

Speech comprehension across time, space, frequency, and age: MEG-MVPA classification of intertrial phase coherence

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ABSTRACT

Language is a key part of human cognition, essential for our well-being at all stages of our lives. Whereas many neurocognitive abilities decline with age, for language the picture is much less clear, and how exactly speech comprehension changes with ageing is still unknown. To investigate this, we employed magnetoencephalography (MEG) and recorded neuromagnetic brain responses to auditory linguistic stimuli in healthy participants of younger and older age using a passive task-free paradigm and a range of different linguistic stimulus contrasts, which enabled us to assess neural processing of spoken language at multiple levels (lexical, semantic, morphosyntactic). Using machine learning-based classification algorithms to scrutinise intertrial phase coherence of MEG responses in cortical source space, we found that patterns of oscillatory neural activity diverged between younger and older participants across several frequency bands (alpha, beta, gamma) for all tested linguistic information types. The results suggest multiple age-related changes in the brain's neurolinguistic circuits, which may be due to both healthy ageing in general and compensatory processes in particular.

Credit statement

MJ: Data analysis, Conceptualisation, Methodology, Software, Original draft preparation, Revision. **RH:** Stimulus preparation, Data acquisition, Conceptualisation. **BUW:** Data analysis, Conceptualisation, Methodology, Writing, Revision. **AH:** Stimulus preparation, Conceptualisation, Writing, Revision. **YS:** Supervision, Conceptualisation, Writing, Revision, Funding acquisition.

1. Introduction

Language is a key part of the human cognitive inventory, acquired early in life and used until death. As we age, some cognitive abilities decline, which goes in parallel with several physical changes in the brain (Raz et al., 2005). However, people can normally understand language until the very end of their lifespan, and ageing comes with both negative (such as difficulties in name retrieval) and positive (increased vocabulary) alterations in language functions (Abrams and Farrell, 2011). But exactly how the language comprehension changes with age and what mechanisms ensure its resilience is still poorly understood. Another

reason why age-related dynamics in language functions are important is that several neurodegenerative diseases typically linked with older age (such as Alzheimer's or Parkinson's disease) lead to a cognitive decline. At the same time, cognitive decline is often correlated with age, and healthy ageing effects may thus be difficult to disentangle from pathological changes in patients. To understand the impact that a neurodegenerative disease has on the cognitive aspects of language comprehension, we first need to understand the normal ageing-related changes. Here, we address this question by investigating the impact of age on different types of linguistic information processing in the brain, namely the lexical (word storage), semantic (meaning), and syntactic (linguistic structure parsing) levels of spoken word comprehension.

Structurally, age-related brain changes mostly manifest as shrinkage across most types of brain tissue, including neocortical grey matter, hippocampus, and white matter tracts, affecting various parts of the left-lateralised language network (Davis et al., 2009; Pfefferbaum et al., 2000; Raz et al., 2005). However, these structural changes as such do not lead to a measurable loss in language comprehension (Agarwal et al., 2016), which raises the question of how the language function can resist obvious changes in its neuronal underpinnings. While it is fairly

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uncontroversial to suggest that some form of compensation must take place, it is important to specify what mechanisms underlie such compensatory changes that can keep the functional output the same in spite of neuroanatomical degradation.

A somewhat better described situation where compensatory neuro-linguistic processes are known to take place is during recovery and rehabilitation after brain injuries where core areas of the language system are damaged. Several lesion studies have reported an increase in the right hemisphere's activity after damage to the left-hemispheric language network (Blasi et al., 2002; Kiehl et al., 2016; Thiel et al., 2006; Tyler et al., 2010). This suggests that the right hemisphere can "step in" to help perform language comprehension if needed (although lesion studies by definition do not tell us about what happens in a healthy brain). Similar to these clinical findings, it has also been reported that there is an increase in right-hemispheric activity with normal ageing. For instance, Tyler et al. (2010a,b) argued that, with age, syntactic processing switches from a primarily left-hemispheric fronto-temporal system to a bilateral functional language network. Agarwal et al. (2016) reported that the language areas develop more bihemispheric functional connectivity with age, despite neuroanatomical losses. In another recent study, Gertel et al. (2020) reported a bilateral activation of frontal areas and precuneus in an older group compared to left-lateralised activity in younger individuals in a lexical task. Interestingly, this relative increase in right-hemispheric involvement does not seem to be at the expense of the left hemisphere, but rather reflects a more distributed activation. Still, the nature of this "redistribution" of functional activity remains obscure.

Language comprehension is a highly dynamic process unfolding on a millisecond scale, which is best addressed using time-resolved neuro-imaging methods, such as electro- or magnetoencephalography (EEG, MEG). Traditionally, neurolinguistic EEG/MEG studies have most often focussed on event-related potentials/fields (ERPs/ERFs; see, e.g., Friederici, 2002). In recent years, however, more studies have started to examine the neural oscillatory dynamics underpinning normal language processing. For instance, theta-oscillations (~4–6 Hz) have been shown to play a role in both acoustic processing and sentence parsing (see, e.g., Bastiaansen and Hagoort, 2006; Kösem and van Wassenhove, 2017; Luo and Poeppel, 2007). More importantly in the context of the present report, high-frequency oscillations have been related to different neuro-linguistic processes. Bastiaansen and Hagoort (2006) suggested that both beta (~15–25 Hz) and gamma (>30 Hz) bands are related to the unification of semantic and syntactic information. Towle et al. (2008), in turn, showed that power in the high gamma band (70–100 Hz) is elevated when hearing meaningful words compared to non-speech tones, linking it to lexical processing, while theta and gamma band activity is involved in the processing of the acoustic dynamics of the speech signal (Teng et al., 2017). These and many other studies have led to a more general suggestion that, while low frequencies reflect the analysis of acoustic features, specific linguistic representations are more reflected in a higher-frequency activity. Thus, the entirety of language comprehension is underpinned by an interplay between low- and high-frequency neural oscillations (Kösem and van Wassenhove, 2017). In sum, there is substantial evidence that the brain handles different linguistic information by engaging oscillatory activity at different frequencies, and multiple neurophysiological frequency bands are involved in the functioning of language processing networks in an interactive manner.

Generally, patterns of neural oscillations have been shown to change with age, including those not related to linguistic processing. For instance, using simple visual stimuli, Gaetz et al. (2012) showed that the peak frequency for gamma activity decreases with age. Furthermore, Ziegler et al. (2010) reported, using both real data and simulations, an increase in beta-band activity in the primary somatosensory cortex with age. Another study (Schafer et al., 2014) used spectral analysis of neural oscillations in resting state data to show that there is an increase in inter-regional amplitude correlations with age, largest in alpha and beta

frequency bands. Jointly, these and other results (obtained with non-linguistic paradigms, e.g., Gaetz et al., 2010, 2012; Herrmann et al., 2011) show an influence of age on oscillatory brain activity, even though the direction of those changes (i.e., increase or decrease) vary across individual frequency bands, while the mechanisms and the functional role of these changes still remain to be specified.

Given the link between oscillations and language processing on the one hand, and a change in oscillatory brain dynamics with age on the other one, one way to investigate age-related changes in language processing networks could be to address language-related neural oscillations in different age groups. This was the objective of the present study, where we used MEG to record automatic brain responses to different linguistic contrasts and subsequently applied source modelling and machine learning techniques to disentangle oscillatory signatures of different linguistic processing levels in younger and older participants.

One common issue when addressing neural processes in individuals with different cognitive or neurological status is the risk of potential confounds related to differences between tasks or groups in attentional levels, cognitive resources available for the task or motor vigilance in providing behavioural responses (Gansou et al., 2018). Thus, in order to investigate aspects of language comprehension in younger and older persons in the absence of such task/attention demands and related confounds, we devised a passive task that does not require any stimulus-related behavioural responses from the participants and that could be conducted without relying on any attentional resources. Passive tasks have been used successfully in many studies to show language processing without attention (e.g., Hyder et al., 2020, 2021; Mohr et al., 2016; Shtyrov, 2011; Shtyrov et al., 2008; Whiting et al., 2015; Pulvermüller et al., 2001). In the present MEG study, our participants were exposed to spoken words played over headphones while watching a film without sound, similar to previous studies on automatic language comprehension processes that did not require attention on the auditory input or any responses at all (Näätänen et al., 2007; Pulvermüller and Shtyrov, 2006; Shtyrov, 2010). This allowed us to investigate age-specific processes based on automatic responses to the same stimuli without attentional or motor requirements confounding the results. To assess the neural processing of different types of linguistic information, we used spoken stimuli that diverged lexically (real meaningful words vs. meaningless pseudo-words), semantically (action- vs. object-related), or morphosyntactically (grammatically correct vs. incorrect).

