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The oscillatory mechanisms associated with syntactic binding in healthy ageing

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ABSTRACT

Older adults frequently display differential patterns of brain activity compared to young adults in the same task, alongside widespread neuroanatomical changes. Differing functional activity patterns in older adults are commonly interpreted as being compensatory (e.g., Cabeza et al., 2002). We examined the oscillatory activity in the EEG during syntactic binding in young and older adults, as well as the relationship between oscillatory activity and behavioural performance on a syntactic judgement task within the older adults. 19 young and 41 older adults listened to two-word sentences that differentially load onto morpho-syntactic binding: correct syntactic binding (morpho-syntactically correct, e.g., *"I dotch"*); incorrect syntactic binding (morpho-syntactic agreement violation, e.g., "*they dotches"*) and no syntactic binding (minimizing morpho-syntactic binding, e.g., "*dotches spuff*"). Behavioural performance, assessed in a syntactic judgement task, was characterized by inter-individual variability especially in older adults, with accuracy ranging from 76 to 100% in young adults and 58–100% in older adults. Compared to young adults, older adults were slower, but not less accurate. Functional neural signatures for syntactic binding were assessed as the difference in oscillatory power between the correct and no syntactic binding condition. In older adults, syntactic binding was associated with a *smaller* increase in theta (4–7 Hz), alpha (8–12 Hz) and beta (15–20 Hz) power in a time window surrounding the second word. There was a significant difference between the older and young adults: in the alpha range, the condition difference seemed to be in the opposite direction for older versus young adults. Our findings thus suggest that the neural signature associated with syntactic binding in older adults is different from young adults. However, we found no evidence of a significant association between behavioural performance and the neural signatures of syntactic binding for older adults, which does not readily support the predictions of compensatory models of language and ageing.

1. Introduction

There is clear evidence that advanced age, even in the absence of neurodegenerative disease, is associated with structural changes in the brain (Fjell and Walhovd, 2010). These structural alterations are accompanied by decline across a number of cognitive domains, including working memory (Waters and Caplan, 2001) and processing speed (Salthouse, 1996). At the same time, there exists evidence that language abilities are generally well preserved across the adult lifespan (Campbell et al., 2016; Shafto and Tyler, 2014; Peelle, 2019), despite structural changes in language-relevant brain regions (Antonenko et al., 2013; Raz, 2009). Given the structural and cognitive changes that occur in healthy ageing, it is unlikely that successful performance in older adults is achieved with identical neural processes as in young adults (Peelle, 2019). In fact, a differential pattern of brain activity in older compared to young adults is frequently observed (e.g., Antonenko et al., 2013; Tyler et al., 2010; Wingfield and Grossman, 2006). However, the functional interpretation of these observed differences is not yet well

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understood. A key question in this context is how mechanisms of neural adaptation and concomitant cognitive change relate to better or worse behavioural performance in older adults. The purpose of the current study was to investigate this question in the context of language comprehension by focusing on a specific fundamental building block thereof: syntactic binding. Syntactic binding refers to the combination of words into larger structures, taking into account features that determine syntactic structure, agreement and tense (Segaert et al., 2018). Our first aim was to investigate the oscillatory mechanisms supporting syntactic binding in healthy older compared to young adults using a minimal phrase paradigm that minimizes contributions of semantics and working memory load. Our second aim was to investigate whether age-related changes are compensatory by relating the neural signatures of syntactic processing to the degree to which language comprehension is successful within the group of healthy older adults. Lastly, because healthy ageing is characterized by considerable inter-individual variability (Raz, 2009; Peelle, 2019), we incorporated measures of overall cognitive and physical functioning in addition to our neural measure of syntactic processing to identify factors associated with individual differences in comprehension performance.

1.1. Theoretical perspectives on age differences in brain activity

Neuroimaging studies have provided substantial evidence of distinctively different patterns of neural activation between young and older adults under identical task requirements. By and large, the literature shows a more widespread pattern of activity in older (i.e., above the age of 65) relative to young (i.e., in their 20's) adults (e.g., Cabeza et al., 2002; Davis et al., 2008). Different views exist on how to interpret these age-related changes in brain activity. According to one view, the appearance of more diffuse activity in the older brain reflects a general decline in neural efficiency, or reduced cerebral specialization. The term *dedifferentiation* is commonly used to refer to this account (Baltes and Lindenberger, 1997; Wingfield and Grossman, 2006). An alternative (though not mutually exclusive) interpretation is that increased engagement of brain regions in older compared to young adults reflects focused recruitment as a means to compensate for neurocognitive decline. This is commonly referred to as *compensation* (Wingfield and Grossman, 2006). Some researchers argue that compensatory mechanisms may still exist even if performance is impaired, but even so, the term compensation should be reserved for enhanced activation that is contributing meaningfully to performance (Grady, 2012; Cabeza et al., 2018).

A growing emphasis in the field of the cognitive neuroscience of ageing is placed on individual differences. Indeed, rather than age per se, age-related performance differences could be better explained by individual differences in neuroanatomical features, cognitive abilities and sensory abilities (Peelle, 2019). Consequently, the characterization of factors contributing to the rate of age-related function decline is an important area of interest (Lara et al., 2015). Both processing speed and working memory capacity decline with age (Salthouse, 1996; Waters and Caplan, 2001; Caplan and Waters, 2005) and are known to contribute to language processing (Wingfield et al., 2003; Wingfield and Grossman, 2006). Health characteristics can also explain variability in cognitive ageing (Raz, 2009; Shafto et al., 2019). Specifically, physical health in older adults is positively related to general cognitive functioning (Barnes et al., 2003; Colcombe et al., 2004), brain electrical activity (Sanchez-Lopez et al., 2018) and language processing (Segaert et al., 2018b). These findings highlight the importance of considering healthy ageing in a broader, more holistic sense rather than an exclusive focus on the behavioural and brain decline. In the context of the current study, it seems that examining potential factors contributing to inter-individual variability in comprehension performance and the operations underlying this process could be illuminating in further establishing the conditions under which older adults successfully engage in alternative pathways to language comprehension.

1.2. Age differences in brain activity during language comprehension

Functional magnetic resonance imaging (fMRI) studies have yielded evidence that older adults recruit additional brain regions compared to young adults during syntactic processing (e.g., Grossman et al., 2002; Tyler et al., 2010; Shafto and Tyler, 2014; Peelle et al., 2009). This could indicate the existence of compensatory mechanisms, but an explicit relationship between the observed additional activity and successful performance is often missing (for example: Tyler et al., 2010). When additional activity is not predictive of performance, it is sometimes interpreted as exerting a more indirect compensatory influence, by supporting working memory or processing demands related to task performance (Peelle et al., 2009; Campbell et al., 2016).

Electrophysiological (EEG) measurements, which enable the investigation of neural activity that is concurrent with comprehension processes, offer an alternative approach. By and large, ERP components during sentence comprehension show smaller amplitudes and longer latencies in older compared to younger adults (Federmeier and Kutas, 2005; Federmeier et al., 2002; Wlotko et al., 2010). Later studies suggest the age-related change in the use of contextual information is associated with a decreased reliance on predictive processing in older adults (Wlotko and Federmeier, 2012; Wlotko et al., 2012). In extension of these findings, research suggests that older adults do not seem to engage in mechanisms of binding information the same way young adults do, as evidenced by age-related deficits in the encoding processes thought to underlie memory binding (Johnson, 1996; Mitchell, Johnson, Raye, Mather & D'Esposito, 2000; Sander et al., 2011). Likewise, the P600, an ERP component sensitive to syntactic violations, is less asymmetric and more frontal in older, compared to younger adults (Kemmer et al., 2004; Leckey and Federmeier, 2017; Alatorre-Cruz et al., 2018). In other words, similar to the age-related increases in bilateral activation patterns observed in the fMRI literature, the changed scalp distribution of the P600 effect suggests a qualitative change in syntactic processing with age.However, the functional significance of these changes is still debated.

An alternative approach to investigating event-related changes in the EEG signal, and the one that is our main focus here, is to look at oscillatory activity. An advantage of investigating neural oscillations relative to ERPs is that this method allows for the investigation of event related changes which are time-locked to the event, but not necessarily phase locked (i.e., when the phase of the event-related response is the same or very similar across all individual trials). Sentence comprehension in young adults has been associated with oscillatory changes in the theta (~4–7 Hz); alpha (~8–12 Hz) and beta band (~13–18 Hz; Bastiaansen, van Berkum & Hagoort, 2002a; Meyer, 2018; Prystauka and Lewis, 2019). Syntactic processing, particularly the integration of syntactic information across words, has been associated with increased theta power (Bastiaansen et al., 2010). In addition, while storing syntactic information in verbal working memory and syntactic binding have been associated with a power *increase* in the alpha band (Meyer et al., 2013; Bonhage et al., 2017; Segaert et al., 2018), successful encoding of syntactic information has been linked to a power *decrease* in the alpha band (Vassileiou et al., 2018; Beese et al., 2019a). Finally, it has been suggested that effects in both the alpha and beta band reflect unification, or binding of semantic and syntactic information in sentences (Davidson and Indefrey, 2007; Lam et al., 2016; Bastiaansen et al., 2010).

