, sharing the same set of primes were crafted. In set A, half of the prime words were paired with a congruent target and the other half with incongruent targets. In set B, the same prime stimuli were used in the other condition, i.e., the first half was paired with incongruent and the latter half with congruent targets. Each participant was presented with 216 unique primes paired with targets drawn either from set A or set B, counterbalanced between age groups. The stimulus subsets were matched for word length and word frequency ($p < .05$, independent samples t-test).

2.4. Analysis of behavioral results

In the lexical-semantic judgment task, participants were required to actively categorize the target stimulus as either congruent (semantically related) or incongruent (unrelated) and give their manual response by lifting their right index or middle finger (counterbalanced between age groups). Differences in response times and accuracies between age groups and stimulus conditions were studied with two-tailed independent-samples t-tests. Response accuracy was determined as the ratio between correct and incorrect responses. To further characterize age-group differences in response times, we conducted an ex-Gaussian distributional analysis (Balota and Yap, 2011). An ex-Gaussian decomposition separates the normally distributed bulk of response times, indexed by mu and sigma, from the exponentially distributed right tail, indexed by tau. This is useful as group differences in mean response times may be driven by different parts of the underlying distribution. Ex-Gaussian parameters were here estimated separately for each participant from trials collapsed across conditions. Age-group differences in participant-level mu, sigma, and tau estimates were tested using Welch independent-samples t-tests.

2.5. MEG and MRI recordings

MEG data were recorded at Aalto University MEG Core using a 306-channel (204 gradiometers and 102 magnetometers) Vectorview device (MEGIN Oy, Helsinki, Finland) inside a high-end 3-layer magnetically shielded room (Imedco AG, Hägendorf, Switzerland). MEG signals were acquired at a sampling frequency of 1000 Hz and filtered to 0.1 – 330 Hz during acquisition. Vertical and horizontal electro-oculogram (EOG) signals were recorded to identify eye blinks and saccades. Five head position indicator (HPI) coils were affixed to the head, and their positions relative to anatomical landmarks (nasion and preauricular points) were digitized using an electromagnetic tracking system (Fastrak, Polhemus Inc., Colchester, VT, USA). Continuous head position indication (cHPI) was used to compensate for head movements in relation to the sensor array during the measurement. Structural MR images were acquired at Aalto University Advanced Magnetic Imaging (AMI) Centre using a 3 T Magnetom Skyra whole-body scanner (Siemens Healthcare, Erlangen, Germany) and a standard T1-weighted Magnetization Prepared Rapid Gradient Echo (MPRAGE) sequence.

2.6. MEG preprocessing

MEG data were preprocessed using MaxFilter version 2.2.15 (MEGIN Oy) and MNE-Python version 1.5.1 (Gramfort et al., 2014). Temporally extended signal space separation (tSSS; Taulu and Simola, 2006) was applied to suppress signal artifacts originating from outside the brain. Data from different participants and measurements were transformed into a common head position enabling sensor-level analysis at the group level. Independent component analysis (ICA) using the Extended Infomax algorithm (Lee et al., 1999) and a 30-component decomposition was used to suppress ocular, cardiac, and other physiological artifact components. On average, 3.3 (SD = 2.5) components per participant were removed. The preprocessed MEG data were low-pass filtered at 40 Hz and segmented to event-related epochs from 200 ms before to 1000 ms after the stimulus onset. Baseline correction was applied using the 200 ms interval preceding the stimulus. Epochs with amplitudes exceeding 3000 fT/cm for gradiometers or 4000 fT for magnetometers were discarded (0.40% of all epochs), and the number of epochs was equalized across conditions within each participant. In the younger group, the average number of trials retained per condition was 107.5 (SD 1.4, range 102 – 108), and in the older group it was 107.7 (SD 0.9, range 104 – 108).

2.7. Evoked activity and source modelling

MEG evoked responses were obtained by averaging across epochs for each condition. For source-level visualization, the cortical-level spatio-temporal distribution of the evoked activity was obtained through cortically constrained L2-minimum-norm estimates (Hämäläinen and Ilmoniemi, 1994) using MNE-Python version 1.5.1 (Gramfort et al., 2013). Sources perpendicular to the cortical surface were favored using a loose orientation constraint of.2, and a depth weighting of.8 was used to reduce the bias towards superficial sources. Noise covariance matrices were computed from the 200 ms pre-stimulus baselines of the prime epochs (the initial words in a pair), and noise normalization was applied to obtain dynamic statistical parametric maps (dSPM, Dale et al., 2000). Cortical surfaces needed for anatomically informed source localization were derived from the individual MR images using Freesurfer 6. 0 (Fischl, 2012). Co-registration between structural images and MEG data was performed using digitized anatomical landmarks (nasion and pre-auricular points), coil positions, and additional reference points from the scalp. For each participant, a head conductor model was constructed using a single-layer boundary-element model (BEM) from the inner skull surface consisting of 20484 triangles. A source space with 10242 vertices (ico-5) per hemisphere was employed in the forward model computation. For group-level analyses, the source estimates were morphed onto a template brain (FreeSurfer fsaverage). Anatomical parcellations (Desikan et al., 2006; Glasser et al., 2016) were used to segment the cortical surface into regions of interest (ROI).

2.8. MEG analysis

2.8.1. Difference in evoked activity between conditions

To detect alterations in evoked activity associated with semantic congruency, we first studied the difference between congruent and incongruent conditions at the sensor level. The semantic congruency effect was determined as the point-by-point difference in gradiometer activation by subtracting the evoked responses in the congruent condition from those in the incongruent condition. Each sensor in a gradiometer pair was handled independently. The significance of the congruency effect was studied in three designated time windows (200 – 400 ms, 400 – 600 ms, and 600 – 800 ms) using two-tailed one-sample *t*-tests (H0 = 0). The hypotheses were tested independently for four averaged sensor selections (left temporal, right temporal, left frontal, and right frontal) for each age group. To account for multiple comparisons, the p-values were adjusted using the Benjamini–Hochberg procedure (false discovery rate, FDR).

2.8.2. Region of interest analysis

Age-related differences in the source-level congruency effects were examined by comparing activation differences between age groups within two regions of interest (ROIs). For each participant, the semantic congruency effect was computed as the point-by-point difference between the stimulus conditions. The first ROI was defined in the left superior and middle temporal cortex (auditory label; Glasser et al., 2016), corresponding to the typical neural correlates of the N400 (Helenius et al., 1998; Kutas and Federmeier, 2011; Lau et al., 2008), and the second ROI covered the left frontal cortex, which has been implicated as a key neural substrate of late, controlled semantic responses (Badre and Wagner, 2007; Lau et al., 2008; Thompson-Schill et al., 1997; Wagner et al., 2001). Mean activation time courses within these ROIs were derived using the PCA flip method, which applies singular value decomposition to extract the dominant component and implements scaling and sign-flipping to ensure consistent orientation across source estimates. Group differences were assessed within three time windows (200 – 400 ms, 400 – 600 ms, and 600 – 800 ms) using two-tailed independent-samples *t*-tests, with FDR correction applied to control for multiple comparisons.