We have previously shown that oscillations linked to automatic processing of spoken words can be used to classify different types of linguistic information in the input (M. Jensen et al., 2019), where especially the phase of the oscillatory activity in several frequency bands allowed for successful decoding of language features. We found that this classification was most successful for lexical processing across several distinct gamma sub-bands, for semantic processing – in the alpha and beta bands, and for syntactic processing – in the low gamma band. Thus, to investigate age-related processing differences, we focused on analysing inter-trial phase coherence (ITPC) in five canonical frequency bands (alpha, beta, and low, medium, and high gamma), within two different age groups consisting of healthy younger and older participants. Further, for neuroanatomical localisation of the cortical oscillatory dynamics, we opted to compute the ITPC in source space using a cortically constrained linearly-constrained minimum variance (LCMV) beamformer (Van Veen et al., 1997), calculated using individual brain-based boundary element models (BEMs). We chose multivariate pattern analysis (MVPA) as our statistical approach since, compared to traditional frequentist statistics, it can handle large amounts of data and allows for unbiased data driven analysis without having to a priori specify either locations, time points, or frequency bands of interest.

In an exploratory manner, we employed this MVPA approach to decode different language properties over time in the individual frequency bands within the groups of younger and older participants. We hypothesised that we would find differences when comparing the decoding patterns of these two groups with respect to the relevant

frequency bands, time points, and brain areas. In light of the literature reviewed above, these differences might contain, but not be limited to, a shift in frequency and a change in latencies (e.g., a delayed lexical and semantic response with age), as well as a wider network of brain areas in the older as compared to the younger participants, including a shift from a more left-lateralised towards more bilateral activity. At higher bands in the gamma range, we might expect an age-related drop in frequency, whereas at the lower end of the scale, a shift towards more beta activity might take place, given this frequency's connection to cross-hemispheric transfer. The semantic contrast between action- and object-related words is likely to involve the known signatures of the motor system activity (including reduced activity for the action words, as the motor system is known to deteriorate with age) as opposed to the involvement of the ventral stream (e.g., occipitotemporal and anterior temporal areas) for the object-related words.

2. Methods

2.1. Participants

MEG data were acquired for two groups of participants, all right-handed (assessed according to Oldfield, 1971) healthy native Danish speakers with normal hearing and no record of neurological impairments: seventeen healthy younger participants (age range 18–27 years, mean age 23 years, 12 females) and sixteen older participants (age range 51–75 years, mean age 64 years, 11 females). All participants gave written consent and received remuneration for their participation. The experiment was approved by the Central Denmark Region Committees on Health Research Ethics and was conducted according to the principles of the Helsinki Declaration.

2.2. Stimuli

To address a range of different neurolinguistic processes at the lexical, semantic, and syntactic levels, we chose stimulus items which could enable us to contrast a combination of different linguistic phenomena while controlling for acoustic features (see Fig. 1 for examples of the stimuli used). To this end, we followed a previously suggested strategy (Gansonne et al., 2018) and selected a set of spoken Danish-language stimuli which (i) belonged to different lexical and semantic categories (action-related verb, abstract verb, object-related noun and meaningless pseudo-word), (ii) were close in terms of phonology so we could compare them directly with minimal acoustic/phonetic confounds, and

(iii) could be modified morpho-syntactically in the exact same way and nonetheless exhibit different syntactic properties (i.e., grammatically correct vs. incorrect) such that we could test the very same contrasts in different linguistic contexts in a counterbalanced fashion.

This led to a choice of four main base stimuli: *bide* ([bi:ðə], *to bite*), *gide* ([gi:ðə], *to bother*), *mide* ([mi:ðə], *a mite*), **nide* ([ni:ðə], **pseudo-word*). Note that these words have identical CVCV phonological structure and only differ in the first consonant. The second syllable [ðə], which allows recognition of the lexical items, was the same across all items, which was achieved by cross-splicing (see below). To ensure that the full recognition of each word form in the restricted experimental context is only possible at the second syllable, we also included, in a 1:1 ratio with all other stimuli, all four first syllables in isolation: [bi:], [gi:], [mi:] and [ni:]. These served as fillers to ensure identical acoustic divergence points across the four types of stimuli, to which we time-locked the brain activity for the main stimulus items, and were thus not analysed as such.

The above stimulus quadruplet provided us with a way to address both lexical and semantic contrasts. By estimating the brain activity elicited by the same word-final syllable [ðə], we could compare, on the one hand, word vs. meaningless pseudo-word activation, putatively indicating lexical access, which we expected to be reflected in an automatic activation of the core left temporo-frontal language system (Pulvermüller and Shtyrov, 2009; Tyler and Marslen-Wilson, 2008). On the other hand, by comparing action vs. non-action items, we could address semantically-specific aspects of these activations. Previous EEG, MEG and fMRI research has indicated automatic involvement of the brain's motor system in the comprehension of action-related verbs (Pulvermüller, 2005; Shtyrov et al., 2004, 2014; Pulvermüller and Fadiga, 2010); we therefore expected more pronounced centro-frontal activity for the action verb *bide*, but not for the concrete noun *mide*, which might be expected to activate object-related networks with more occipitotemporal distribution.

We produced, based on the forms above, further stimuli that included a balanced morphosyntactic contrast. We took advantage of Danish morphology and the fact that the morphemes *-(e)t* and *-(e)n* can be used to express the past participle of verbs and definiteness on common nouns. Hence, we compared the inflected items based on their syntactic congruence or incongruence, e.g. *-n* in *miden* vs. **giden*, and *-t* in *gidet* vs. **midet* (where * indicates a violation of the stem/affix syntactic agreement). Note that all of these pairs have identical codas (*t/n*) that lead to grammatical/morphosyntactic violation in a counterbalanced fashion: each of them is correct in combination with one but

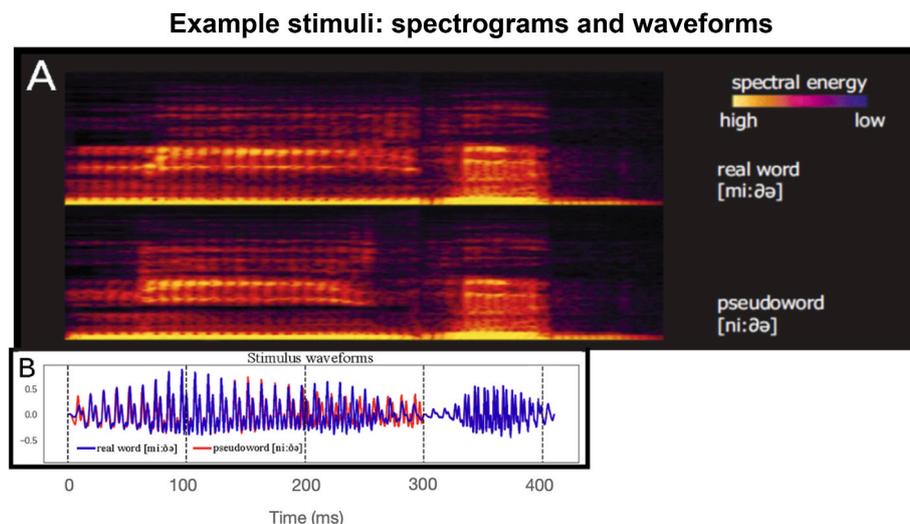


Fig. 1. A: Examples of spectrograms of spoken stimuli used in the experiment. B: Examples of waveforms plotted on top of each other. (Adapted from M. Jensen et al., 2019).

not with the other stem. These were presented, in equal proportion along with the other stimuli above, to make sure syntactic properties were only recognised at the very last consonant. To balance for these acoustic modifications, we also included similar items based on other forms (*bide[n/t] and *nide[n/t], all meaningless), which were used to make an acoustically balanced design, but not analysed as such.

The stimuli were made based on a digital recording of a male native speaker of Danish in an anechoic chamber (recording bandwidth: 44k Hz, 16bit, stereo). The first and second syllables of the four CVCV stimuli were recorded independently in order to avoid possible coarticulation effects and cross-spliced together such that the second syllables were physically identical across all items. The second syllable commenced at 300 ms after the onset of the first one, and this was the earliest time (the so-called disambiguation or divergence point, DP) when any lexical or semantic effects could be expected to commence in the MEG data.