Few studies have investigated age-related changes in the oscillatory dynamics associated with sentence processing. However, research by Beese et al. (2019a) reports age differences in the lower alpha-band (~8–10 Hz) in sentence encoding. Specifically, using an auditory sentence comprehension task, oscillatory power differences between correctly and incorrectly encoded sentences were compared across age groups. Interestingly, the authors found an age-related inversion in the alpha band, from a relative *decrease* in correctly remembered relative to later-not-remembered sentences in young adults, to an *increase* in correctly remembered relative to later-not-remembered sentences in

older adults. The authors suggest this shift likely reflects a change from cortical disinhibition to inhibition during sentence encoding.

1.3. Isolating syntactic binding in sentence comprehension

In the current study, we use a minimal two-word sentence paradigm to investigate syntactic binding processes in online sentence comprehension. At its most fundamental level, syntactic binding refers to the combination of words into larger structures, taking into account features that determine syntactic structure, agreement and tense (Segaert et al., 2018). This elementary computation, otherwise known as *merge* (Chomsky, 1995; Zaccarella and Friederici, 2015) or *unification* (Hagoort, 2005, 2009, 2016) forms the foundation of structure building of increasing syntactic complexity. Investigating elementary syntactic binding by means of a minimal phrase paradigm offers the advantage of minimizing contributions of other processes involved in sentence comprehension, such as working memory load. This advantage is particularly salient when studying the effect of age on online sentence comprehension, given the large number of factors that are influenced by age.

In a previous study, Segaert et al. (2018) employed a minimal phrase paradigm to investigate the oscillatory mechanisms associated with syntactic binding in young adults. To substantially reduce the infuence of semantic processing on syntactic binding, pseudowords were used instead of existing words. Specifically, participants listened to two-word sentences consisting of a pronoun paired to a pseudoverb (e.g., "*I grush*", "*they dotch*"), forming a morpho-syntactically correct combination (i.e., syntactic binding condition) and to wordlists, consisting of two pseudoverbs paired together (e.g., *"ploffs grush*", "*spuffs dotch*"), eliciting no syntactic binding (i.e., no binding condition). Pseudoverbs, such as "*grush"* and "*dotch",* are present in both conditions, equally eliciting morphological parsing of stems and inflectional affixes, which indicate the number and tense for each instance of a pseudoverb. The two conditions thus differ from each other only with respect to binding taking place. The aspects of syntactic binding that are manipulated in this paradigm are: (1) establishing agreement of number and person between the pronoun and the pseudoverb; and (2) structure building: 'subject verb' is a sentence with a syntactic structure, while for wordlists with two verbs, no syntactic structure can be established. The paradigm thus allows us to focus on syntactic binding, with only a minimal contribution from semantics and working memory load. Preceding the presentation of the second word, Segaert et al. (2018) observed a larger increase in alpha and beta power in the syntactic binding condition relative to the no binding condition, which was maximal over a cluster of frontal-central electrodes. In addition, following the presentation of the second word, a larger increase in alpha power was observed in the syntactic binding condition relative to the no binding condition, which was maximal over a left-lateralized cluster of fronto-temporal electrodes. Using a paradigm similar to the one used in Segaert et al. (2018), the current study aims to investigate the oscillatory mechanisms associated with syntactic binding in older compared to young adults.

In another study (Poulisse et al., 2019), we have used a minimal phrase paradigm to specifically investigate age differences in comprehension performance for elementary syntactic structures. Minimal phrases consisting of a pronoun and a verb were used in an auditory syntactic judgement task to investigate performance differences between young and older adults. The degree of semantic support was varied by comparing sentences containing real-verbs (e.g., "*I cook*") to sentences containing pseudoverbs (e.g., "*I spuff*"). Older adults were less accurate and slower in detecting syntactic agreement errors than young adults, but this decrease in performance was modulated by the level of semantic information provided. Specifically, the age-related decline in accuracy was smaller for pseudoverb compared to real verb sentences, but this difference was associated with disproportionately slower response times in the pseudoverb compared to the real verb sentence condition. Although older adults as a group showed declined comprehension performance, there was a large degree of inter-individual variability, which was partly explained by individual differences in processing speed. Specifically, older adults with higher processing speed abilities performed better in the real verb condition and were faster in the more challenging pseudoverb condition. In addition, performance was moderated by working memory capacity, such that a higher working memory capacity was associated with higher performance in the older age group. These findings on individual differences in performance highlight the importance of adopting an inter-individual variability approach to the investigation of age differences in language performance. In sum, the results of this study show that comprehension performance in older adults declines even when syntactic constructions are reduced to just two words, thus extending previous work that suggests performance is particularly susceptible to age-related decline for the comprehension of syntactically complex sentences (Kemtes and Kemper, 1997; Obler et al., 1991; Wingfield et al., 2006).

Taken together, Segaert et al. (2018) suggest syntactic binding in young adults is associated with oscillatory power changes in the alpha and beta band. A behavioural study targeting the same fundamental syntactic computation (Poulisse et al., 2019) shows comprehension performance is subject to age-related changes, yet is characterized by a large degree of inter-individual variability. However, no study to date has looked into the oscillatory mechanisms associated with syntactic binding in older adults. This is the motivation for the current work.

1.4. Current study

The goal of this study was to investigate the oscillatory mechanisms associated with syntactic processing in healthy ageing. We examined a group of healthy older adults, aged 65–80 years and compared their performance to that of a group of young adults. Secondly, we explored whether age-related changes in oscillatory mechanisms are predictive of performance success in syntactic comprehension. In doing so, we also incorporated factors associated with individual differences in comprehension performance, namely, working memory capacity, processing speed and indicators of physical health (i.e., amount of regular physical activity and handgrip strength).

To collect our behavioural and functional measures, we used a minimal phrase paradigm in a separate behavioural and EEG experiment (similar to Segaert et al., 2018 – described above). This paradigm targets elementary syntactic binding operations by using minimal phrases consisting of a pronoun and a pseudo verb (e.g., "*I dotch*", "*she spuffs*"). The use of pseudoverbs instead of real verbs limits the influence of lexical-semantic content to syntactic binding, as pesudoverbs lack a representation in the mental lexicon. In addition, the load on working memory required to process these phrases is kept to a minimum.

We obtained a behavioural performance measure with a syntactic judgement task. Participants listened to the minimal phrases and indicated with a button press whether the phrases were morpho-syntactically correct (yes/no). Syntactic comprehension was assessed as the mean accuracy and response time (RT) for correctly rejecting and detecting morpho-syntactic agreement errors.

To obtain our neural measure associated with syntactic processing, EEG was recorded while participants listened to the same minimal phrases. Since we were concerned with syntactic binding, a process that inherently unfolds over time rather than being time locked to a specific event, we especially focused on the oscillatory dynamics related to syntactic binding. Specifically, we compared the oscillatory response to a correct syntactic binding condition (e.g., "*I dotch*") with the response to a no syntactic binding condition (e.g., "*spuffs dotch*"). The analysis focused on power changes surrounding the onset of the *second* word ("*dotch*" in this example). In the correct syntactic binding condition, agreement of number and person is established between the pronoun and the target word "*dotch*", whereas this is absent in the no syntactic binding condition. In addition, the subject-verb combination in the

correct syntactic binding condition forms a morpho-syntactic structure. In contrast, in the no syntactic binding condition, a morpho-syntactic structure cannot be established. In other words, the target word in those two conditions differs in terms of syntactic binding taking place. The power difference between the correct syntactic binding and no binding condition served as our neural measure for syntactic processing.

Age-related changes in oscillatory mechanisms (i.e., oscillatory mechanisms supporting syntactic comprehension in older, but not young adults) that are predictive of performance success would indicate that these changes are compensatory.

2. Methods

2.1. Participants

20 young university students and 48 older adults participated in the study (details on participant characteristics are below). All participants were native British English speakers and reported to be in good health with no known history of neurological, speech or language disorders. No participant had audiometer measurements indicating severe hearing impairment on both ears [specifically, > 70 db or more on the Etymotic Hearing Task (Etymotic Research, Inc.)]. One older adult had an audiometer measurement indicating severe hearing impairment on the left, but mild hearing impairment on the right and was included in the final sample. All participants had a minimum education level of A levels (or A levels equivalent). 7 older adults obtained a score below the cut-off value of 26 on the Montreal Cognitive Assessment test (MoCa; version 7.1) and were not included in the analysis. One young participant was excluded from the EEG analyses due to noisy EEG data. Taken together, these exclusions resulted in a final sample of 19 young adults (13 women, mean age: 21, SD: 2.46; 6 men, mean age: 21, SD: 2.32) and 41 older adults (26 women, mean age: 69, SD: 3.37, 15 men, mean age: 69, SD: 5). Participants were recruited via the database of the University of Birmingham and the Join Dementia Research database. Students were given university credits or a monetary compensation, older adults received monetary compensation. All participants gave informed consent. This research was conducted at the University of Birmingham and had full ethical approval (ERN 15–0866).