2.8.3. Laterality Index and Temporal-Frontal Index

To study age-related differences in activation distribution across the hemispheres, we used Laterality Index (LI) which has been used in previous studies to determine language lateralization (Doss et al., 2009; Raghavan et al., 2017; Tanaka et al., 2013). Following the approach of Tanaka et al. (2013) and Raghavan et al. (2017), we defined individual activation thresholds as 50% of the maximum value over both hemispheres within each of the three selected time windows (200 – 400, 400 – 600, and 600 – 800 ms). The 50% threshold was chosen to maintain comparability with prior lateralization studies (Bidula et al., 2017; Fernández et al., 2003, 2001; Raghavan et al., 2017; Tanaka et al., 2013; Weber et al., 2006). LIs were defined as:

$$LI = \frac{N_L - N_R}{N_L + N_R} \times 100$$

where N_L and N_R represent the number of above-threshold vertices in the left and right hemispheres. The LI values range between −100 and 100, and LI $\geq$ 10 was considered left hemisphere dominance, LI $\leq$ −10 right hemisphere dominance, and LI between −10 and 10 bilateral (Doss et al., 2009; Raghavan et al., 2017; Tanaka et al., 2013).

Following a similar approach, we determined Temporal-Frontal Indices (TFI) to investigate the age-related differences in activation distribution between temporal and frontal brain regions. Here, we used the Desikan-Killiany parcellation (Desikan et al., 2006) to construct two bilateral ROIs covering the entire temporal and frontal cortices in both hemispheres. The activation thresholds were defined as 50% of the maximum value over both ROIs within each time window. TFIs were defined as:

$$TFI = \frac{N_T - N_F}{N_T + N_F} \times 100$$

where N_T and N_F represent the number of above-threshold vertices in the temporal and frontal ROIs. Ranging between −100 and 100 the more positive values correspond with temporal-over-frontal emphasis, and the more negative values with frontal-over-temporal emphasis. Since the vertex count between the ROIs is not equal, this index is not symmetrical, unlike the LI, but it describes the relative ratio between temporal and frontal activation.

2.8.4. Temporal decoding of the semantic congruency

A time-resolved within-participant decoding analysis was conducted to investigate the temporal dynamics of the semantic congruency effect. The analysis was performed using MNE-Python (version 1.5.1; Gramfort et al., 2014) and scikit-learn (version 1.3.1; Pedregosa et al., 2011). Logistic regression classifiers were employed with stratified 10-fold cross-validation, and classifier performance was evaluated using the Area Under the Receiver Operating Characteristic Curve (ROC-AUC) scores. Binary classification between congruent and incongruent epochs was repeated at each time point, generating a time-series of ROC-AUC scores describing the evolution of classification performance over time. Group-level results were obtained by averaging within-participant results. To determine whether decoding scores deviated significantly from chance level, cluster-based permutation tests were conducted with 1000 permutations based on random sign-flipping and a cluster-forming threshold of $p < .05$. Similar analysis was performed to assess between-group differences.

To examine the spatial origin of the semantic congruency effect, classifier weights for each participant were transformed into activation patterns using the method proposed by Haufe et al. (2014). The neural generators of these reconstructed patterns were localized using the inverse solutions described earlier. The resulting relevance patterns indicate the extent to which different cortical regions contain condition-specific information about the stimuli. Prior to group-level averaging, individual relevance patterns were morphed onto the fsaverage template brain.

Furthermore, Pearson's correlation analysis was conducted to evaluate the relationship between decodability and behavioral performance. Decodability scores were averaged across 200 – 400 ms, 400 – 600 ms, and 600 – 800 ms time windows, and the correlations between the resulting mean scores and behavioral reaction times were analyzed, applying FDR correction to control for multiple comparisons. To test whether the decodability–behavior relationship differed between age groups, we fitted additional linear regression models predicting participant-level mean reaction time from age group, z-scored decodability, and the age group × decodability interaction. Models were fitted separately for the 200 – 400 ms, 400 – 600 ms, and 600 – 800 ms windows and p-values were FDR-corrected across the three windows. To further assess whether decodability was associated with broader cognitive performance, we correlated decodability scores from the same three time windows with neuropsychological test scores.

2.8.5. Temporal decoding of the age group

A similar time-resolved decoding approach was employed to directly assess differences in the semantic congruency effect between the younger and the older age groups. Here, logistic regression classifiers were trained to classify between the younger and older age groups at distinct time points based on the evoked contrast responses (incongruent minus congruent). To mitigate overfitting, a group shuffle-split cross-validation scheme was implemented, adhering to participant boundaries and ensuring that the test set did not incorporate samples from participants present in the training set. In practice, the data was shuffled and

randomly divided into training and test sets, with six participants included in each test split. This re-shuffling and splitting process was repeated 50 times. Age groups were initially split separately from each other and subsequently combined to ensure equal representation of each age group in the training and test sets. As in the previous analysis, classifier weights were used to compute cross-group relevance patterns (Haufe et al., 2014). Source reconstruction was performed at the individual level following the previously described steps, and the final cross-group cortical relevance patterns were obtained by averaging these source estimates.

3. Results

3.1. Neuropsychological assessments

The general cognitive performance of the participants in the two age groups, assessed using a neuropsychological test battery, is described in Fig. 1. The older group scored lower in perceptual reasoning and processing speed tests (Trail Making Test A [$p = .002$], Trail Making Test B [$p = .003$], WAIS-IV Block design [$p < .001$], WAIS-IV Digit-Symbol-Coding [$p = .001$]), whereas no age-related differences were found in verbal tests (WAIS-IV Similarities [$p = .283$], WAIS-IV Vocabulary [$p = .287$], Phonemic Verbal Fluency [$p = .663$], Semantic Verbal Fluency [$p = .797$]) (Fig. 1 upper section). When adjusted for age, both groups exhibited slightly higher performance than their respective age-matched reference populations (Fig. 1 lower section). However, this advantage was more pronounced among older adults than the younger in Trail Making Test A ($p < .001$), Trail Making Test B ($p = .046$), WAIS-IV Digit-Symbol Coding ($p = .001$), and Phonemic Verbal Fluency test ($p = .048$).