To produce the morphosyntactic items ending in [t] or [n], we cross-spliced recordings of these two morphemes onto the four main stems in order to obtain words either violating or respecting Danish morphology rules such that the exact same phonemes completed syntactic or asyntactic forms in a counterbalanced fashion. These morphemes became distinct at 408 ms after the word onset, this point therefore being the earliest time any morphosyntactic contrasts could affect the brain responses.

The sounds were matched for loudness, with a 1.93 dB drop between the first and the second syllables so that our stimuli sounded as natural as possible, and were normalised to have identical power (measured as root-mean-square, RMS). All sound editing was done using Adobe Audition CS6 software (Adobe Inc., San Jose, CA).

To summarise, the stimulus set included four CV syllables, four CVCV stems, four CVCV+[t] and four CVCV+[n] forms, all strictly controlled for phonological and acoustic properties. These were combined in a pseudorandom fashion in a single auditory sequence ensuring that the stimuli's lexical, semantic and syntactic properties were available at stringently defined times.

2.3. Procedure

The MEG recording was conducted in an electromagnetically shielded and acoustically attenuated room (Vacuumschmelze GmbH, Hanau, Germany). During the recordings, participants were placed in supine position and instructed to focus on watching a silent film (displayed using a bespoke mirror system attached to the MEG dewar) and to pay no attention to the sound input. The auditory stimuli were controlled using Neurobehavioral Systems Presentation v16 (www.neurobs.com) and presented through in-ear-tubes (Etymotic ER-30) binaurally at 50 dB above individual auditory threshold.

All sixteen stimuli were presented equiprobably, inter-mixed in a single continuous data acquisition session, with 100 pseudo-random repetitions of each stimulus which resulted in 1600 epochs in total. The total recording time was 28 min, ensuring its ease for all participants regardless of their age.

MEG data were acquired with an Elekta Neuromag Triux MEG (MEGIN Oy, Helsinki, Finland) with 102 magnetometers and 204 planar gradiometers. For eye movement and heartbeat artefact detection, two bipolar electrooculogram (EOG) and one bipolar electrocardiogram (ECG) recordings were taken. Cardinal landmarks and additional head points were digitised using a Polhemus FASTRAK setup (Polhemus, Vermont, USA). Data were recorded at 1000 Hz, a high-pass filter of 0.1 Hz and low-pass of 330 Hz were applied online. Head position and head movements were continuously tracked using four Head Position Indicator (HPI) coils. The participants were lying still on a non-magnetic patient bed, with their head as close to the top of the helmet as possible, the MEG dewar being in supine position, and the display mirror fixed above the head.

2.4. MEG data preprocessing

All data were preprocessed using the MNE-Python open source software package, v. 0.19 (Gramfort et al., 2013). First, the raw continuous data were bandpass-filtered between 1 and 95 Hz, down-sampled to 500 Hz, and epoched into single-trial epochs of 1000-ms duration, starting 100 ms before and ending 900 ms after stimulus onset. Bad channels were detected automatically and interpolated using an automatic approach as integrated in the AutoReject package (Jas et al., 2017). This approach calculates an individual threshold for each channel independently. Epochs with excessive bad channels were discarded and outlier trials (e.g., due to eye blinks) removed. No other corrections for ocular artefacts were applied. For the younger group, there were on average 23.2 bad channels (median: 32, SD: 10.9) and 12.9 (SD: 18.7) bad epochs. For the older group, there were on average 2.6 bad channels (median: 2, SD: 1.6) and 8.8 (SD: 78.7) bad epochs. Finally, cleaned epoched data were bandpass-filtered into five frequency bands (Dalal et al., 2011): alpha (8–12 Hz), beta (13–30 Hz), low-gamma (30–45 Hz), medium-gamma (55–70 Hz) and high-gamma (70–90 Hz).

2.5. Source reconstruction

For each participant, a T1 structural magnetic-resonance image (MRI) was obtained using a Siemens Prisma 3T MRI scanner (Siemens Healthcare GmbH, Germany). The images were segmented in order to create surfaces for the inner skull using SimNIBS software (Thielscher et al., 2015). For each subject, an individual 1-layer boundary element model (BEM) and individual forward model were calculated. A common template grey matter surface was created by averaging all the study participants using the Freesurfer software (Dale et al., 1999).

Source reconstruction was carried out based on planar gradiometer data using a unit-noise-gain scalar LCMV beamformer (Van Veen et al., 1997) and a Hilbert transformation-based beamforming technique (Westner, 2017; Westner and Dalal, 2017). For the adaptive filter, source orientation was optimised by using the orientation of maximum signal power; the output value selected was the neural activity index (NAI, Sekihara and Nagarajan, 2008). The strategy of using only gradiometer data was chosen as planar gradiometers are less sensitive to external magnetic interference and have a better signal-to-noise ratio compared to magnetometers; furthermore, combining channel types is not trivial due to magnetometers and gradiometers producing values of different scales and units (Hari et al., 1988). The source reconstruction process was as follows. First, for each frequency band of interest (alpha, beta, low-gamma, medium-gamma, and high-gamma), the epochs were bandpass-filtered for each subject without subtracting the evoked signal from the single trials, as we were interested in investigating the complete information in the responses time-locked to the auditory stimuli. Second, an adaptive filter was created by combining responses to all the stimuli in the paradigm using a 1-layer BEM and a cortically constrained source space. The adaptive filter was computed using a data covariance matrix based on all time points of the bandpass-filtered epochs; the covariance matrix was not regularised prior to inversion. Third, after the adaptive filters were created, the single-trial epoched data were Hilbert-transformed and the adaptive filter was applied to the complex Hilbert-transformed data providing a source reconstruction for each single trial. Last, we calculated the intertrial phase coherence (ITPC) of the obtained single-trial source space data. This was done for each time point and in each source space location independently using the equation below:

$$ITPC_{tf} = \left| n^{-1} \sum_{r=1}^n e^{ik_{tr}} \right|,$$

where n is the number of trials, e^{ik} provides a complex polar representation of the phase angle k on trial r for the time-frequency point tf where

frequency is the frequency band (for a review, see Cohen, 2014, Chapter 19, esp. pp. 244–245). This resulted in a single ITPC time course for each frequency band and source point for each subject.

After the source-space ITPC data were calculated for each subject, the individual data were morphed onto the common template surface (5124 vertices). Finally, the data were smoothed with a 10-ms rolling windowed mean in the temporal dimension for each source independently.

2.6. Multivariate pattern analysis

For each participant, the morphed ITPC time series per source point was extracted based on the contrast in question. Common to all the multivariate pattern analyses (MVPA) implemented for the different contrasts was the strategy of classification over time. For each time sample independently, a classifier pipeline was applied providing a classification score for this sample. Moving sample by sample, we created a classification score over time. We used the entire cortical source space as input for the classification at each time sample, providing 5124 features per time sample.

The classifier pipeline was constructed in MNE-Python using scikit-learn (Pedregosa et al., 2011) and composed of three steps. First, the features were standardised (z-scored), which was done across all vertices in the source space at each time sample independently using the training set and then applied to the test set. Second, the best 1024 features were selected using F-values (implemented in scikit-learn's SelectKBest algorithm)¹. Last, a logistic regression ($C = 1$, L-BFGS solver, number of max iterations = 1000) was used to classify the two contrasts, and the receiver operating characteristic area under the curve (ROC-AUC) was used as the classification score. This pipeline was applied across subjects. This was done in order to avoid overfitting of the MVPA models. We used cross-validation where we created a training set of all the subjects except one and then used the left-out participant for testing the model (called leave-one-subject-out; see Varoquaux et al., 2017 for details and strategies for cross-validating brain imaging data). This was done iteratively across participants, until all subjects had been used as a testing set once. In the end, we obtained one ROC-AUC score for each participant. The presented classification score is the average of the ROC-AUC across all participants.

This pipeline was repeated for both groups and each frequency band within each linguistic condition independently, resulting in an average ROC-AUC score for each band and contrast for each group. To assess the statistical significance of the classification, we opted for a two-step approach. In the first step, we calculated the threshold for a significant binomial test based on the number of participants and stimuli following Combrisson and Jerbi (2015). In the second step, we corrected for multiple comparisons using a cluster-based approach; based on previous literature (Edmonds and Krumbholz, 2014; Hagoort and Brown, 2000; Wang et al., 2012), we deployed a threshold of 10 ms such that only clusters lasting 10 ms or longer were considered of interest. (For example, in Table 1 we report for the older group that there is a significant cluster in the beta band from 266 ms until 280 ms after divergence point; for that cluster the maximum ROC-AUC score is 78.12 with a standard deviation of 3.99 across subjects, the mean ROC-AUC score for the entire cluster is 72.77 (SD: 3.99). In other words, we find consecutive times when the classification score is above the threshold calculated from the binomial test (Combrisson and Jerbi, 2015)).