2.2. Overview of study design

Our study consisted of a behavioural experiment, an EEG experiment (see overview Table 1) and a set of domain general cognitive and physical functions of healthy ageing.

A. Behavioural syntactic judgement task: The behavioural experiment served to measure syntactic comprehension performance. Participants were instructed to listen to minimal phrases and were asked to indicate whether the phrase was grammatically correct or not. Performance was measured as the mean accuracy and mean response time for rejecting and detecting morpho-syntactic agreement errors in respectively correct and incorrect phrases. This is a measure of a participants' ability to perform syntactic binding and served as a proxy for syntactic comprehension performance.

B. Neural signature of syntactic binding (EEG experiment): To measure the oscillatory mechanisms associated with syntactic binding, the same participants subsequently completed an EEG experiment during which they listened to the same phrases as in the behavioural task. Syntactic binding was measured by comparing the correct syntactic binding to the no syntactic binding condition (Segaert et al., 2018). A reversed speech detection task ensured participants remained focused on the stimuli throughout the task. Participants were instructed to press a button (left mouse click) whenever they heard one of the two words played in reverse. No button press was required for any of the trials in which both words were played normally. This ensured maximal similarity in the response decision processes between the critical conditions of interest.

The condition contrasts that were used to assess behavioural performance and brain function were specifically chosen to best capture the underlying constructs they were set out to measure. At the neural level, we capture the signatures of binding by contrasting the presence vs. absence of binding, whereas at the behavioural level, a performance measure is required and thus we need to ask participants to make a decision on whether binding is correct.

C. Domain general cognitive and physical functions: Lastly, a set of measures of cognitive processing and physical function were included to examine individual differences in cognitive and physical decline in the older adult group.

Table 1
Conditions of interest and measures obtained for the behavioural experiment (panel A) and the EEG experiment (panel B).

Conditions	Explanation	Example	Measurement
A. Behavioural experiment			
correct or incorrect syntactic binding	Detecting whether a phrase is morpho-syntactically correct or incorrect	correct: I spuff incorrect: I spuffs	**Syntactic comprehension performance:** the mean accuracy and response time (RT) of rejecting and detecting agreement violations
B. EEG experiment			
correct syntactic binding	Morpho-syntactically correct phrase	I spuff, they dotched	**Functional neural signature of syntactic binding:** the difference in time frequency power between correct syntactic binding and no syntactic binding
no syntactic binding	No morpho-syntactic binding is possible	plams spuff, grush dotched	

2.3. Materials for the behavioural and EEG experiment

The stimuli for this experiment were based on a set of 20 non-existent, monosyllabic English verbs created by Ullman et al. (1997): brop, crog, cug, dotch, grush, plag, plam, pob, prap, prass, satch, scash, scur, slub, spuff, stoff, trab, traff, tunch, vask. The words had an average word length of four letters. Despite having no meaning in the mental lexicon, these pseudoverbs can be inflected according to the grammar rules for regular verbs in English. Consequently, combining the pseudoverbs with one of the six pronouns I, you, he, she, we, or they, yields a minimal phrase, for example: "*I dotch*", "*she dotches*", or "*they dotched*". The stimuli were digitally recorded using a male native speaker of English. All pseudoverbs were recorded in first, second and third singular and plural present tense. For each word, the clearest recording out of three attempts was selected. Using the software program Adobe Audition, a reversed speech version of all recordings was created. Lastly, all audio files in wav format were normalized to 1 db in order to equalize the volume of the individual recordings.

These stimuli were combined to form three conditions that differentially load on morpho-syntactic binding, serving the basis for our behavioural and EEG experiment (see Table 1). In the correct syntactic binding condition, the pronoun and pseudo verb form a morpho-syntactically correct phrase (e.g., "*I spuff*", "*they dotched*"). In the incorrect syntactic binding condition, a pronoun was paired with a pseudoverb but the inflectional suffix of the verb did not match the pronoun, resulting in a morpho-syntactic agreement violation (e.g., "*I spuffs*", "*they dotches*"). In the no syntactic binding condition, two pseudoverbs were paired together (e.g., "*dotches spuff*"), preventing the establishment of a morpho-syntactic structure.

A potential concern may be that specific combinations in the no syntactic binding condition could be interpreted as noun-verb rather than verb-verb pairings (e.g., in "*dotch spuffs*" and "*dotches spuff*", the first word could be interpreted as a singular and plural noun respectively). However, previous research established that participants do not syntactically bind such pairings (Segaert et al., 2018). Specifically, in

that study, 66% of the no syntactic binding trials[1] consisted of pseudoverb combinations in which both verbs were either first, or second person singular. If the first word in such pairings would have been interpreted as a pseudonoun, this would have been identified as having an agreement mistake in number and person by the Dutch-speaking participants tested in the study. However, performance accuracy for correctly rejecting mistakes was found to be 97.4%, suggesting participants were not performing syntactic binding in this condition.

2.4. Behavioural syntactic comprehension experiment

Conditions: Conditions of interest were the correct and incorrect syntactic binding condition. An average performance measure was calculated for 24 trials of each. Correct syntactic binding trials could be formed with three possible pronoun-pseudoverb combinations. Specifically, the pseudoverb *stem* combined with either 'I', 'you', 'we' or 'they'; the pseudoverb stem plus *–s* combined with 'he' or 'she', or the pseudoverb stem plus *–ed* combined with each of the six pronouns. Each form occurred 8 times and each verb would occur only once in each form. The incorrect syntactic binding word pairs were formed according to the same criteria, but only the *stem* and *-s forms* were possible, as no incorrect combination can be composed with the *–ed form*.

In addition, there were two other conditions that were not analysed (24 trials in each): a no syntactic binding condition (i.e., two pseudoverbs), to ensure similarity to the EEG task, and a pronoun filler condition (i.e., two pronouns, e.g., "*we he*"), to prevent predictability in the potential engagement of binding processes after the presentation of a pronoun as the first word.

Each participant received a unique randomized stimulus list, which was divided into two blocks, separated with a self-paced break. The experiment had 96 trials in total and was preceded by a practice block of 14 trials.

Trial timing: Each trial started with a fixation cross for 1000 ms, followed by a blank screen for 1000 ms, followed by a word-by-word presentation of the minimal phrase, with a Stimulus Onset Asynchrony of 1200 ms. The Inter Stimulus Interval (ISI) between the first and the second word varied as a function of the duration of the first word and ranged between 300 and 600 ms. A response screen (self-paced) showing the text: *"Did you hear a grammatical mistake?"* appeared 1605 ms after the onset of the second word, followed by an inter trial interval (6 ms).

Performance behavioural experiment: To confirm the overall effectiveness of our experimental manipulation, the results of the behavioural experiment are reported here. Data points with RT's above or below 2 standard deviations of the participant mean were removed from analyses, resulting in an exclusion of 5% of the data points. Table 2 shows the group average performance accuracy and response time for the younger and older age group on the conditions of interest. For the sake of completeness, performance on the other two conditions is reported as well. In the older age group, the group average performance accuracy for rejecting (for correct syntactic binding trials) and detecting (for incorrect syntactic binding) syntactic agreement errors was 91% (SD = 28%) and 86% (SD = 35%) respectively. In addition, the group average response time for correct responses was 2734 ms (SD = 1773 ms) for the correct syntactic binding trials and 2977 ms (SD = 1839 ms) for the incorrect syntactic binding trials. In the younger age group, the group average performance accuracy for rejecting (for correct syntactic binding trials) and detecting (for incorrect syntactic binding) syntactic agreement errors was 93% (SD = 26%) and 90% (SD = 30%) respectively. In addition, the group average response time for correct responses was 1885 ms (SD = 1332 ms) for the correct syntactic binding trials and 2301 ms (SD = 1585 ms) for the incorrect syntactic binding trials.

[2] In the original Segaert et al. (2018) paper, the condition in which two pseudoverbs were paired together was called 'wordlist condition', while in the current work, this condition is referred to as 'no syntactic binding' condition.

Due to the unequal sample sizes, Dunnett's tests were run to identify group differences in performance for every condition separately at a significance level of $p = 0.05$. There were no differences in performance accuracy between the younger and older age group, but older adults were slower compared younger adults. This is in line with Poulisse et al. (2019), who found that in the challenging pseudoverb conditions, older adults slowed down to make more accurate decisions.

In the results section we used a performance measure for individual participants (average of the accuracy/reaction for the correct and incorrect syntactic binding trials) and related these to our functional neural measures.