3.2. Behavioral results

During the MEG recordings, the participants performed a lexical-semantic judgment task during which they were required to actively categorize the target stimulus as either congruent (semantically related) or incongruent (unrelated). The performance in the task for younger and older age groups, with respect to response times and accuracy, is presented in Fig. 2. The older group had significantly faster response times in both the congruent and incongruent conditions (mean 809.4 ms, SD

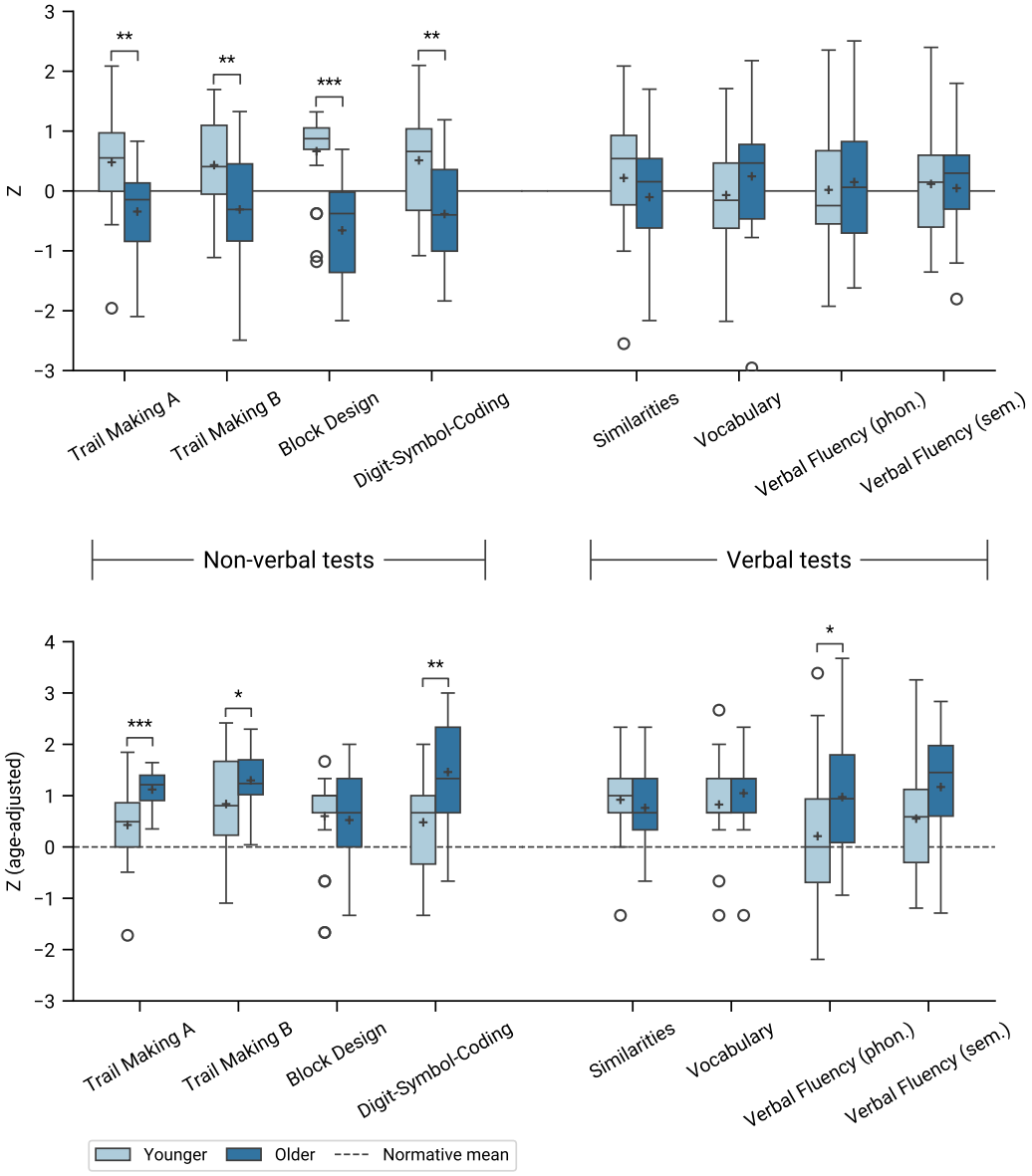


Fig. 1. Neuropsychological assessment results. The upper section presents raw sample-based Z-scores, while the lower section displays Z-scores standardized using age-matched normative data. Significant differences between age groups are highlighted (independent-samples *t*-tests).

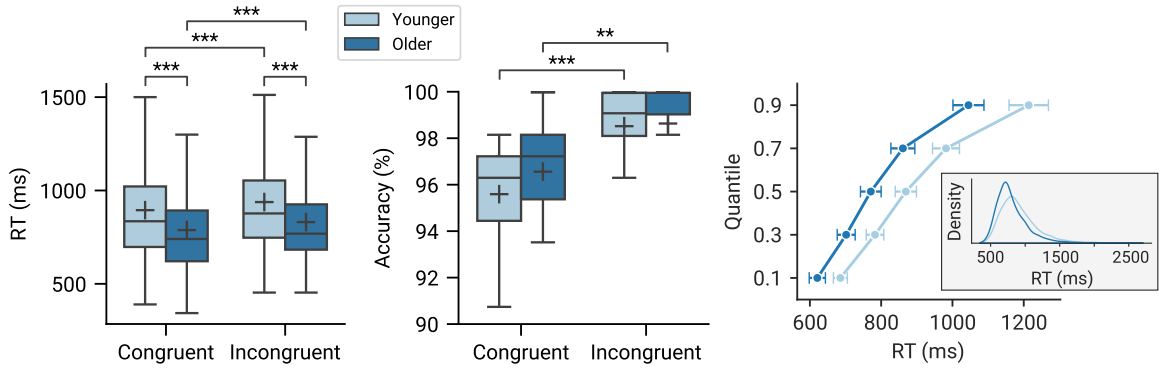


Fig. 2. Left: Behavioral response times and accuracy rates (defined as the ratio of correct to incorrect responses). Comparisons between age groups and stimulus conditions were conducted using independent samples *t*-tests (*** p < .001, ** p < .01, * p < .05). Right: Cumulative response time quantiles and density distributions for younger and older participants, collapsed across conditions.

235.9) than the younger (mean 916.3 ms, SD 228.4, $p < .001$). On average, the gap between age groups was 106.9 ms with no discernible difference between conditions. On the other hand, response times for incongruent stimuli were significantly slower than for congruent stimuli in both younger (congruent: mean 894.6 ms, SD 287.1, incongruent: 938.0 ms, SD 289.7) and older age groups (congruent: mean 788.0 ms, SD 241.5, incongruent: mean 830.7 ms, SD 230.4, $p < .001$). On average, the difference between conditions was 43.1 ms. Here, no age-related variation was observed.

To further characterize the age-group difference in response times, we conducted an ex-Gaussian distributional analysis. Older adults showed a smaller tau than younger adults (older: 169.5 ms; younger: 215.1 ms; Welch $t = -2.139$, $p = .0390$), indicating a smaller slow-response tail. Older adults also showed a numerically smaller, but statistically nonsignificant, mu than younger adults (older: 639.6 ms; younger: 702.5 ms; Welch $t = -2.008$, $p = .0510$), indicating possible age-group difference in the central bulk of the response time distribution. No significant age-group difference was observed for sigma (older: 72.1 ms; younger: 84.2 ms; Welch $t = -1.371$, $p = .1779$). Response time distributions are visualized in Fig. 2.