The linguistic contrasts that we tested for within groups were: (1) *lexical contrast*: real words (bide, gide, mide) vs. meaningless pseudo-word (nide); (2) *semantic contrast*: action verb (bide) vs. object-related noun (mide); (3) *syntactical contrast*: gidet, miden vs. *midet, *giden; the latter two violate the stem-affix syntactic agreement, whereas the

former two are syntactically correct forms.

3. Results

3.1. Lexical contrast

In the lexical contrast, we found that we could successfully classify real words vs. pseudo-words for both the younger and the older groups. The times and frequency bands of successful classification, however, varied for the two groups. Decoding clusters in both groups encompassed both the left and the right hemispheres. The **highest ROC-AUC score** for the **younger group** was 81.58% (SD: 5.00) in the **medium-gamma** band in a time-cluster at 74–100 ms after the divergence point. For the **older group**, it was 78.12% (SD: 3.44) in the **medium-gamma** band in a time-cluster at 276–294 ms after the divergence point.

Frequency bands. For the **younger group** we obtained significant classification in the alpha, medium-gamma, and high-gamma bands in seven different time-clusters (see Table 1); in the **older group**, we obtained significant classification in the beta and medium-gamma bands with two different time-clusters.

Time. The earliest time point of decoding was for the **younger group** in the high-gamma already at 48 ms after the divergence point. For the **older group**, the earliest decoding point was in the beta band at 266 ms after the divergence point (see Table 1 and Fig. 2 for an overview).

Brain areas. Inspection of the left-hemispheric source space patterns in the time-cluster with the peak ROC-AUC score for the **younger group** showed a pattern of activity predicting the real words in Brodmann areas (BA) 39, 40, 41, 44 as well as BA 1, 4, 6 and 7. In the right hemisphere, we found patterns predicting the real words in BAs 21–22, 39 as well as 6 and 8, with a small cluster in BA 6 predicting the pseudo-word. For the other, less prominent time-clusters, we found mostly bilateral patterns that predicted both the real words and the pseudo-word. For the **older group**, the patterns in the cluster with the peak ROC-AUC score in the left hemisphere showed smaller patterns of activity, which could predict the real words, in BA 21–22, as well as 3 and 6. There were also smaller patterns predicting the pseudo-word in BA 38, 39, 46 as well as 2, 3, and 11. In the right hemisphere, we found patterns predicting the real words in BA 6, 8, 19 and BA 43. Predicting the pseudo-word were right-hemispheric patterns in BA 22, 39, 40, 46 as well as 1, 2, 3, and 11.

3.2. Semantic contrast

For the semantic contrast, we could successfully classify action verb vs. object noun for both groups. Again, the times and frequency bands of successful classification varied. The **highest ROC-AUC score** for the **younger group** was 78.95% (SD: 4.73) in the **beta** band in the time-cluster at 142–158 ms after the divergence point. For the **older group**, it was 79.41% (SD: 1.96) in the **alpha** band in the 192–226 ms cluster.

Frequency bands. For the **younger group**, we found significant classification in the beta and medium-gamma bands in two different time-clusters, while in the **older group** five different time-clusters were found in the alpha and medium-gamma bands.

Time. The first time point of decoding for the **younger group** was in the beta band at 142 ms after the divergence point, while for the **older group** it was in the alpha band at 154 ms after the divergence point (see Table 2 and Fig. 3 for an overview).

Brain areas. Inspecting the patterns from the time-cluster with the peak ROC-AUC score in the left hemisphere for the **younger group** showed a pattern with activity predicting the action verb in a large set of areas: BA 6, 44, 20, BA 22 and 40, and BA 37. In the right hemisphere, we also found patterns predicting the action verb in sensorimotor areas: BA 2, 4 and 6; the patterns predicting the object noun was, in turn, found in inferior-temporal cortex (fusiform gyrus, BA 37). Also, a small medium-gamma cluster in BA 22 predicting the action verb and another one in BA 10 predicting the object noun, were found. In the right

¹ The number of features was selected through a grid search between 512, 1024, and 2048 features at a single time point.

Table 1

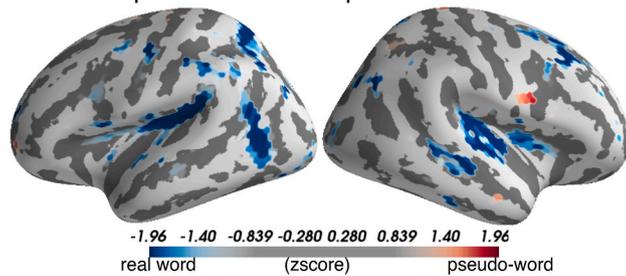
Summary of significant clusters in the lexical condition. *Cluster start* is the start time of the cluster from divergence point (DP) and *cluster end* is the end time of the cluster from DP, in milliseconds. *Cluster max* is the highest ROC-AUC score within the cluster. *Cluster mean ROC-AUC* is the mean ROC-AUC score of the cluster. The *cluster ROC-AUC SD* is the standard deviation of the cluster mean across cross-validation folds.

Older group					
frequency band	cluster start (ms)	cluster end (ms)	cluster max (ms)	cluster mean ROC-AUC	cluster ROC-AUC SD
beta	266	280	78.12	72.77	3.99
medium-gamma	276	294	78.12	71.53	3.44
Younger group					
frequency band	cluster start	cluster end	cluster max	cluster mean ROC-AUC	cluster ROC-AUC SD
high-gamma	48	64	76.32	70.39	3.66
medium-gamma	74	100	81.58	73.89	5.00
high-gamma	196	214	78.95	74.56	4.64
alpha	230	242	68.42	67.98	0.98
alpha	246	258	71.05	67.98	2.36
medium-gamma	274	288	78.95	72.93	3.91
alpha	412	424	68.42	67.98	0.98

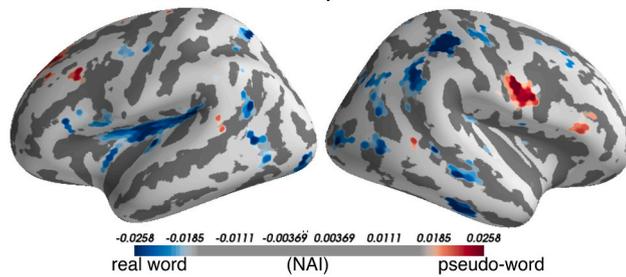
Lexical condition

Younger group, medium gamma, 74-100 ms

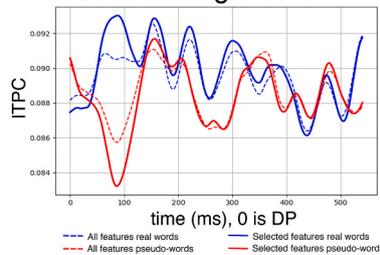
A Model patterns: real vs. pseudo-words



B ITPC contrast: real vs. pseudo-words

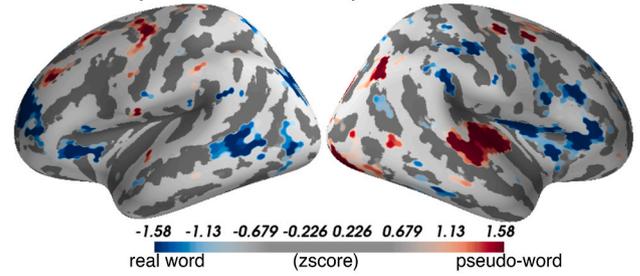


C Time course of average ITPC

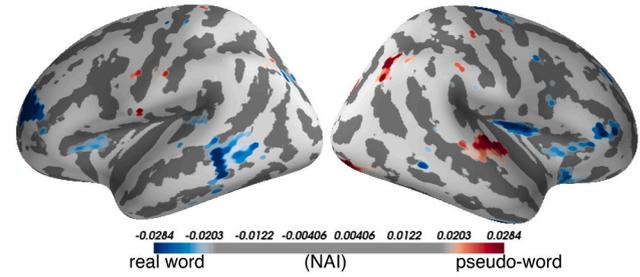


Older group, medium gamma, 276-294 ms

D Model patterns: real vs. pseudo-words



E ITPC contrast: real vs. pseudo-words



F Time course of average ITPC

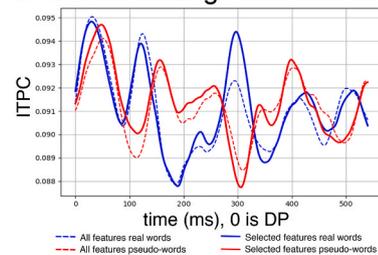


Fig. 2. Lexical condition: model patterns, ITPC contrasts and time courses. **Left:** results from the younger group. **Right:** results from the older group. **A:** Model patterns; in order to interpret the coefficients of the machine learning model we use model patterns (for details, see Haufe et al., 2014). We show the top and bottom 5% of the patterns in the medium-gamma band, from 74 to 100 ms after the divergence point for the younger group. Blue colours are areas of activation that predict real words, and red are areas used to predict pseudo-words. **B:** Average top and bottom 5% of intertrial phase coherence (ITPC) differences; blue colours indicate higher ITPC for real words and red colours indicate higher ITPC for the pseudo-word for the medium-gamma band from 74 to 100 ms. **C:** Average ITPC over time; solid lines are the average of the selected features, dashed lines are the average of all vertices in the source space. Time 0 is the divergence point when stimuli could be distinguished from the available acoustic information. **D:** Like A, but showing the model patterns in the medium-gamma band, from 276 to 294 ms in the older group. **E:** Like B, but depicting the ITPC from 276 to 294 ms in the older group. **F:** Like C, depicting average ITPC over time, but for the older group. Note that all time points are expressed relative to the divergence point (0 ms).