2.5. EEG experiment: neural signature of syntactic binding

Conditions: After the behavioural experiment, participants completed an EEG task in order to collect our functional measure of syntactic processing. Conditions of interest were the correct syntactic binding and the no syntactic binding condition, each consisting of 72 trials. Comparing these two conditions provides a maximum contrast in terms of morpho-syntactic binding and hence served as our measure of syntactic processing.

In the correct syntactic binding condition, each possible verb form (i.e., *stem form*, *-s form* and *–ed form*) occurred 24 times, such that each possible pronoun in the stem form (i.e., *I, you, we, they)* occurred 6 times, each possible pronoun in the –s form (i.e., *he, she*) occurred 12 times and each possible pronoun in the ed-form (i.e., *I, you, we, they, he, she*) occurred 4 times. Similarly, each possible verb form occurred 24 times in the no syntactic binding condition. To avoid repetition effects, the first word of the pair in this condition could neither be the same verb nor have the same ending as the second word of the pair (e.g., combinations such as "*dotches dotched*", or "*plammed dotched*" were not possible).

In addition, the EEG experiment included three other conditions that were not analysed: an incorrect syntactic binding condition (64 trials), to ensure similarity to the behavioural experiment; a pronoun filler condition, (72 trials; i.e., two pronouns, e.g., "*we he*"), to prevent predictability in the potential engagement of binding processes after the presentation of a pronoun as the first word; and a reversed speech condition (80 trials, i.e., one of the two words was played in reverse), to ensure participants remained focused on the stimuli throughout the experiment. This resulted in a total of 360 trials, divided into 8 blocks and separated by self-paced breaks. The experiment was preceded by a practice block consisting of 30 trials. Each participant received a unique randomised stimulus list.

Trial timing: Each trial started with a fixation cross for 1000 ms, which was followed by a blank screen for 1000 ms, followed by a word-by word presentation of the minimal phrase. The screen remained blank throughout auditory word presentation. The second word was presented 1200 ms after the onset of the first word. A response screen showing the text: "*Reversed?"* was presented 1400 ms after the onset of the second word, to ensure the response screen would not interfere with the processing of the stimuli. The response screen lasted for 4000 ms or until a button press. This was followed by the presentation of a blank screen for 500 ms. A schematic representation of a trial is presented in Fig. 1.

EEG recording: EEG recordings were made using a 64 electrode cap-mounted Ag/AgCl electrodes arranged in a 10/10 system layout (including left and right mastoids, CPz as reference and AFz as ground). Recordings were acquired using the EEGO Sports system (ANT Neuro, Enschede, The Netherlands). Horizontal eye movements were monitored by means of two electrodes placed at the outer left and right canthi. The EEG data were high-pass filtered at 0.3 Hz and low-passed at 30 Hz. All impedances were kept below 20 kΩ. Signals were recorded at a 500 Hz sampling rate.

EEG preprocessing: The preprocessing and analyses of the data were performed using functions from EEGLAB (version 13.6.5b; Delorme and Makeig, 2004) and the Fieldtrip software package (Oostenveld et al., 2011). The data was average referenced and epoched from −2.2s to 4.5s,

Table 2
Means and standard deviations of group average performance accuracy and RT for the younger and older age group and the results of comparisons between the age group (Dunnett's Test).

	Younger age group (N = 20)		Older age group (N = 41)		Comparison Dunnett's Test			
	mean	sd	mean	sd	diff	lower CI	upper CI	sign
Accuracy (% correct)								
correct syntactic binding	93	26	91	28	0.01	−0.05	0.06	
incorrect syntactic binding	90	30	86	35	0.05	−0.01	0.11	
no syntactic binding	99	11	98	14	0.01	−0.02	0.04	
pronoun filler	91	28	92	28	−0.01	−0.15	0.14	
Response time (ms)								
correct syntactic binding	1885	1332	2763	1804	−845	−1470	−237	*
incorrect syntactic binding	2301	1585	3055	1925	−780	−1441	−118	*
no syntactic binding	905	973	1182	1179	−556	−1134	22	*
pronoun filler	728	723	1182	1179	−605	−1065	−144	*

Diff = pairwise mean differences between two means under comparison; CI = confidence interval.
* = significant difference between two means at alpha 0.05

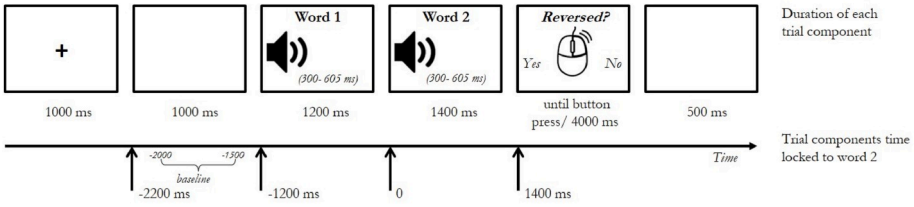

Fig. 1. Timing of each component in one EEG trial.

time-locked to the onset of the second word. Next, all trials from the reversed speech condition (i.e., reversed speech detection task trials) were removed as well as false positive button presses to non-reversed speech trials and trials containing artefacts. One young participant was removed from the analyses because of muscle artefacts caused by excessive coughing. In addition, trials containing non-biological as well as movement artefacts were rejected based on visual inspection. This resulted in an average loss of 5 trials per participant in the younger age group (SD: 11) and 23 trials per participant in the older age group (SD: 23). An approximately equal amount of trials was excluded across conditions. Following this, eye movements and blinks were removed using independent component analyses (infomax algorithm) incorporated as the default "*runica*" function, with the first step of a PCA to reduce the dimensionality of the data. This resulted in an average exclusion of approximately 2.2 components in the young age group and 3.5 components in the older age group. A similar pipeline has been used for data analysis in previous EEG studies (e.g., van Diepen et al., 2016; van Diepen and Mazaheri, 2017).

2.6. Inter-individual variability measures on cognitive processing, physical capability and physical activity

A number of additional measures were included to examine the effect of individual differences, an overview of which can be found in Table 3. All are established biomarkers of healthy ageing (Lara et al., 2015).

Table 3
Overview of additional measurements.

Measure	*Task*	*Scoring*
Working memory: Backward Digit (BD) and Subtract 2 (S2) Span task (Waters; Caplan, 2003)	Listening to a series of digits of increasing length, starting with 2 digits, up to 7. There were 5 trials of each digit length. *Task BD*: repeat digits in backward order. *Task S2:* repeat digits after subtracting 2 from each digit.	Span size: longest digit length for which 3 out of 5 trials are correctly recalled; 0.5 point is added if 2 out of 5 is correctly recalled. Composite score: (span BD + span S2)/2.
Processing speed: WISC-IV Coding subtest (WAIS-IV; Wechsler, 2008)	Copying symbols that are paired with numbers within 120 s.	One point for each correctly drawn symbol completed within time limit. Total score: number of correctly drawn symbols. Raw scores converted to scaled score equivalents according to age group.
Physical activity: New Zealand Physical Activities Survey Short Form (Sport and Recreation New Zealand, 2001)	A self-report measure of habitual practice of physical activity.	Composite score: adding the duration (in minutes) of moderate activity and two times the duration of vigorous activity.
Handgrip Strength: Hand dynamometer (Takei Scientific Instruments, Japan).	The dynamometer is held towards the ceiling with an outstretched arm whilst standing upright, shoulder and elbow are fully flexed. While the arm moves downwards in 3 s, the meter is squeezed at maximum force.	Three measurements were recorded for both hands. The highest value of the dominant hand was used for analyses. Raw scores were converted to standardised z-scores within gender groups.

2.7. Procedure

The behavioural and EEG tasks were completed on the same day for both the young and the older adults. The procedure was the same for each participant and can be summarized as follows: (1) *Volume check:* Participants listened to 10 randomly selected pseudoverbs through headphones and were asked to repeat what they heard. Special attention was paid to participants' ability to distinguish between words in *stem form*, *-s form* and *–ed form.* Volume settings were adjusted if necessary. (2) *Behavioural task:* During the practice block, participants received verbal feedback on their performance and only proceeded to the real experiment when they had a clear understanding of the task. The behavioural task took on average 30 min to complete, including the

practice session and a break. (3) *EEG task*: EEG recordings were conducted in a quiet, dimly lit room. After the completion of the capping procedure, participants started with a practice block to familiarize themselves with the task. The experiment was divided into 8 blocks (~5 min each), separated by self-paced breaks. The EEG recording lasted around 1 h in total. Both the behavioural and EEG experiment were run using the E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA).

A second session was scheduled with the older participants to collect the additional measurements. These tests were administered in the following order: Hearing Task, Backward Digit Span Task, Forward Digit Span Task, Hand Grip Strength, Coding, Physical Activity questionnaire and MoCa. The average time interval between the first and the second session was 87 days (SD: 53).

2.8. Statistical analyses

2.8.1. Group level statistical analyses

Our first research objective was to establish a functional neural EEG signature for syntactic binding in older compared to young adults. To this end, we examined differences in oscillatory power between the correct syntactic binding and no syntactic binding condition between and within groups.