Response accuracy (proportion of correct responses) exceeded 95% across both age groups and conditions, and no differences in accuracies were found between the groups. Accuracies for incongruent stimuli were marginally greater than those for congruent stimuli in both younger (congruent: mean 95.6%, SD 2.3, incongruent: mean 98.5%, SD 2.1, $p < .001$) and older (congruent: mean 96.6%, SD 2.5, incongruent: mean 98.6%, SD 2.1, $p = .006$) participants.

3.3. *Age-related differences in semantic MEG responses and their neural correlates*

We examined variations in MEG responses associated with the semantic judgment task across the two age groups, with a particular focus on the semantic congruency effect, defined as the difference in neural responses between incongruent and congruent conditions.

Significant congruency effects in sensor-level MEG evoked responses ($p < .05$, two-tailed one-sample *t*-test, FDR-corrected) were observed in both age groups within the 200 – 800 ms window following stimulus onset (Fig. 3). In the younger group, the effect was prominent in all the time windows at the left temporal (200 – 400 ms [$p = .001$], 400 – 600 ms [$p < .001$], 600 – 800 ms [$p = .013$]), and left frontal (200 – 400 ms [$p = .002$], 400 – 600 ms [$p = .003$], 600 – 800 ms [$p = .002$]) sensors, and at the right temporal (200 – 400 ms [$p = .030$], 400 – 600 ms [$p = .022$]) and right frontal (400 – 600 ms [$p = .031$]) sensors. In the older group, a congruency effect was observed at the left temporal (200 – 400 ms [$p = .011$]), left frontal (200 – 400 ms [$p = .002$], 400 – 600 ms [$p < .001$], 600 – 800 ms [$p = .031$]), right temporal (200 – 400 ms [$p = .020$]), and right frontal sensors (400 – 600 ms [$p = .002$]).

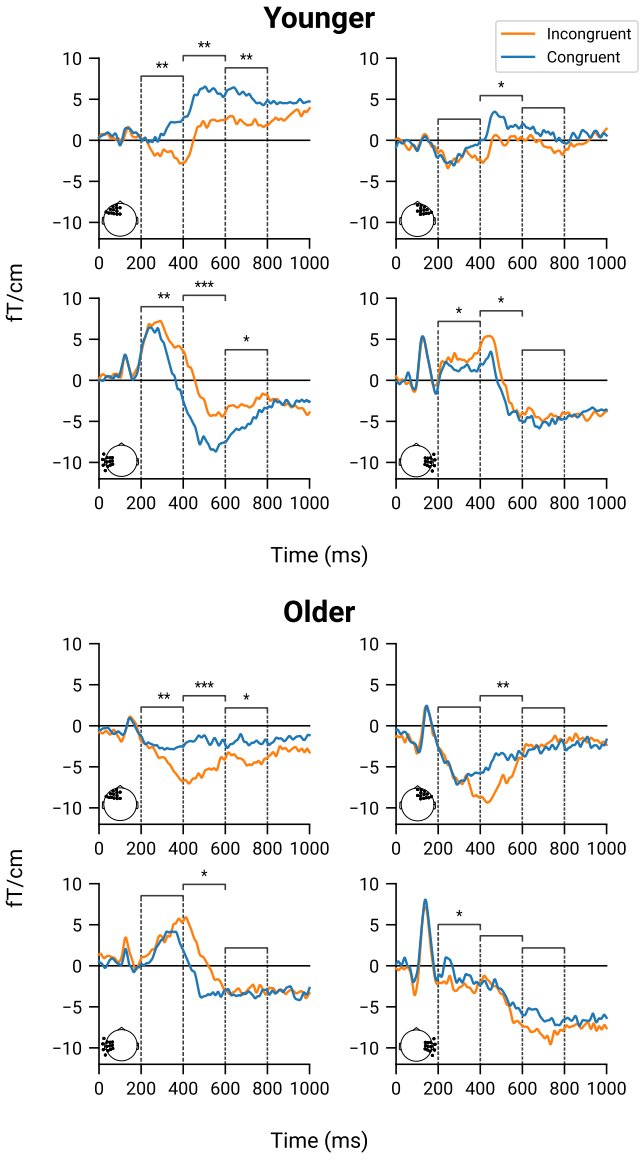


Fig. 3. Evoked responses by age group over four sensor selections: left-frontal, right-frontal, left-temporal, and right-temporal. The significance of the congruency effect between conditions was tested in three time windows: 200 – 400 ms, 400 – 600 ms, and 600 – 800 ms (two-tailed one-sample *t*-test, *** p < .001, ** p < .01, * p < .05, FDR-corrected).

In the younger group, a characteristic N400 effect (incongruent > congruent), originating from the left superior temporal and middle temporal cortices, was observed between 300 and 400 ms (Fig. 4A). Similar neural correlates have previously been associated with the N400 response in younger individuals (Helenius et al., 1998; Kutas and Federmeier, 2011; Lau et al., 2008). In the older group, the N400 response peaked slightly later, just after 400 ms, in the left temporal sensors (Fig. 3). No distinct source-level equivalent of the N400 effect (incongruent > congruent) was identified for the older participants, and the congruency effect exhibited significant age-related attenuation during the 200 – 400 ms interval in the left superior and middle temporal ROI ($T = 2.74$, $p = .027$, FDR-corrected). Instead, the N400 response in the older group was associated with widespread activation in left inferior frontal, middle frontal, and posterior temporal regions, as well as right superior temporal, middle temporal, and middle frontal regions (Fig. 4A).

In the younger group, a later, inverted congruency effect (congruent > incongruent) was observed from 400 to 800 ms (Fig. 3). The neural correlates of this late semantic effect extended from the left temporal to the left middle frontal and inferior frontal regions (Fig. 4A). In the older group, activation patterns associated with the late semantic response were observed both in the left and right middle frontal and inferior frontal regions, as well as in the right middle temporal regions (Fig. 4A). However, older participants demonstrated a significantly weaker congruency effect than the younger during the 600 – 800 ms interval in the left superior and middle temporal ROI ($T = -2.91$, $p = .027$, FDR-corrected).

To assess the overall distribution of cortical activation during the task, Laterality Indices (LI) and Temporal-Frontal Indices (TFI) were computed for selected time windows (Fig. 4B). The younger group exhibited significantly greater left-hemisphere-dominant activation ($LI \geq 10$) across all time windows compared to the older group ($p = .049$, FDR-corrected), whose activation patterns were generally more bilateral (LIs between −10 and 10). Furthermore, in examining the relative balance of activation between temporal and frontal regions, the younger participants demonstrated significantly greater emphasis on the temporal cortex (positive TFIs) during the 200 – 600 ms time window ($p = .003$, FDR-corrected), whereas in the older group, activation was significantly more frontally distributed (negative TFIs). In the later processing stage (600 – 800 ms), activation distribution in the younger group shifted towards frontal regions, and no TFI differences between age groups were observed ($p = .519$, FDR-corrected).