Table 2

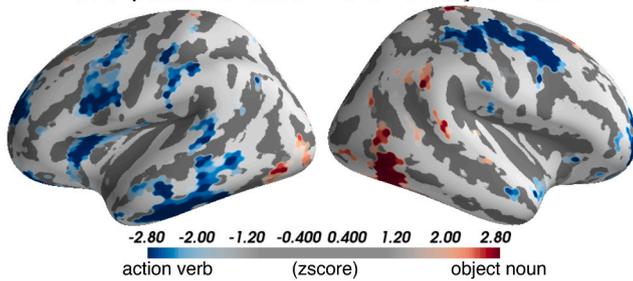
Significant clusters in the semantic condition. *Cluster start* is the start time of the cluster from divergence point (DP) and *cluster end* is the end time of the cluster from DP, in milliseconds. *Cluster max* is the highest ROC-AUC score within the cluster. *Cluster mean ROC-AUC* is the mean ROC-AUC score of the cluster. *Cluster ROC-AUC SD* is the standard deviation of the cluster mean across cross-validation folds.

Older group					
frequency band	cluster start (ms)	cluster end (ms)	cluster max (ms)	cluster mean ROC-AUC	cluster ROC-AUC SD
alpha	154	170	73.53	71.32	1.95
alpha	192	226	76.47	73.18	2.45
medium-gamma	256	276	79.41	72.65	3.73
alpha	382	414	79.41	75.37	3.10
medium-gamma	464	476	76.47	72.55	2.77
Younger group					
frequency band	cluster start (ms)	cluster end (ms)	cluster max (ms)	cluster mean ROC-AUC	cluster ROC-AUC SD
beta	142	158	78.95	74.34	3.89
medium-gamma	486	498	71.05	70.18	1.96

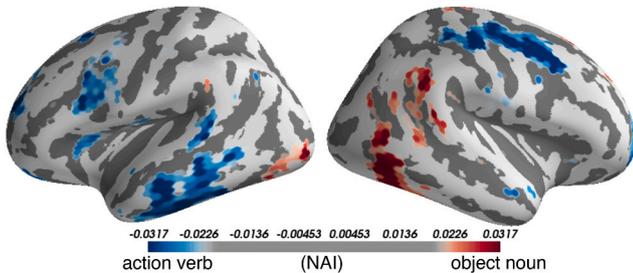
Semantic condition

Younger group, beta, 142-158 ms

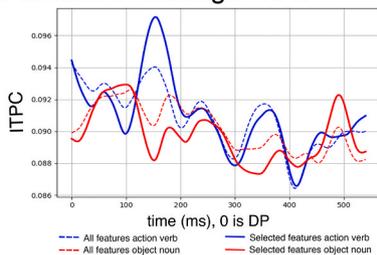
A Model patterns: action verb vs. object noun



B ITPC contrast: action verb vs. object noun

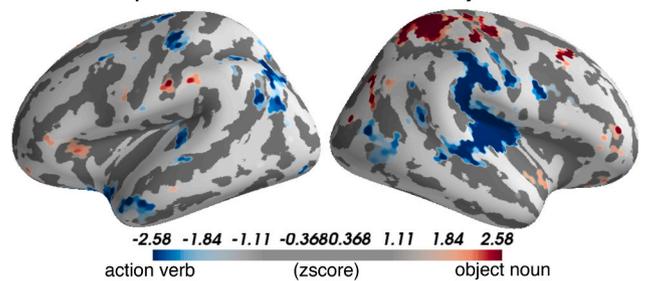


C Time course of average ITPC

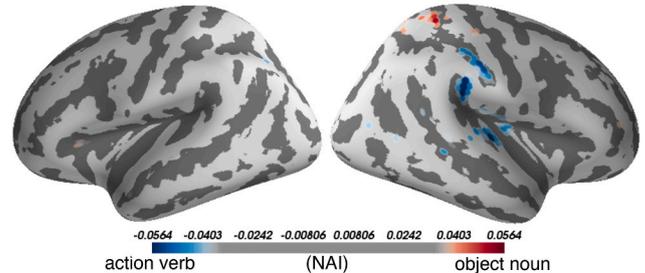


Older group, alpha, 382-414 ms

D Model patterns: action verb vs. object noun



E ITPC contrast: action verb vs. object noun



F Time course of average ITPC

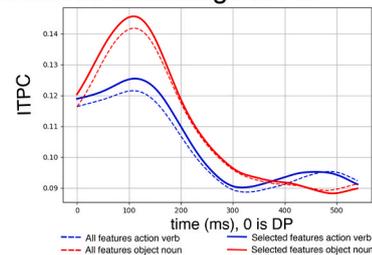


Fig. 3. Semantic condition: model patterns, ITPC contrasts and time courses. **Left:** younger group. **Right:** older group. **A:** Model patterns (see also Fig. 2 legend): top and bottom 5% of the patterns in the beta band from 142 to 158 ms in the younger group. Blue colours are areas used to predict the action verb, and red are areas used to predict the object noun. **B:** Average top and bottom 5% of ITPC differences, blue colours showing higher ITPC for the action verb and red indicating higher ITPC for the object noun for the beta band from 142 to 158 ms in the younger group. **C:** Average ITPC over time, solid lines are the average of the selected features, dashed lines are the average of all vertices in the source space. Time 0 is the divergence point when stimuli could be recognised from the available acoustic information. **D:** Like A, but showing the model patterns in the alpha band from 382 to 414 ms in the older group. **E:** Like B, but depicting the ITPC for the alpha band from 382 to 414 ms in the older group. **F:** Like C, but for the older group.

hemisphere, object noun-predicting clusters were located in BA 44, 4, 6. For the **older group**, the patterns from the time-cluster with the peak ROC-AUC score in the left hemisphere showed activity predicting the

object noun in temporal areas BA 22, 37 and 38. In the right hemisphere, a cluster predicting the object noun was at the temporo-parietal junction (TPJ; BA 39).

3.3. Morphosyntactic contrast

We could successfully classify correct vs. incorrect morphosyntax for both groups. As with the lexical and semantic contrasts, the times and frequency bands of successful classification varied between the two groups. The **highest ROC-AUC score** for the **younger group** was 65.79% (SD: 2.63) in the **alpha** band in a time-cluster at 412–424 ms after the divergence point. For the **older group**, it was 72.06% (SD: 1.71) in the **beta** band in the 148–158 ms time-cluster.

Frequency bands. For the **younger group**, significant classification was achieved in the alpha and high-gamma bands in two different time-clusters; in the **older group**, it was achieved in the beta and high-gamma bands in four different time-clusters.

Time. The earliest time point of successful decoding was for the **younger group** in the beta band at 346 ms after the divergence point, whereas in the **older group** it was at 104 ms in the alpha band (see Table 3 and Fig. 4).

Brain areas. The time-cluster with the peak ROC-AUC score for the alpha band in the **younger group** showed a pattern in the left hemisphere with activity predicting incorrect morphosyntax in BA 22, BA 39, BA 40, and BA 42; BA 20, BA 22 and BA 40, and BA 37. In the right hemisphere, we found patterns predicting the incorrect morphosyntax in BA 22 and BA 7, and a pattern predicting correct morphosyntax in BA 22 and BA 39. For the high-gamma, we found a smaller cluster in the left-hemispheric TPJ (BA 39) predicting correct morphosyntax, and some smaller left-hemispheric clusters in BA 1–2 and 4 predicting incorrect morphosyntax. In the right hemisphere, we found high-gamma clusters in BA 7 predicting incorrect morphosyntax and BA 44 predicting correct morphosyntax. For the **older group**, the peak ROC-AUC score showed a cluster in the left hemisphere predicting correct morphosyntax, distributed across the BA 10, BA 39, BA 44, and BA 46. In the right hemisphere, there was a cluster predicting incorrect morphosyntax in the BA 39 and BA19.