Time frequency analyses: Time-frequency representations (TFR) of power were calculated for each condition using the Fieldtrip function '*ft_freqanalysis_mtmconvol*'. Power was analysed from 2 to 30 Hz in steps of 1 Hz for every 50 ms. We used sliding Hanning tapers with an adaptive time window of three cycles for each frequency of interest ($\Delta T = 3/f$), utilizing a similar approach as used in previous studies (e.g., van Diepen et al., 2015; Whitmarsh et al., 2011). After assessing there were no differences in baseline oscillatory power for the frequency bands of interest between our conditions of interest, power changes in oscillatory activity were expressed in terms of change scores from baseline (ΔPt) using the following formula: $\Delta Pt = (Pt–Pr)/Pr$, where Pr, was the mean power during the baseline period −2000 to −1500 ms before the onset of the second word and Pt was the power at each specific time point. In order to distinguish between induced responses (i.e., activity that is time-locked but not phase-locked to the event) from evoked responses (i.e., activity that is both time and phase locked to event), the ERP components were removed from the TFR (Bastiaansen and Hagoort, 2003). This step was done to reduce the likelihood that the oscillatory phenomena we observed were simply the spectral-representation of the event-related potentials. First, a time frequency decomposition of the ERP data was performed on each participant for each condition separately, using the approach described above. Following this, the time frequency spectra of the ERPs were subtracted from the time-frequency spectra of the EEG epochs for each condition separately. A similar procedure has been used in previous studies (e.g., Mazaheri and Picton, 2005; Segaert et al., 2018). The resulting subject averaged power changes were subjected to statistical analysis to test for condition differences in the temporal and spectral dynamics of oscillatory modulations induced by the minimal phrases.

To examine group differences between young and older adults, we compared the neural signature associated with syntactic binding in the young age group to the neural signature in the older age group. Specifically, we computed the power difference between conditions for each individual participant (i.e., correct syntactic binding minus no syntactic binding). To assess the difference values of the young adults to the difference values of the older adults while accounting for multiple-comparisons (i.e., multiple electrodes and time points), a non-parametric cluster level (over-electrodes) randomization routine was performed (Maris and Oostenveld, 2007). In this procedure, the power of the frequencies of interest, in each channel and time point within a time window of interest, was clustered depending on if it exceeded a dependent samples *t*-test threshold of $p < 0.05$ (two-tailed). In doing so, the *triangulation method* was used to determine neighbouring channels. A minimum of two neighbouring electrodes was considered a cluster. Probability values for the clusters were obtained by a Monte Carlo simulation involving randomly swapping the labels (i.e., conditions) in participants 5000 times and calculating the maximum cluster-level test statistic for each permutation. These analyses were performed by collapsing within the theta (4–7 Hz), alpha (8–12 Hz) and low beta (15–20 Hz) frequency band, using a time window from −1.2 to 1.4 s surrounding the second word. In sum, this procedure resulted in the identification of a cluster of electrodes that showed the greatest difference in amplitude between the difference values in the young adults compared to the difference values in the older adults in each of the three frequency bands. Following this, the statistical difference between conditions (i.e., the correct syntactic binding condition compared to the no syntactic binding condition) was assessed in each age group separately using the same procedure, frequency bands, and time window that was used in the between group analyses.

We should note that some previous studies have found that the peak alpha band frequency is reduced in older adults (Klimesch, 1999; Chiang et al., 2011). Furthermore, individual alpha frequency has been found to correlate with individual differences in cognitive performance (Klimesch, 1999; Grandy et al., 2013a, 2013b). Peak individual alpha frequency qualifies as a stable neurophysiological trait marker in healthy young and older adults (Grandy et al., 2013b). To ensure that we were not creating differences in oscillatory patterns of activity between age groups due to our choice of frequencies to include in our predefined frequency bands, we ran an additional analysis getting the individual peak alpha frequency of each participant in a baseline window before the onset of the first word (−2.2 to −1.2s). Individual alpha peak frequency was estimated using the centre of gravity (CoG) method proposed by Klimesh, Schimke & Pfurtscheller (1993). We defined CoG as:

$$CoG = \frac{\sum_{i=1}^{n} f_i * a_i}{\sum_{i=1}^{n} a_i}$$

Here, f_i is the ith frequency bin including and above 7 Hz, n is the number of frequency bins between 7 and 14 Hz, and a_i the spectral amplitude for f_i. The individual alpha peak frequencies ranged from 9 to 11 Hz (older adults, mean: 10.6 Hz, SD: 0.48; young adults, mean:10.7 Hz, SD: 0.32). These individual alpha peak frequencies were thus captured in our chosen predefined frequency bandwidth for alpha.

Event Related Potentials: ERPs were computed for each individual and for each condition separately, using the Fieldtrip function '*ft_timelockanalysis*'. Differences in the ERP amplitudes between the conditions were assessed by means of cluster based analyses. Using a 100-ms prestimulus baseline, we examined amplitude differences elicited by the second word, that is, the target word in our primary TFR analyses. Specifically, based on inspection of the grand average data collapsed across conditions and previous reports in the literature (i.e., Friederici, 2004 for P1, N400 and P600; Rentzsch et al., 2008 for N1), we examined the following latency windows synchronized to the onset of the second word (i.e., at time 0s): 0.1–0.14s (i.e., corresponding to P1); 0.17–0.2s (i.e., corresponding to N1); 0.25–0.35s (i.e., corresponding to P300); 0.4–0.5s (i.e., corresponding to N400); 0.6–0.7s (i.e., corresponding to the late positivity component/P600). The amplitude was larger in the correct syntactic binding, compared to the no binding condition for the P1, P300 and late positivity ($p = 0.02$; $p < 0.001$ and $p = 0.02$ respectively). This overall positivity shift in the first 300 ms post word onset could have been brought about by the difference in amplitude asymmetric (i.e., non-Gaussian) alpha power between the two conditions (Mazaheri and Jensen, 2008; Nikulin et al., 2007, van Dijk, van der Werf, Mazaheri, Medendorp & Jensen, 2010).

2.8.2. Individual differences analysis

Our second aim was to explain the variability among healthy older adults in syntactic performance as a function of their neural signatures, as well as the domain general cognitive and physical measures. We

created linear regression models (LM's, *lme4* package, version 1.1–10; Bates et al., 2014) using the *lm* function in R version 3.5.1 (R Development Core Team, 2015). Separate models were created to predict accuracy and response time of syntactic comprehension performance (i.e., the dependent variables). The independent variables were the neural signatures of syntactic processing derived from the EEG task and our inter-individual variability measures on cognitive and physical functioning. Specifically, the regression models for predicting both accuracy and RT included the following predictors (i.e., independent variables): working memory capacity, processing speed, hand grip strength, regular physical activity and age. All individual difference measures were centred. Table 4 provides an overview of the group average and standard deviation for each measure. The scaled processing speed scores were used in the analyses, but for the sake of completeness, the raw processing speed scores are reported as well. The neural signatures of syntactic processing were calculated in the following way. First, a power difference TFR was created for each individual participant by subtracting the no syntactic binding condition from the correct syntactic binding condition. Following this, power was averaged over the electrodes and time points that were obtained by the cluster level randomization tests described above, and averaged over the predefined frequency bands that were used in those analyses. This resulted in a power difference value for each individual subject.

3. Results

3.1. Syntactic binding is associated with different oscillatory signatures in young compared to older participants

3.1.1. Differences in syntactic binding signatures between young and older adults

Fig. 2 summarizes the results for the difference in syntactic binding between the young and older age group. Fig. 2A shows the TFR of correct syntactic binding minus no syntactic binding for the youngadults. Likewise, Fig. 2B shows the TFR of correct syntactic binding minus no syntactic binding for the older adults. The comparison of the condition difference (i.e., correct vs. no syntactic binding) between young and older adults revealed a difference in alpha power in a time window from 0.6 to 1.05s following presentation of the second word ($p = 0.03$). Specifically, there was a *larger* power increase in the correct syntactic binding relative to the no syntactic binding in the young adults, but a *smaller* power increase in the correct syntactic binding relative to no binding in the older adults (Fig. 2C). This difference was most pronounced in a cluster of electrodes over frontal and left parietal regions (Fig. 2D).

3.1.2. Syntactic binding in young adults

The group level results of the younger age group are summarized in Fig. 3. Fig. 3A and B shows the individual grand mean TFRs of the correct and no syntactic binding condition respectively, after removal of the spectral components of the ERP. Qualitatively, in both conditions, there was a power increase in alpha (8–12 Hz) and low beta (15–20 Hz) activity surrounding the presentation of the second word (at 0 s). This was followed by a suppression in the theta range (4–7 Hz) starting around 1s.

Table 4
Means and Standard Deviations of predictor variables in the older age group (N = 41).