3.4. Temporal decoding

3.4.1. Decoding the stimulus condition

We examined the temporal evolution of the semantic congruency effect by training a series of logistic regression classifiers to differentiate between congruent and incongruent evoked responses at each time point within each participant. Classifier performance was subsequently evaluated and plotted as a function of time (Fig. 5A**)**. Stimulus conditions became decodable approximately 300 ms after stimulus onset, with peak decoding performance occurring shortly after 400 ms. At this peak, ROC-AUC scores reached.6 in the younger cohort and.7 in the older cohort. A gradual decline in decoding performance was observed in the older group after 500 ms, whereas performance in the younger group remained relatively stable between 400 and 800 ms. Decoding performance was significantly higher in the older than in the younger group from 400 ms onward ($p < .05$).

Cortical relevance patterns were derived by transforming classifier weights into activation patterns and projecting them onto the cortical surface. The activation patterns presented in Fig. 5A highlight the brain regions most relevant for congruent-incongruent classification within specific time windows, separately for both age groups. In the younger group, the decoder performance between 200 and 400 ms was predominantly associated with the left middle and superior temporal regions, corresponding to the neural correlates of the N400 effect observed (Fig. 4A). In the older group, similar left temporal patterns emerged, albeit with a more posterior distribution (Fig. 5A). During the 400 – 600 ms window, these relevance patterns shifted toward the left frontal regions, as well as the right anterior temporal and inferior frontal regions, similarly to the cortical source estimates (Fig. 4A).

In the younger group, post-N400 relevance patterns in the 400 – 600 ms window extended to the left inferior frontal and inferior temporal regions, as well as right middle temporal and inferior frontal regions. Subsequently, between 600 – 800 ms, a pronounced left posterior temporal emphasis was observed. Compared to the late semantic response source estimates for the younger group in Fig. 4A, these relevance patterns exhibited greater temporal and reduced frontal distribution. In the older group, the late semantic response relevance patterns between 600 and 800 ms were associated with left and right middle frontal and inferior frontal, as well as right middle temporal regions (Fig. 5A), corresponding to the source estimate results.

The relationship between MEG response decodability (averaged across 200 – 400 ms, 400 – 600 ms and 600 – 800 ms time windows) and behavioral reaction times (averaged across conditions) was examined using Pearson's correlation analysis. Higher decodability scores were associated with faster reaction times in both age groups (Fig. 5B). Significant negative correlations were observed in both younger (200 – 800 ms) and older (400 – 600 ms) participants: the higher an individual's stimulus condition decodability within a given time window, the faster their response time.

To determine whether the relationship between decodability and behavioral reaction time differed between age groups, we fitted linear regression models predicting reaction time from age group, z-scored decodability, and their interaction. The age group × decodability interaction was not significant in any of the time windows: 200 – 400 ms, $\beta = 29.12$, $T(42) = 0.72$, $p = .712$; 400 – 600 ms, $\beta = 6.38$, $T(42) = 0.13$, $p = .895$; 600 – 800 ms, $\beta = 62.50$, $T(42) = 1.20$, $p = .706$, FDR-corrected. Thus, there was no evidence that the association between decodability and reaction time differed between younger and older adults. We additionally examined whether decodability was associated with neuropsychological test performance within age groups by correlating decodability scores from the same three time windows with neuropsychological test scores. No significant associations with neuropsychological test performance were observed.

3.4.2. Decoding the age group

Age-related differences in the semantic congruency effect were examined using a similar temporal decoding approach. Logistic regression models were trained to classify between the younger and older age groups at distinct time points based on the evoked contrast responses (incongruent minus congruent). Age group classification was successful within the 200 – 800 ms time window, with ROC-AUC scores peaking at.8 (Fig. 6).

The cortical relevance patterns in Fig. 6 highlight several brain regions that contributed to the decoding performance, thereby reflecting functional age-related differences in the semantic task. Within the 200 – 400 ms window, the primary contributing regions included the left middle temporal, superior temporal, and inferior frontal cortices. Between 400 and 800 ms, a prominent shift was observed toward the left middle frontal, as well as right anterior temporal and inferior frontal regions. Finally, in the 600 – 800 ms window, decoder performance was predominantly associated with age-related activation differences in the left middle frontal cortex.

4. Discussion

This study examined the effects of healthy aging on the neural underpinnings of semantic congruency judgments by integrating MEG and behavioral measures in younger and older adults. While behavioral performance remained stable across age groups, age-related differences