4. Discussion

We aimed at investigating the brain's automatic speech comprehension processes in healthy individuals of different ages at lexical, semantic, and morphosyntactic levels by scrutinising oscillatory brain activity elicited by spoken words in different frequency bands. By using a beamformer source reconstruction and calculating ITPC for each point in source space for each word independently, we first combined the different words into contrasts, one for each linguistic level (i.e., lexical, semantic, and morphosyntactic). We then proceeded to classify these contrasts in each of the five pre-defined frequency bands for both the younger and the older group. As a result, we could successfully classify the different language processes, and found different time courses across the frequency bands, in line with previous research (M. Jensen et al., 2019). Crucially, the classification features diverged not only between the linguistic contrasts but also between the age groups. In line with the global hypothesis of our investigation, these differences encompassed frequency, time, and space. In the following, we will discuss these findings in more detail, grouped by linguistic contrasts.

4.1. Lexical processing

For the lexical condition, we found that the younger group had the fastest response differentiating meaningful vs. meaningless items starting already at ~50 ms after the divergence point and peaking at ~70–100 ms. This is in line with some of the earliest lexical effects

reported previously for unattended spoken words and pseudo-words (MacGregor et al., 2012; Shtyrov and Lenzen, 2017). Importantly, unlike these ERP/ERF-based findings, the lexicality effects in the present study were found in oscillatory signal, predominantly in the gamma range². Previously, gamma-band activity has been linked to lexical processing (Towle et al., 2008; Tavabi et al., 2011; Chrabaszcz et al., 2021) which aligns with our findings of significant clusters in the gamma bands: for the younger group in both medium-gamma and high-gamma band within the first 100 ms after the divergence point, and for the older group in the medium-gamma band (although later, at about 280 ms). Gamma-band activity at ~50 ms was also suggested to reflect the rapid processing of native speech sounds (Palva et al., 2002), which, in combination with the present results, suggests a certain parallelism in early phonological and lexical processes. The lack of expressed high-gamma effects in the older participants might be due (at least in part) to a gradual decrease in gamma peak frequency which takes place with age (Gaetz et al., 2012). However, we still found high-gamma dynamics for the morphosyntactic contrast (see below), implying that at least for the present sample the lack of lexical high-gamma effects cannot be explained by the mere absence of activity in this band. Furthermore, given the relative preservation of semantic effects at ~150 ms (see below) and a syntactic response in the older group from already ~100 ms, it seems unlikely that the lexical processing was postponed by as much as over 200 ms. A potential explanation could be a larger temporal variance across participants of different ages for this specific contrast, which, along with some drop in signal power, may have led to the loss of significant findings. This, however, cannot be verified based on the present data and needs further investigations.

At lower frequencies, the younger group had two alpha-band clusters (at ~230–260 ms), while the older group showed significant beta-band effects at a similar, albeit slightly later latency (266–280 ms). This frequency shift aligns well with the suggestion that an increase in beta band activity is related to cross-hemispheric connectivity (Schafer et al., 2014; Ziegler et al., 2010), which, in turn, may be involved in ageing-related compensatory processes, whereby right hemisphere putatively becomes increasingly involved in previously left-dominant function (Agarwal et al., 2016; Blasi et al., 2002; Manenti et al., 2013). More generally, both alpha and beta modulations have been found in lexical tasks (e.g., Bakker et al., 2015; Chrabaszcz et al., 2021; Krause et al., 2006), although the evidence of their specificity to language is limited. In its turn, the ageing-related beta increase is also not specific to language and can, e.g., be found in the motor system (Rossiter et al., 2014). On the other hand, a drop in beta-band with ageing has also been reported for tasks requiring alertness (Gola et al., 2012), which is, however, not the case of the presently used passive paradigm. Crucially, both of these bands have been linked to cortical excitation-inhibition balance (O. Jensen et al., 2005; Klimesch et al., 2007), which is also known to undergo age-related changes (Legon et al., 2016; Rossiter et al., 2014), potentially linked to changes in the GABA and glutamate regulatory systems (Huang et al., 2017). The exact mechanisms connecting excitation-inhibition balance and EEG/MEG dynamics are still unknown (Ulanov and Shtyrov, 2022), and more studies are needed to understand how their changes with ageing may be linked to language comprehension.

Of particular note here is the divergence in the temporal dynamics of neural processes between the groups. The late (~300 ms) medium-gamma lexical effect in the older adults is not unusual on its own, with similar latencies previously reported for lexicality processing in younger adults' gamma oscillations (Tavabi et al., 2011; van Ackeren et al., 2014), also visible in the present ITPC dynamics (Fig. 2). The lack

² Although some oscillatory dynamics can also reflect or be influenced by slower ERP/ERF phenomena (and vice versa), this confound does not apply to all frequency bands equally, and rather concerns frequencies lower than the medium and high gamma bands here.

Table 3

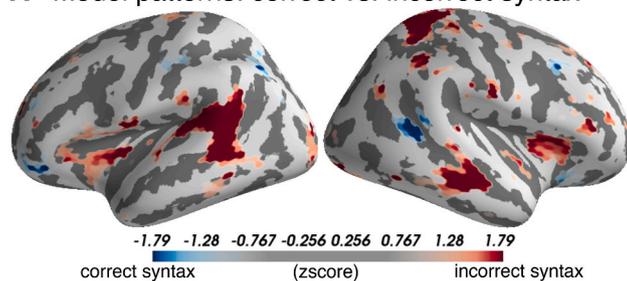
Significant clusters in the morphosyntactic condition. *Cluster start* is the start time of the cluster from divergence point (DP) and *cluster end* is the end time of the cluster from DP, in milliseconds. *Cluster max* is the highest ROC-AUC score within the cluster. *Cluster mean ROC-AUC* is the mean ROC-AUC score of the cluster. *Cluster ROC-AUC SD* is the standard deviation of the cluster mean across cross-validation folds.

Older group					
frequency band	cluster start (ms)	cluster end (ms)	cluster max (ms)	cluster mean ROC-AUC	cluster ROC-AUC SD
beta	104	124	72.06	67.94	4.45
beta	148	158	72.06	68.82	1.71
high-gamma	256	270	70.59	62.61	4.37
beta	430	440	67.65	65	3.14
Younger group					
frequency band	cluster start (ms)	cluster end (ms)	cluster max (ms)	cluster mean ROC-AUC	cluster ROC-AUC SD
high-gamma	346	356	64.47	51.84	10.08
alpha	412	424	65.79	61.84	2.63

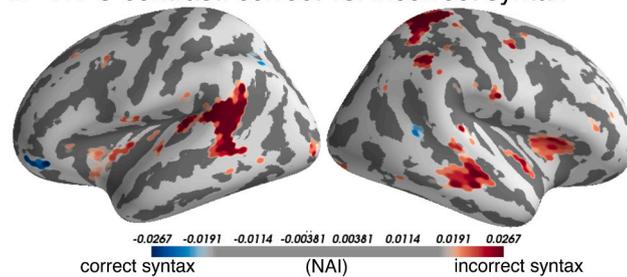
Morphosyntactic condition

Younger group, alpha, 412-424 ms

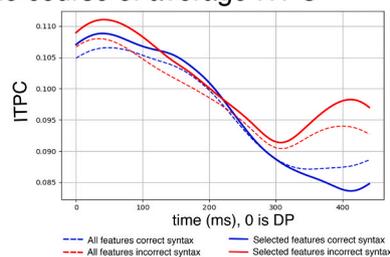
A Model patterns: correct vs. incorrect syntax