Measurements	mean	sd
Working Memory	4.89	0.91
Processing Speed (Raw)	11.59	2.09
Processing Speed (Scaled)	60.00	10.50
Physical Activity	145.98	165.54
Hand grip	30.11	8.62
Age	69.29	3.98

Fig. 3C shows the TFR of the correct syntactic binding minus the no syntactic binding condition. Immediately preceding and following the onset of the second word, there appears to be a *larger* increase in alpha power (8–12 Hz) in the correct syntactic binding condition, a pattern opposite to that of the older adults. The pattern in young adults we observe in the present study is consistent with the young adults' patterns observed in Segaert et al. (2018). However, unlike in Segaert et al. (2018), the pattern did not yield a significant condition difference, in any of the frequency ranges (i.e., theta; alpha or low beta).[2] However, the larger increase in the alpha band in correct syntactic binding relative to no syntactic binding approaches significance ($p = 0.1$) in a time window between 0.65 and 0.76 s following the presentation of the second word (i.e., within the time window where a significant between-group difference was found).

3.1.3. Syntactic binding in older adults

The group level results are summarized in Fig. 4. Fig. 4A and B shows the individual grand mean TFRs of the correct syntactic binding and no syntactic binding condition respectively, after removal of the spectral components of the ERP. Qualitatively, in both conditions, the presentation of the first word (at −1.2s) induced a transient power increase in the theta and alpha range (likely reflecting the sensory responses to the onset of the sound stimuli). Following this, there was a power increase in alpha and low beta activity surrounding the presentation of the second word (at 0s), followed by a suppression in the alpha and beta range.

Fig. 4C shows the TFR of the correct syntactic binding condition minus the no syntactic binding condition. There was a significant difference in theta power (4–7 Hz) between the correct syntactic binding condition and the no syntactic binding condition, in the time window from −0.25- 0.1s relative to the presentation of the second word ($p = 0.05$). Power in the theta range returned to baseline in the correct syntactic binding condition during this time window, in contrast to a continued power increase in the no syntactic binding condition. The mean condition difference within this time interval was most pronounced over a cluster of left frontal and left-parietal electrodes for correct syntactic binding compared to no syntactic binding (Fig. 4D). In addition, a significantly smaller increase in alpha power (8–12 Hz) was observed in the correct syntactic binding condition from −0.25 to 0.3 s relative to the presentation of the second word ($p = 0.02$). This difference was most pronounced in a cluster of electrodes over left-frontal central and parietal regions (Fig. 4E). Lastly, there was a significant difference in beta power (15–20 Hz) in the time window −0.3 to 0.15s around the presentation of the second word ($p = 0.002$), such that the power increase was less sustained in the correct syntactic binding condition, compared to the no syntactic binding condition. This difference was most pronounced in a frontal-posterior cluster of electrodes (Fig. 4F).

To gain insight into the individual variation that underlies the grand average of these significant clusters, we calculated the power difference between the correct and no syntactic binding condition for each individual participant and averaged the power over the electrodes and time points of each significant cluster. The individual power difference values are shown in Fig. 4G–I. The participants plotted below the red lines show, in line with the grand mean of all participants, a *smaller* theta, alpha and beta increase for correct compared to no syntactic binding. The participants plotted above the red lines show, in contrast to the grand mean, a *larger* theta, alpha and beta power increase for the correct syntactic binding compared to the no binding condition. The individual participant values suggest there is considerable variability in the

[3] We also ran an ROI analysis using the frequency ranges and time windows where Segaert et al. (2018) reports condition differences, specifically in alpha (8–12 Hz) in the time window −0.4 to 0 and 0.05 to 0.35 relative to word 2 and in low beta (15–20 Hz) in the time window −0.25 to −0.15 relative to word 2. No significant differences were found.

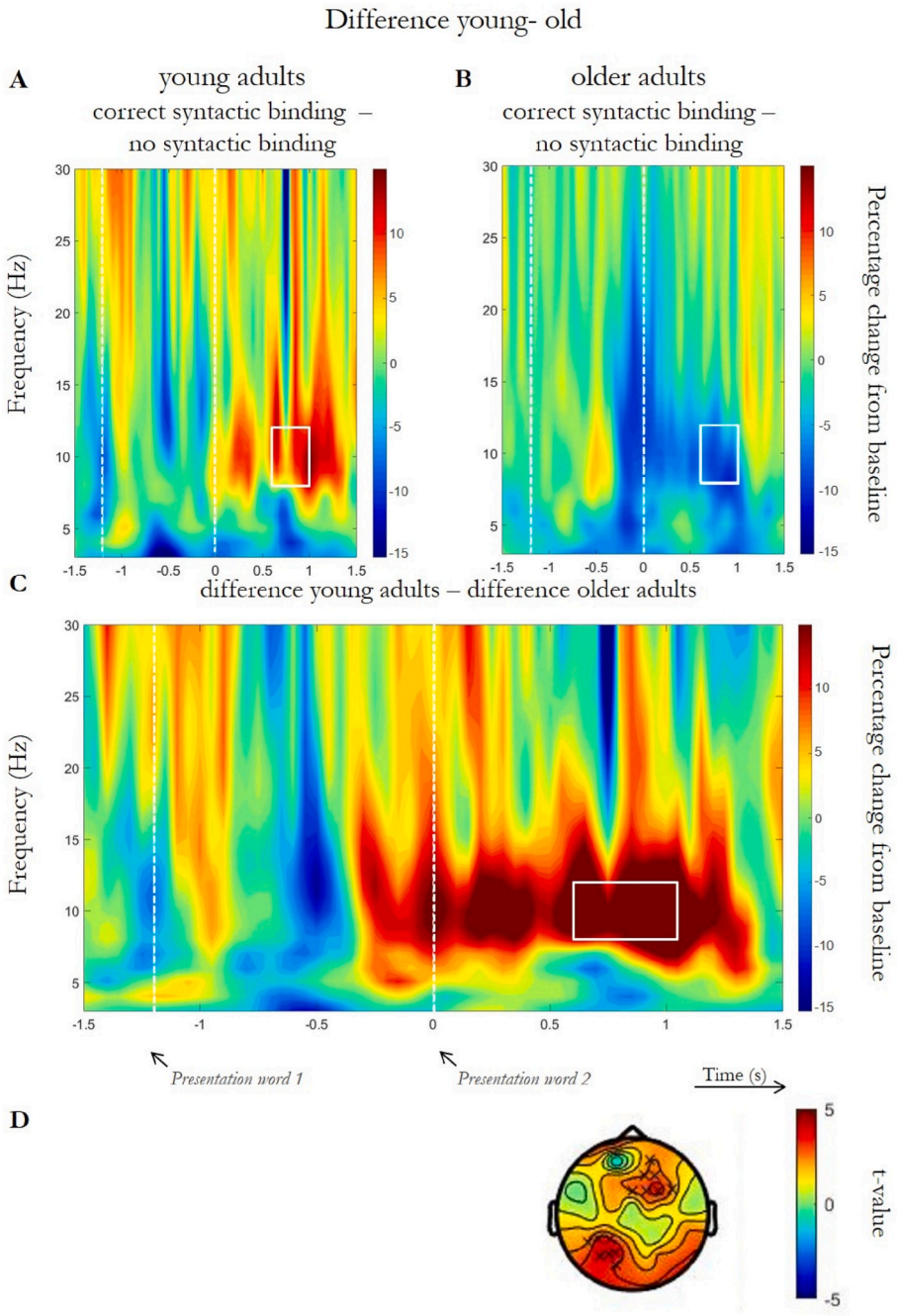

Fig. 2. TFRs of power for the contrast between correct syntactic binding and no syntactic binding. (A–B). Grand mean TFR (collapsed across electrode locations) for the contrast between the correct syntactic binding condition (e.g., *I sploff*) and the no syntactic binding condition (e.g., *dotches sploff*) for (A) young adults, and (B) older adults. (C) The comparison of the condition difference (correct vs. no syntactic binding) between young and older adults revealed a difference in alpha power in a time window from 0.6 to 1.05s following presentation of the second word (p = 0.03). Specifically, there was a larger power increase in the correct syntactic binding relative to the no syntactic binding in the younger adults, but a smaller power increase in the correct syntactic binding relative to no binding in the older adults. (D) The crosses ('x') illustrate the cluster of electrodes that show the most pronounced condition difference for alpha power, over the averaged time interval of 0.6–1.05s (rectangle in panel).

magnitude and the direction of the neural signature of syntactic binding.