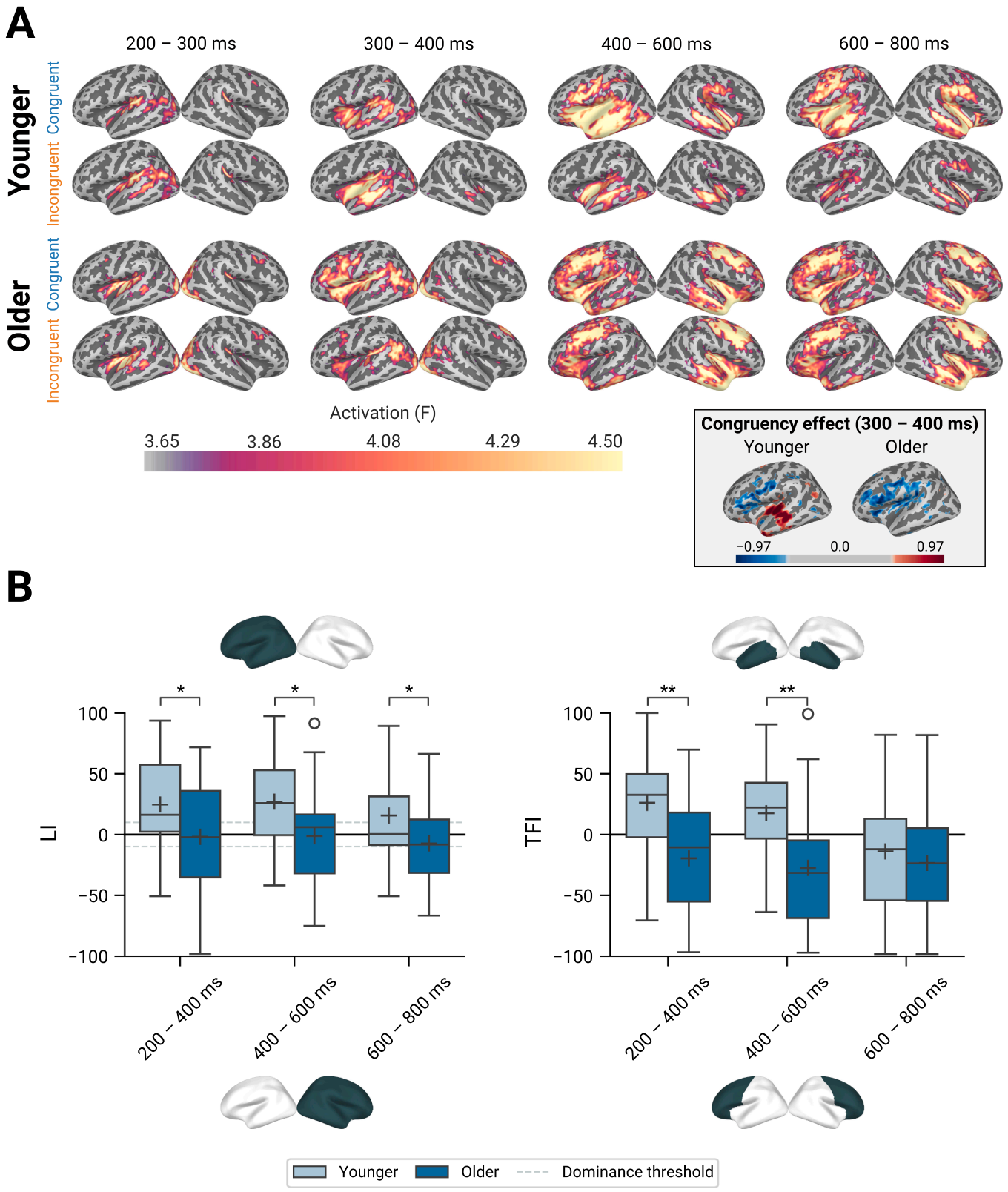


Fig. 4. Minimum-norm estimates. A. Cortical source estimates (dSPM) of congruent and incongruent word pairs and the N400 congruency effect (incongruent − congruent). B. Differences in Laterality Indices (LI) and Temporal-Frontal Indices (TFI) between age groups tested in three time windows (two-tailed independent samples *t*-test, *** $p < .001$, ** $p < .01$, * $p < .05$, FDR-corrected). LI > 0: left hemisphere emphasis; LI < 0: right hemisphere emphasis. TFI > 0: temporal-over-frontal activity; TFI < 0: frontal-over-temporal activity. The dashed line refers to the threshold of hemispheric dominance (LI ≥ 10: left hemisphere dominance, LI ≤ −10: right hemisphere dominance [Doss et al., 2009; Tanaka et al., 2013; Raghavan et al., 2017]).

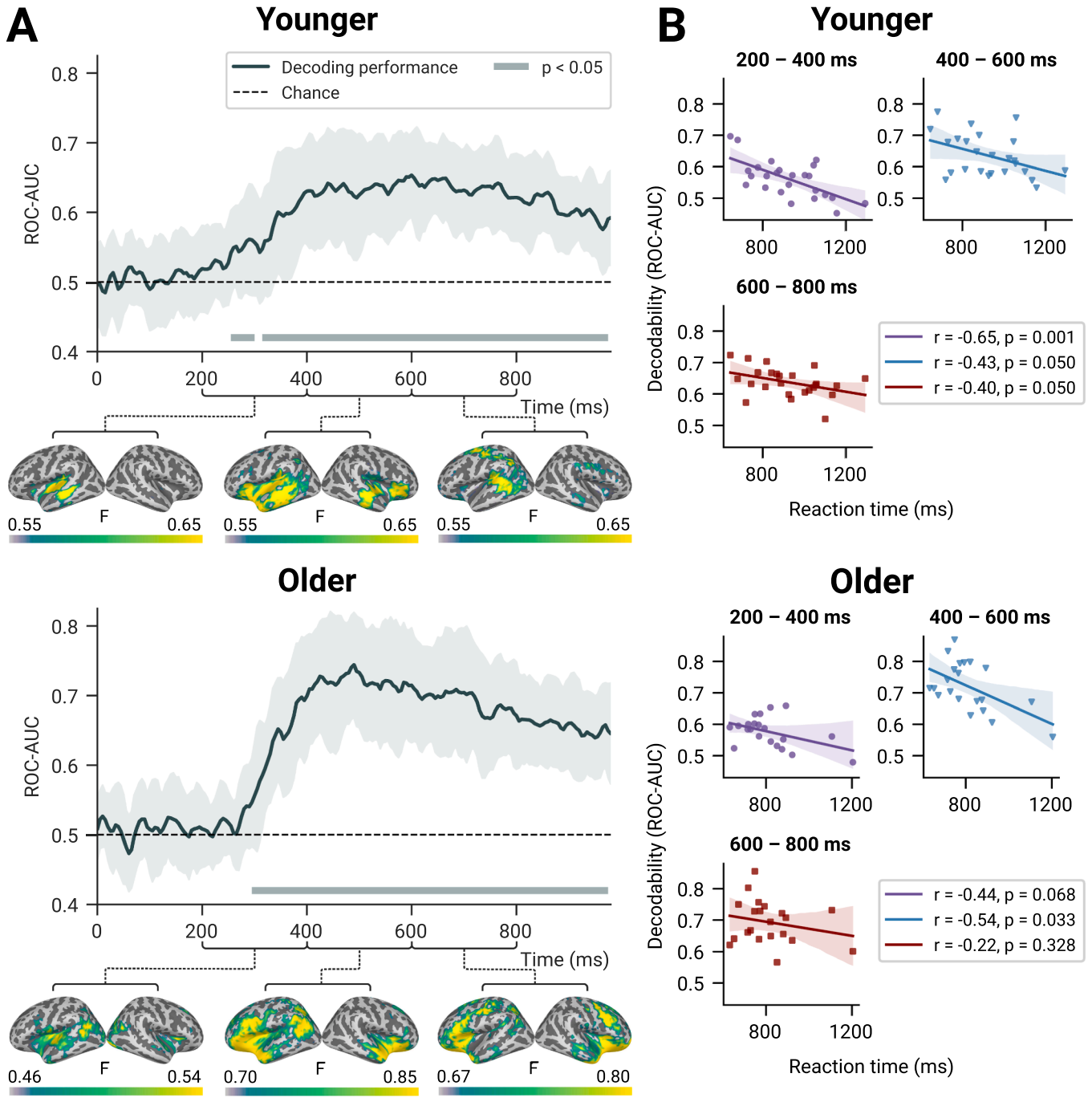


Fig. 5. Decodability of stimulus condition (congruent vs. incongruent). A. Time-resolved decoder performance (± SD), quantified by the area under the receiver operating characteristic curve (ROC-AUC), is presented. Gray bars indicate time intervals during which decoding accuracy significantly exceeded chance level ($p < .05$, two-tailed, within-group cluster-based permutation tests). Corresponding cortical relevance patterns (Haufe et al., 2014) highlight the neural sources contributing to classifier performance based on MEG signal features. B. Correlation between decodability (averaged across 200 – 400 ms, 400 – 600 ms and 600 – 800 ms) and behavioral reaction times (Pearson's r ± SD).

emerged in the time-resolved neuronal responses. In older participants, the activation pattern was more bilateral and shifted towards the frontal cortex. Notably, higher semantic decodability, which correlated with faster reaction times, was observed in the older group, indicating that greater neural separation between semantic concepts was associated with faster decision-making. Together, these findings suggest a functional reorganization of neural systems linked to preserved semantic proficiency in aging.