B ITPC contrast: correct vs. incorrect syntax

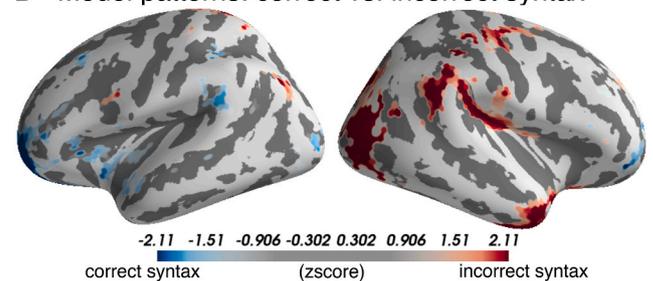


C Time course of average ITPC

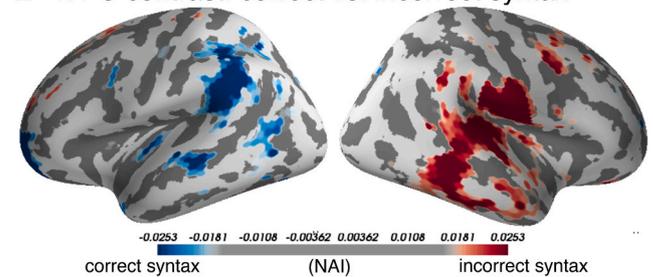


Older group, beta, 148-158 ms

D Model patterns: correct vs. incorrect syntax



E ITPC contrast: correct vs. incorrect syntax



F Time course of average ITPC

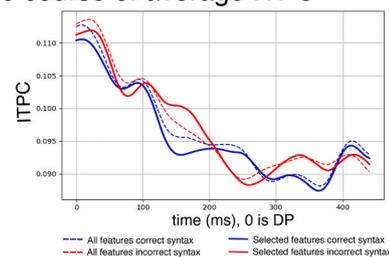


Fig. 4. Morphosyntactic condition: model patterns, ITPC contrasts and time courses. **Left:** younger group. **Right:** older group. **A:** Model patterns (see also Fig. 2 legend): top and bottom 5% of the patterns in the alpha band, from 412 to 424 ms in the younger group. Blue colours are areas used to predict correct syntax, and red are areas used to predict incorrect syntax. **B:** Average top and bottom 5% of ITPC differences, blue colours showing higher ITPC for correct syntax and yellow/red showing higher ITPC for incorrect syntax from 412 to 424 ms in the younger group. **C:** Average ITPC over time, solid lines are the average of the selected features, dashed lines are the average of all vertices in the source space. Time 0 is the divergence point when stimuli could be recognised from the available acoustic information. **D:** Like A, but showing the model patterns in the beta band, from 148 to 158 ms in the older group. **E:** Like B, but depicting the ITPC for the beta band from 148 to 158 ms in the older group. **F:** Like C, but for the older group.

of early activity before 100 ms (present in the younger sample) in the older group, on the other hand, does suggest a certain delay at least in the initial automatic stage of lexical parsing. This is further supported by

a minor latency increment found in lower frequency ranges (alpha/beta) at a later time. Based on the idea of an increased compensatory involvement or the right-hemisphere with age (Agarwal et al., 2016;

Gertel et al., 2020; Tyler et al., 2010a,b), a cautious proposition could be that more cross-hemispheric activity needs more time to transmit and to synchronise information across the more distributed bilateral network, which may contribute to the later onset of significant effects in the older group. Neuroanatomically, we found the lexical contrast to show bilateral patterns, involving the temporo-frontal language system as well as other, more distributed areas. Interestingly, whereas in the younger participants the number of areas with clusters predicting real word was eight in the left hemisphere vs. five in the right one, in the older subjects this ratio was four vs. four, potentially supporting the laterality shift hypothesis. (However, when interpreting these patterns, it is important to keep in mind that they demonstrate the most successful classification which does not necessarily correspond to the strongest activity in absolute terms).

4.2. Semantic processing

In the semantic condition, as in the lexical one, we found patterns diverging in both time and frequency between the two groups. The earliest successful decoding was for the younger group in the beta band at ~142 ms, as opposed to 154 ms for the older group in the alpha band. The overall highest ROC-AUC score was for the younger group; it was higher in frequency and earlier (~150 ms; beta) than for the older group (~200 ms; alpha).

Furthermore, the patterns from the classifiers also differed in other aspects. For the younger group, most of the features in the beta band predicted the action verb with activity in both hemispheres in both precentral motor (BAs 4 and 6) and inferior-frontal language-related (BA 44) areas. In contrast, the patterns of the older group were first predictive of the object noun in the alpha band, and only much later of the action verb in the medium-gamma band. Furthermore, the activity used for the prediction of the action verb was mainly found in the right hemisphere for the older group, which may imply a cross-hemispheric compensation involving cortical redistribution of semantic information processing.

The timing of the earliest effects was approximately the same for both groups, implying certain robustness of this level of processing, in line with the general view of language's resilience towards ageing (Abrams and Farrell, 2011). Interestingly, this activity, at least in the younger controls, was later than the earliest lexical classification, which may entail a certain delay between lexical identification and semantic classification of word forms (Friederici, 2002). Crucially, whereas the younger group's decoding patterns were mostly expressed in the beta band, the patterns for the older group were expressed in the alpha range instead. Whereas one might speculate that the lower-frequency might be due to an age-related decrease in peak frequency (Gola et al., 2012), this would contradict the explanation we put forward for the opposite shift in the lexical contrast above. Indeed, an increase in beta with age has been reported (Gaetz et al., 2010; Ziegler et al., 2010), which, as discussed, may in part be related to cross-hemispheric transfer. In principle, it could also represent an increased inter-regional (rather than cross-hemispheric) amplitude correlation known to involve the alpha band (Schafer et al., 2014); however, the number of areas involved in this contrast was comparatively low in the older group (with only one in the right hemisphere), which makes these explanations less likely.

Notably, the specific contrast here involved the action word vs. object word, which may be at the root of this divergence. Whereas semantic activity in the beta band in the younger group is in line with previously reported findings for word processing in general (Bastiaansen and Hagoort, 2006; M. Jensen et al., 2019), more interestingly, beta-band activity in the motor system has been linked to both motor control and the processing of movement-related words (O. Jensen et al., 2014; Vukovic and Shtyrov, 2014). The latter is in line with the view of motor cortex involvement in processing action-related language (Pulvermüller et al., 2005; Pulvermüller and Fadiga, 2010; Shtyrov et al., 2004, 2014) and embodied/grounded cognition frameworks in general

(Barsalou, 2008). Thus, the beta-range finding in the younger group for this stimulus contrast is more likely related to the motor semantics specifically than to a generic lexico-semantic processing. The motor system, in turn, is well-known to deteriorate with age (Seidler et al., 2010), which may explain the lack of similar beta band activity in the older group. This explanation is further supported by the more successful classification for the visually related object noun. The latter was in the alpha band, which, in turn, is heavily engaged in visual information processing (e.g., O. Jensen and Mazaheri, 2010). Indeed, these patterns here involved, among others, occipitotemporal areas (BA37), part of the object-recognition network (Stewart et al., 2001), as well as classical language-processing areas in the temporal lobe, including, importantly, the anterior-temporal cortex, argued to be the hub of lexical semantics (Lambon Ralph and Patterson, 2008). Whereas this explanation aligns well with the framework of distributed modality-specific neural circuits acting as word memory traces, it remains tentative, and further research is needed to address the observed divergence in temporo-spectral dynamics of these semantic effects, as well as their neuroanatomical underpinnings.

In addition to these lower frequencies, both groups also exhibited responses in the medium-gamma band, which have been linked to semantic processing in previous studies (Bastiaansen and Hagoort, 2006; Lam et al., 2016; Levy et al., 2014). However, this semantic aspect of gamma dynamics is most often linked to semantic processing in context, such as sentence comprehension (Hald et al., 2006; Penolazzi et al., 2009). Furthermore, Wang et al. (2012a,b) reported an increase in gamma power tied to the predictability of a word rather than semantic integration. Thus, the present relatively modest gamma-band effect for the semantic contrast might be explained by the lack of contextual information and a randomised stimulus presentation design with very low predictability of the stimuli. Given the gamma-band known involvement at different neurolinguistic processing levels, further research in its role in automatic semantic processes (including contextual and pragmatic levels, not addressed in the present study) appear warranted.

4.3. Morphosyntactic processing

For the morphosyntactic condition, we were able to successfully classify correct vs. incorrect morphosyntax for both groups. The findings in the two groups again diverged, although with a pattern different from the previous two contrasts, which is in line with the general concept of syntax and lexical semantics being underpinned by distinct neurolinguistic systems (Friederici, 2002, 2012; Shtyrov, 2010; Ullman, 2001).