3.2. No evidence for a relationship between syntactic comprehension performance (accuracy and reaction time) and neural signatures associated with syntactic binding within the older adult group

Our second aim was to investigate whether age-related changes in oscillatory signatures contribute to performance, and hence, are compensatory. Individual variability in syntactic comprehension performance is visualised in Fig. 5. The group average performance accuracy was 89%, with individual accuracy scores ranging from 58% up to 100% (Fig. 5A). We have used a cut-off score of 50% for accuracy, similar to previous work (Poulisse et al., 2019). However, using a more conservative cut-off of 65% did not affect the outcomes, for either the accuracy model or the response time model. The group average performance response time was 2883 ms, with individual scores ranging from 1145 ms to 6055 ms (Fig. 5B). Internal consistency estimates for accuracy and response time were calculated as Cronbach's alpha and as the correlation between an odd/even trial split, utilizing a similar approach as used in previous studies (e.g., Jackson, Rothmann & van de Vijver, 2006). Both accuracy and response time were found to be reliable measures (α = 0.87 and 0.97 respectively).

We first turn to the analyses of the relationship between the accuracy data and the neural signatures associated with syntactic binding. Table 5 presents the results from the multiple regression model predicting syntactic comprehension accuracy with the neural signatures of syntactic binding (that is, the theta, alpha and beta cluster), together with processing speed, working memory, physical activity, handgrip and age. The overall model fit was R^2 = 0.19. The model did not reach statistical significance (p = 0.50). The included predictors are therefore not able to

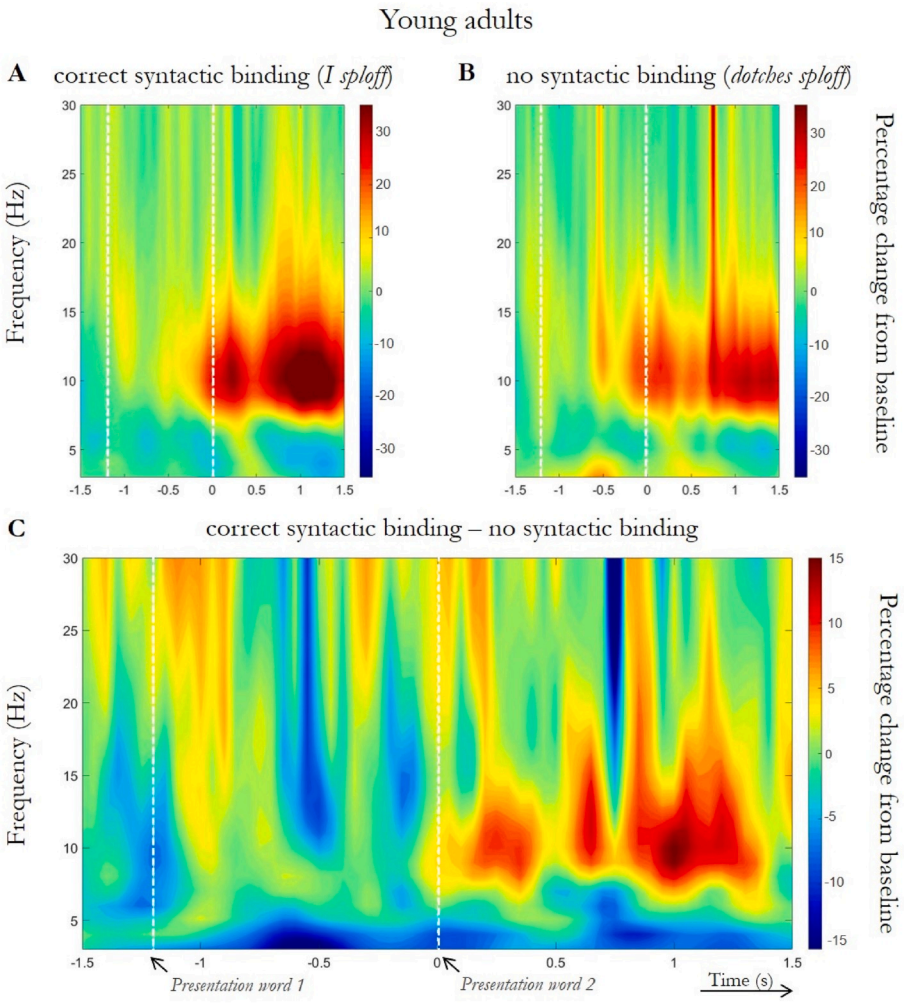

Fig. 3. Differences in theta (θ), alpha (α) and beta (β) power between the correct syntactic binding condition (e.g., *I sploff*) and the no syntactic binding condition (e.g., *dotches sploff*) in young adults. (A–C) TFR of conditions of interest for all electrodes after removal of the spectral components of the ERP, expressed as a percentage change from baseline (-2s to −1.5s before the onset of word 2) for (A) the correct syntactic binding condition; (B) the no syntactic binding condition and (C) correct minus no syntactic binding. While there was a larger increase in the alpha band in correct syntactic binding relative to no syntactic binding observed, this effect did not reach significance when accounting for multiple comparisons (p = 0.1).

explain variability in comprehension accuracy.

To estimate the statistical power of our model with our available sample size, we ran a post hoc power analysis using the *pwr.f2.test* function for general linear models of the *pwr package* in R (Champely et al., 2018). This revealed a statistical power of 0.46, given the current sample size (n = 41); the number of coefficients in the model (8) and the effect size (R^2 = 0.19) at an alpha level of 0.05.

Next, we turn to the analyses of the relationship between the reaction time data and the neural signatures associated with syntactic binding. Table 6 presents the results from the multiple regression model predicting response time with the neural signatures of syntactic binding (that is, the theta, alpha and beta cluster), together with processing speed, working memory, physical activity, handgrip and age. The overall model fit was R^2 = 0.20. The model did not reach statistical significance (p = 0.48); the included predictors are therefore not able to explain variability in comprehension accuracy.

To estimate the statistical power of our model with our available sample size, we ran a post hoc power analysis using the *pwr.f2.test* function for general linear models of the *pwr package* in R (Champely et al., 2018). This revealed a statistical power of 0.48, given the current sample size (n = 41); the number of coefficients in the model (8) and the effect size (R^2 = 0.20) at an alpha level of 0.05.

4. Discussion

We investigated age-related changes in the oscillatory mechanisms associated with syntactic binding in healthy ageing and whether these mechanisms are compensatory in nature, in that they support successful behavioural performance. Firstly, we found that syntactic binding (i.e., oscillatory power induced by the second word in the correct syntactic binding versus the no binding condition) was supported by different oscillatory patterns in older compared to young adults. At the group level, syntactic binding in young adults was associated with a *larger* increase in alpha (8–12 Hz) power, however, this difference did not reach statistical significance. In contrast, syntactic binding in older adults was associated with a *smaller* increase in theta (4–7 Hz), in alpha (8–12 Hz) and in beta (15–20 Hz) power. Interestingly, the different neural signatures in older compared to young adults were observed in the context of near equivalent behavioural performance. However, we did not find evidence that the age-related changes in oscillatory signatures associated with syntactic binding were related to the level of behavioural performance in older adults, thereby providing no support for the hypothesis that these age-related changes are compensatory in nature. We expand on the implications of these findings below.

4.1. Age-related differences in oscillatory activity associated with syntactic binding

At the group level, older adults show a different neural signature of syntactic binding compared to young adults. The young-old comparison showed a significant difference in alpha power in a time window from 0.6 to 1.05s following the presentation of the second word: young adults showed a *larger* increase in alpha power in the correct syntactic binding (relative to the no binding) condition, while the older adults showed a