4.1. Preserved behavioral performance in older adults may reflect benefits of accumulated knowledge

Both age groups completed the lexical-semantic judgment task with high accuracy, exceeding 95% correct responses. Older adults, however, demonstrated significantly faster response times than their younger counterparts, indicating that advancing age was not associated with impaired task performance. On the contrary, healthy and motivated older adults may even outperform younger adults. Preserved performance is consistent with prior psycholinguistic research indicating that

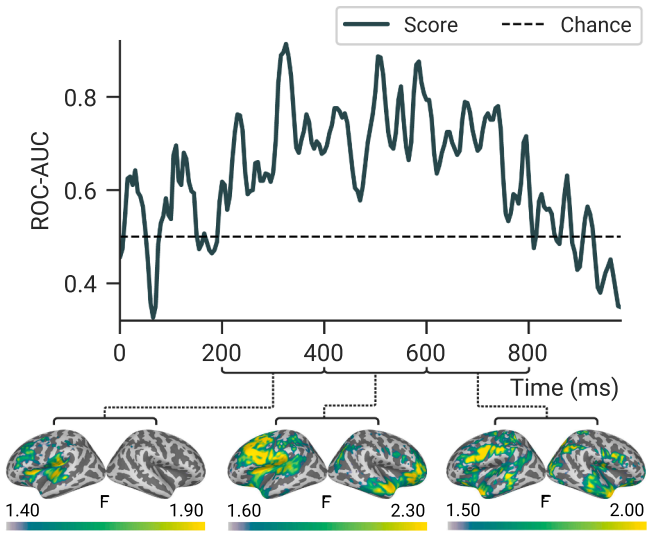


Fig. 6. Decodability of age group, based on the semantic congruency effect in the MEG responses. Time-resolved decoder performance (ROC-AUC) over time is shown for the classification between younger and older adults based on the semantic congruency effect (incongruent minus congruent). Corresponding cortical relevance patterns (Haufe et al., 2014) indicate the neural sources contributing to classification performance.

semantic cognition remains largely stable across the lifespan (Burke and MacKay, 1997; Park et al., 2002).

The observation that older adults exhibited faster response times than younger adults in the semantic judgment task was, still, somewhat unexpected, given that processing speed generally declines by age (Salthouse, 1996). Age-related slowing in reaction times has frequently been reported also in semantic aging (Gold et al., 2009; Hoffman, 2018; Lacombe et al., 2015; Cheimariou et al., 2019), although it is often attributed to general, non-semantic processing decline (Balota and Duchek, 1988). In tasks requiring little semantic control, the impact of general age-related slowing may be reduced. Older adults' greater knowledge reserve, accumulated through life experience, could also facilitate more efficient decision-making. Older adults are likely to favor automatic strategies grounded in experience-based knowledge and semantic networks acquired over years, which are largely preserved beyond age 60 (Li et al., 2004; Salthouse, 2004; Spreng and Turner, 2019; Zaval et al., 2015). Computational modeling studies have further demonstrated a reshaping of semantic networks with age, associated with increased distance between semantic categories and higher within-category coherence in the semantic network (Cosgrove et al., 2023; Wulff et al., 2022). Although such changes reduce network flexibility and efficiency, in relatively simple word association tasks, more cohesive category representations in older individuals could support rapid pattern recognition, particularly for strongly associated words. The faster response times observed in older adults in our task are thus more likely to reflect knowledge and familiarity benefits than globally faster processing. The neuropsychological assessments support this notion, showing comparable verbal performance across age groups, but poorer non-verbal reasoning and slower processing speed in older adults.

An ex-Gaussian distributional analysis of the response times revealed that the most reliable distributional difference in reaction times between groups was in the slow tail, suggesting that the older adults' faster mean response times were driven primarily by fewer or less extreme slow responses. Prior work has suggested that such effects may be attributed to factors such as attentional fluctuations (Roelofs and Piai, 2017), practice effects (Balota et al., 2008), or ease of access due to familiarity from previous exposure (Konopka, 2012). The faster response times observed in the older adults in our task may thus reflect knowledge and familiarity effects, or more consistent task engagement, rather than globally faster processing. The neuropsychological assessments support this notion, showing comparable verbal performance across age groups, but poorer non-verbal reasoning and slower processing speed in older adults.

Many previous aging studies have focused on slightly older individuals (Gold et al., 2009; Hoffman, 2018; Lacombe et al., 2015), whereas our older group consisted of individuals in their sixties who were in good health, partly owing to the exclusion of COVID-19 risk groups, and scored above average on age-adjusted neuropsychological tests. In an older cohort, general age-related slowing would likely outweigh the benefits of accumulated knowledge and familiarity, leading to slower responses. Nonetheless, our findings demonstrate that older adults can maintain, and under certain conditions even exceed, the proficiency of younger adults in processing semantic relationships, particularly in tasks that capitalize on acquired knowledge.

4.2. Frontal shift and increased bilaterality in semantic MEG responses may reflect neural reorganization in older adults

Despite the preserved behavioral performance, we observed age-related alterations in the MEG responses. As anticipated, younger adults demonstrated an N400 response peaking between 300 and 400 ms in the temporal cortex. In the older group, the N400 peaked slightly later, after 400 ms, and lacked a specific neural correlate, instead showing widespread activation in the left frontal and posterior temporal regions. Furthermore, the characteristic N400 congruency effect, marked by greater activation for incongruent versus congruent stimuli, was more prominent in the younger group than the older, consistent with prior research (Federmeier and Kutas, 2005; Kemmotsu et al., 2012; Kutas and Iragui, 1998; Wlotko and Federmeier, 2012). Despite these differences, decodability of semantic congruency showed a sharp increase from 300 ms onward in both age groups, indicating preserved sensitivity to congruency with age. Thus, the attenuated localized N400 effect in older adults is more likely to reflect a broader functional reorganization of semantic processing rather than diminished contextual utilization or semantic deficits.