Both the younger and the older groups showed activity in the high-gamma band. Previously, gamma band power has been suggested to reflect temporal binding in language processing (Peña and Melloni, 2012). More specifically, sentence-level syntactic binding has previously been reported to be linked to low gamma-band activity (Weiss et al., 2005) as well as beta-band synchrony (Wang et al., 2012), with both bands putatively related to working memory (Lundqvist et al., 2016, 2018) that must be involved in binding temporally distant elements together. The present high-gamma effect, however, cannot be explained by sentence-level binding due to the single-word nature of our stimuli presented outside of any sentences and the unattended nature of the paradigm. Little evidence is available on gamma's involvement in morphology, particularly regarding the oscillatory dynamics for morphosyntactically correct vs. incorrect complex words. Still, considering a degree of similarity between sentence-level and morphosyntactic word-level structural dependencies, it stands to reason that the present effects may be related to the more local binding processes in word parsing. Indeed, morphologically well-formed complex words have been shown to engage a distributed gamma-band network involving left temporal and (bilateral) inferior frontal regions (Fonteneau et al., 2015), suggesting that temporo-frontal cortico-cortical interactions underpin morphosyntactic computations, which is at least partially compatible

with our findings. More specifically, our finding of the left TPJ cluster of activity predicting correct syntax is highly similar to the previous suggestion of high-gamma oscillations linked to morphological unification (Levy et al., 2014). The latter result was obtained for written words (hence the activity peaking more occipitally) in an active task, whereas we find this for unattended spoken words, supporting the previously claimed automaticity in spoken syntactic parsing (Alekseeva et al., 2022; Hahne and Friederici, 1999). Interestingly, in the older group this high-gamma cluster involved additional areas in the left, but not the right hemisphere, which suggests that the compensation processes in the case of morphological unification of real words are confined to the left-hemispheric language network (in contrast to the lexical level of processing above, and to incorrect syntax – see below).

At the lower frequencies, while the older group exhibited beta-band effects, the younger participants showed alpha activity. These findings of preserved gamma activity across ages and beta rather than alpha patterns in the older group are interesting as they suggest that the decrease in gamma activity may not only be due to a decrease in physiological capacity but may also (or even instead) reflect a change that is functionally specific to particular neurocognitive processes, which again supports the notion of distinct syntactic vs. lexical systems (Friederici and Weissenborn, 2007; Ullman, 2001). The shift from alpha to beta is also in line with the general concept of beta-activity increase with age, similar to that already discussed for the lexical processing above.

Regarding the timings of these effects, the younger group showed them at ~350 ms and ~400 ms, i.e., almost 300 ms after the first lexical results. Although this may partially be explained by the later onset of the affixes (but note that the times were measured from the respective divergence points), this latency is remarkably similar to that of syntactically-related phenomena such as left-anterior negativity (LAN), including those reflecting syntactic agreement (De Vincenzi et al., 2003). Somewhat surprisingly (and in stark contrast to the lexical pattern), effects for the older group started earlier and extended for longer, with clusters ranging from 104 to 440 ms after the divergence point. Whilst this may in principle suggest less effortful early-stage processing in the younger brain, as opposed to more resource-demanding and extended processing later in life, this suggestion is highly speculative, and further studies are needed to both replicate this finding and explore its underpinnings.

In the ERP/ERF literature, syntactic effects are typically reported in the left-lateralised core language areas, most commonly showing larger responses for grammatical anomalies in left inferior-frontal gyrus as well as in the left superior temporal areas (Hanna et al., 2014; Herrmann et al., 2011; Pulvermüller et al., 2008; Shtyrov et al., 2003). In our study, the ITPC classification patterns were in line with those previous results, though somewhat more complex: left temporal and temporo-parietal areas predicted incorrect morphosyntax in the younger subjects alongside right-hemispheric activity (including right IFG for correct morphosyntax). For the older group, we found a very different pattern: temporo-parietal and frontal activity in the left hemisphere predicted correct morphosyntax, whereas the right-hemispheric activity indicated incorrect morphosyntax. A cautious interpretation could be that the highly automatized syntactic processing (Hahne and Friederici, 1999; Pulvermüller et al., 2008) involves rather limited resources under normal conditions with an additional activity/effort required to handle syntactic anomalies in the left temporo-frontal systems, which is what we observe in the younger subjects. With ageing, more resources are required, and, as compensation processes kick in, right-hemispheric activation becomes necessary for processing syntactic anomalies, whereas even the well-formed items lead to extended activation in the left temporo-frontal systems.

4.4. General remarks, limitations and conclusions

Taking the three contrasts together, we found that the

spatiotemporal dynamics diverged between the younger and the older groups. In accordance with previous studies (e.g., Bastiaansen and Hagoort, 2006; M. Jensen et al., 2019; Lam et al., 2016), we found a difference in the frequency bands for the different linguistic processes. Furthermore, there is little overlap between the frequency bands for the younger and the older groups in each specific contrast. While this needs further investigation to be fully explained, some preliminary interpretations can still be offered based on diverging functional properties of the different frequency bands.

Gamma activity has been linked to GABA-ergic systems in the brain (Buzsáki and Wang, 2012; O. Jensen et al., 2014). GABA levels are lower in older than younger individuals (Maes et al., 2018), so a change in activity in this band is to be expected. Furthermore, gamma activity is related to local processing (Buzsáki and Schomburg, 2015; Buzsáki and Silva, 2012) so the changes in the gamma bands can be a way to investigate the compensation that happens with age. In that regard, we found a difference between the younger and the older group especially for the lexical condition, with the younger group showing multiple clusters in the high-gamma and medium-gamma bands, which were not present in the older group. Another reason why we do not see early gamma responses in the older group could be that the decrease in gamma-power (Gaetz et al., 2012) and lower GABA levels result in more variable and inconsistent high-gamma and medium-gamma responses, which in turn leads to statistically less robust responses in the older group, although they are still preserved in the morphosyntactic contrast, which clearly requires further investigation.

In contrast to gamma, we found activity in the beta band for the older group in the morphosyntactic condition, not expressed for the younger group. This activity appeared at the latencies where we found no medium-gamma activity in the younger group, so it is unlikely to represent just a linear drop in peak frequency with age. In a similar trend, we also found the appearance of beta patterns in the older group in the lexical contrast. The increase in beta-band contribution with age could be related to cross-hemispheric communication, which becomes more prominent with age in order to engage right-hemispheric compensation processes, although further studies are needed to confirm this. In turn, oscillatory activity in the alpha band has been connected to both inhibition (O. Jensen and Mazaheri, 2010) and inter-regional communication (Bonnetfond et al., 2017) and, as we mentioned above, both of those mechanisms may be at play in the semantic condition, which also requires further investigation.

The novel paradigm, which allows testing multiple linguistic processes without relying on the participant's overt responses, also has its limitations. For instance, the repetitive nature of the auditory stimulation may have led to some habituation in the brain responses, the process which on its own may have different dynamics with ageing (Richardson et al., 2011). On the other hand, such a repetition has previously been shown to lead to rapid learning of novel patterns in the auditory input (e.g., Kimppa et al., 2016; Partanen et al., 2017), something that has not been studied in aged participants. Whereas the present paradigm and analysis approach did not allow for such a comparison of exposure-related response dynamics, future studies could do that by further improving our paradigm. On the same note, this analysis precluded direct between-group tests, which should also be done in future studies with larger samples, in order to replicate, verify and extend our findings. Finally, the present study was focussed on assessing highly automatic early language comprehension processes in a short patient-friendly design, leaving some important aspects of language processing such as sentence-level syntax/grammar, contextual semantics and pragmatics (Hald et al., 2006; Hanna et al., 2014; Tomasello, 2023) outside the scope of this investigation. Future studies could use a similar machine-learning approach to MEG analysis in combination with different stimulus designs to investigate patterns of activity in different frequency bands whilst modulating semantic, grammatical and pragmatic conditions.

In sum, using source-space MVPA analysis of ITPC MEG data, we

have shown a detailed and complex picture of alpha-, beta-, and gamma-band activity involved in different neural processes taking place during spoken language perception. Without any a priori selected times and/or areas of interest, this approach allowed for a controlled exploratory whole-brain analysis that revealed the spatiotemporal dynamics of the diverse neurocognitive processes underpinning automatic speech comprehension as well as their putative changes with ageing. The open-ended exploratory nature of this approach allowed for a comprehensive look at ageing in speech comprehension but warrants further follow-up investigations and replications of our findings. Furthermore, we used a very short and passive paradigm where the participants did not need to attend, respond or actively react to the stimuli. This methodology (i.e., both the paradigm and the analysis techniques) can thus be applied not only to healthy younger and older participants, but also to patient groups, whose conditions prevent them from full cooperation with more active tasks and participation in long recording sessions, in order to further our understanding of the neural dynamics underpinning speech comprehension in both health and disease.

Data availability

The authors do not have permission to share data.

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