Following the N400, a later, frontotemporal response emerged between 400 – 800 ms in the younger group, showing a clear congruency effect opposite to the N400 effect (congruent > incongruent). This response was less pronounced in older adults, with significant age-related attenuation of the congruency effect in the temporal regions between 600 – 800 ms. Nonetheless, overall decodability of semantic congruency was high in both groups. Although this effect occurs in a time window often associated with late positivities, its direction is atypical for a conventional anomaly- or reanalysis-driven response. Late post-N400 responses have been linked to a range of processes, including prediction mismatch, plausibility or anomaly, reanalysis, and task- or decision-related processing (Brouwer et al., 2012; Hoshino and Thierry, 2012; Kim and Osterhout, 2005; Kutas and Federmeier, 2011; van de Meerendonk et al., 2009; Yang et al., 2019). As the participants performed an explicit semantic relatedness judgment on isolated word pairs, the observed congruent > incongruent effect may reflect the accumulation of semantic-match evidence used for the overt decision, similar to previous findings that semantically matching cross-modal stimuli elicit stronger neural responses than nonmatching stimuli (Laurienti et al., 2003): congruent targets provided positive evidence for a coherent prime–target relation, which could be read out by fronto-temporal decision mechanisms to support the explicit "related" response. The involvement of inferior and middle frontal regions is compatible with a transition from semantic access and integration to controlled semantic retrieval, selection, and decision-related processing (Badre and Wagner, 2007; Jackson, 2021; Thompson-Schill et al., 1997; Wagner et al., 2001). However, future studies are needed to test this interpretation directly by manipulating decision demands independently of semantic relatedness.

Overall, a distinct activation distribution across cortical regions was observed between younger and older adults, characterized by a shift from temporal to frontal regions and from left-lateralized to more bilateral processing in older adults. These findings align with previous fMRI findings on posterior–anterior shifts and reduced hemispheric asymmetry in aging (Cabeza, 2002; Davis et al., 2008; Hoffman and Morcom, 2018). Furthermore, frontal cortex follows a rostro–caudal gradient, with progressively anterior regions supporting more abstract and control-dependent processing (Badre et al., 2009; Badre and D'Esposito, 2007). This organization appears to be preserved in aging, although older adults tend to show stronger and more distributed activation as control demands increase (Yao and Hsieh, 2022). Thus, increased frontal and bilateral recruitment in older adults may reflect greater reliance on control-supported semantic processing. Similarly, decoding analyses revealed that successful congruency classifications relied predominantly on left anterior temporal regions in younger adults but more on frontal and bilateral regions in older adults. Spatially distributed representations in older participants appeared to be more readily captured by the classifier algorithm, resulting in higher decodability in the older group.

Successful classification of age groups based on evoked contrast responses peaked between 300 and 600 ms, with ROC-AUC values reaching up to.8, indicating strong discriminative power of the logistic regression models during this time interval. This period of maximal divergence in neural activity patterns between age groups, appears to mark a critical window for semantic processing, during which age-related changes are most pronounced. Notably, this interval spans both the N400 and late semantic effects. These findings align with a growing body of literature identifying mid-latency neural responses as particularly sensitive to cognitive aging (Federmeier et al., 2010; Federmeier and Kutas, 2005; Kemmotsu et al., 2012; Kutas and Iragui, 1998; Wlotko and Federmeier, 2012; Xu et al., 2017), demonstrating age-related neural reorganization and recruitment of alternative neural resources (Shafto and Tyler, 2014; Wlotko et al., 2010).

Given the older participants' faster response times and preserved verbal skills, the observed neural reorganization likely reflects age-related changes in the semantic network rather than semantic decline. Recent network-level accounts of aging point to an increased prominence of connector hubs in frontal and temporal regions (Martin et al., 2023) and a shift toward a more modular and sparser network organization (Cosgrove et al., 2023; Wulff et al., 2022). In line with broader views that aging is accompanied by increasing reliance on accumulated knowledge and experience (Spreng and Turner, 2019), we suggest that such network changes may support alternative routes to successful semantic processing.

4.3. Distinctive neural representations for related vs. unrelated words support semantic judgments

Higher decodability of semantic congruency was associated with faster semantic decisions across younger (200 – 800 ms) and older (400 – 600 ms) age groups, and this relationship did not differ significantly between age groups. The association between decodability and response time provides a functional link between neural organization and behavior: the neural differentiation between congruent and incongruent words, as reflected in high decoding performance, was coupled with the efficiency of semantic judgments in terms of response times. This is similar to the concept of distance-to-boundary models, where decision speed is assumed to depend on the distance between neural representations and the classifier boundary, such that stimuli producing more distinct neural representations will yield faster responses (Ashby and Maddox, 1994; Pike, 1973). Although these models were originally proposed to account for speed–accuracy tradeoffs in signal detection, the same principle has also been demonstrated using neural distances derived from MEG and fMRI data (Carlson et al., 2014; Grootswagers et al., 2018; Ritchie et al., 2015; Ritchie and de Beeck, 2019). Consistent with this framework, individual differences in decodability, reflecting more distinct and distributed semantic representations, were associated with more efficient semantic decisions in the present data. This implies that readable information in the brain may be used for behavior: the semantic system projects word meanings into separable activation patterns, which can be tapped into by downstream decision processes to speed responses. As decodability was higher and reaction times faster in the older than in the younger group, this further suggests that this semantic system is well preserved in healthy aging and may even benefit from semantic knowledge accumulated over the lifespan.

At the same time, efficient semantic decisions are not determined solely by the distinctiveness of neural representations. Contextual cues continued to facilitate processing, as shown by shorter reaction times for congruent than incongruent stimuli across both age groups, in line with previous psycholinguistic findings (Laver and Burke, 1993). While distance-to-boundary models can account for individual differences in overall reaction times, these results indicate that semantic decisions are jointly shaped by representational separability and contextual support.

4.4. Conclusion

Our results suggest that the apparent inconsistencies across earlier psycholinguistic and imaging studies on aging and semantic cognition are likely to reflect methodological differences rather than true contradictions. Our findings help reconcile these perspectives by demonstrating that they can be concurrently valid: while the behavioral performance remains intact in older individuals, the spatiotemporal dynamics of neural processing can be altered. Specifically, the reduced N400 congruency effects in older adults aligned with previous electrophysiological evidence of weakened semantic priming, while increased frontal and bilateral activation mirrored fMRI findings of large-scale neural reorganization. Temporal decoding was able to capture differences in neural patterns between age groups, and cortical relevance patterns derived from the decoder weights further mirrored source modelling results. Decoding performance was directly correlated with reaction time, demonstrating a relationship between neuronal response patterns and behavior: increased neural separation between semantic concepts, as indicated by higher decodability, was associated with rapid decision-making. Overall, our findings suggest that healthy aging is associated with a reconfiguration of neural systems that maintain semantic proficiency despite broader age-related cognitive changes. Further investigation into the mechanisms of neural plasticity in late adulthood may facilitate the development of individualized approaches for sustaining linguistic and conceptual vitality throughout life.

Author statement

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CRediT authorship contribution statement

Pietari Nurmi: Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Heidi Ala-Salomäki:** Writing – review & editing, Investigation. **Hanna Renvall:** Writing – review & editing, Supervision. **Mia Liljeström:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare no competing financial or non-financial interests.

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Data availability

The data cannot be publicly released due to Finnish data protection legislation. However, the data may be shared for research collaboration purposes subject to an amendment of the research ethics statement and a corresponding data transfer agreement. The analysis code can be shared upon request.

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