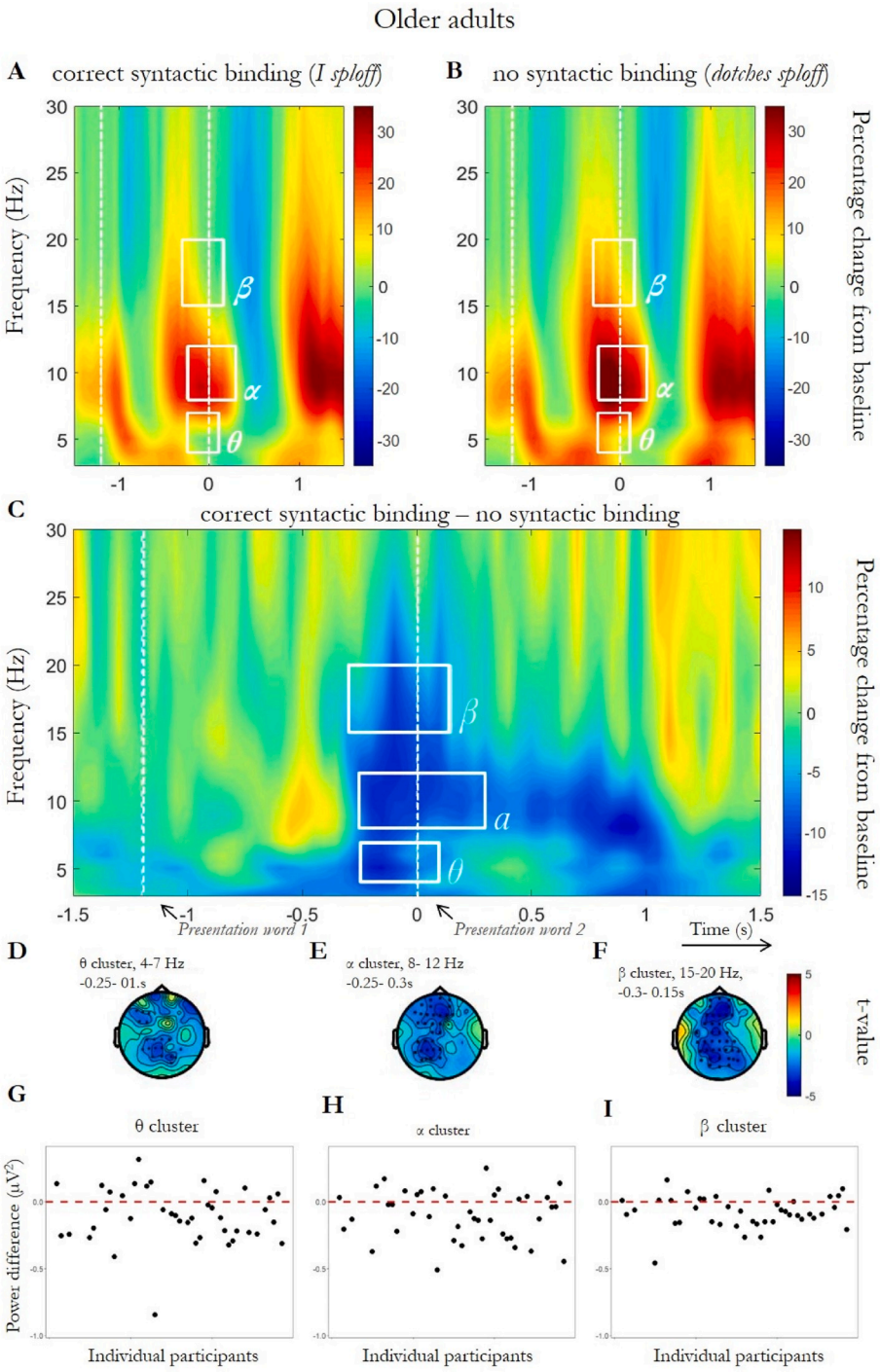

Fig. 4. Differences in theta (θ), alpha (α) and beta (β) power between the correct syntactic binding condition (e.g., *I sploff*) and the no syntactic binding condition (e.g., *dotches sploff*) in the older adults. (A–C) TFR of conditions of interest for all electrodes after removal of the spectral components of the ERP, expressed as a percentage change from baseline (-2s to −1.5s before the onset of word 2) for (A) the correct syntactic binding condition; (B) the no syntactic binding condition and (C) correct minus no syntactic binding. The rectangles indicate the time frequency clusters showing a significant difference between the two conditions: theta (4–7 Hz) in the time window −0.25- 0.1s ($p < 0.05$), alpha (8–12 Hz) in the time window −0.25–0.3s ($p < 0.02$), and beta (15–20 Hz) in the time window −0.3- 0.15s ($p < 0.002$), each showing a smaller increase in the correct syntactic binding vs. no syntactic binding condition. (D–F): The dots ('.') illustrate the cluster of electrodes that show the most pronounced condition difference for theta, alpha and beta power over the averaged time-window where the condition differences were observed. (G–I): Individual power differences between the correct syntactic binding and no syntactic binding condition (each dot represents a participant) for each of the significant time frequency clusters. Individuals plotted below the dotted line had a smaller power increase in the correct syntactic binding condition compared to the no syntactic binding condition, whereas individuals plotted above the line had a larger power increase in the correct, compared to the no syntactic binding condition.

smaller increase in alpha power. This functional neural change was found in the context of age-related slowing, but equivalent behavioural performance accuracy in older compared to young adults. These behavioural findings are in line with Poulisse et al. (2019), who similarly observed that older adults slowed down in the challenging pseudoverb condition, in order to make more accurate decisions. Moreover, the current results of the young adults parallel findings from Segaert et al. (2018), who observed a larger increase in alpha and beta power in syntactic binding (compared to no binding) in younger adults. While the pattern of results was statistically significant in Segaert et al. (2018), the condition differences were not significant within the young adult group in the current study. Importantly however, older adults showed a quantitatively and qualitatively different pattern of results. Specifically, syntactic binding (relative to no binding) in older adults was associated with a smaller increase in theta (4–7 Hz); alpha (8–12 Hz) and beta (15–20 Hz) power.

We will discuss these in turn, starting with the condition effects in the theta band. In older adults, in sentences for which binding occurs, the theta amplitude rebounds to baseline following a strong increase associated with the presentation of the first word. In contrast, in sentences for which no binding occurs, a prolonged increase in theta power was observed, resulting in a condition difference between −0.25s and 0.1s surrounding the presentation of the second word, which was maximal over a cluster of left frontal-parietal electrodes. This difference may be

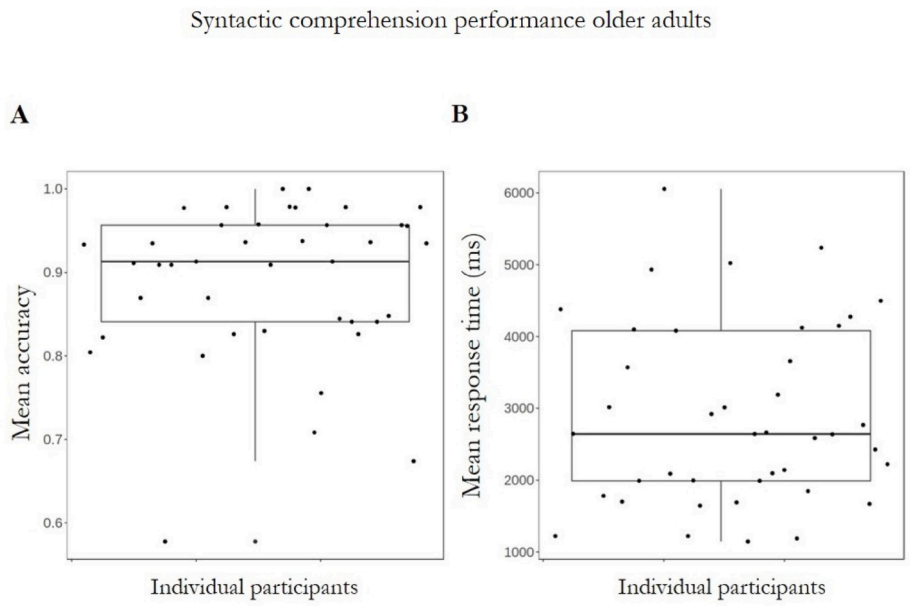

Fig. 5. Group averages and individual variability in behavioural syntactic comprehension performance in the older adults; accuracy (A) and reaction times (B). The performance measure is an average score for rejecting (for correct binding, e.g., "*I sploff*") or detecting (for incorrect binding, e.g., "*I sploffs*") morpho-syntactic agreement errors.

Table 5
Coefficient estimates, standard errors, t values and p values of the multiple regression model predicting accuracy in the older age group with the theta, alpha and beta cluster, processing speed, working memory, handgrip and physical activity as predictors.

Coefficient	Estimate	Std. Error	t value	p	
(Intercept)	1.203e+00	2.939e-01	4.01	<0.001	***
theta cluster	2.458e-02	1.121e-01	0.22	0.83	
alpha cluster	8.799e-02	1.634e-01	0.54	0.59	
beta cluster	−9.952e-02	2.073e-01	−0.48	0.63	
processing speed	−2.337e-03	1.569e-03	−1.49	0.15	
working memory	2.276e-03	1.748e-02	1.30	0.20	
Handgrip	−1.498e-02	1.558e-02	−0.96	0.34	
physical activity	6.662e-06	9.185e-05	0.07	0.94	
Age	−4.476e-03	4.260e-03	−1.05	0.30	

Signif. codes: 0 *** 0.001 ** 0.01 * 0.05. 0.1 ‘’ 1.

Table 6
Coefficient estimates, standard errors, t values and p values of the multiple regression model predicting response time in the older age group with the theta, alpha and beta cluster, processing speed, working memory, handgrip and physical activity as predictors.

Coefficient	Estimate	Std. Error	t value	p
(Intercept)	1981.923	3964.083	0.50	0.62
theta cluster	5.802	1511.928	0.01	0.99
alpha cluster	579.311	2203.282	0.26	0.80
beta cluster	797.280	2796.003	0.29	0.77
processing speed	−24.934	21.162	−1.79	0.25
working memory	−340.868	235.775	−1.45	0.16
Handgrip	−201.718	210.107	−0.96	0.34
physical activity	1.365	1.239	1.10	0.28
Age	14.724	57.449	0.26	0.80

Signif. codes: 0 *** 0.001 ** 0.01 * 0.05. 0.1 ‘’ 1.

related to prolonged lexical-semantic retrieval operations in the no syntactic binding relative to the correct syntactic binding condition. Note that in the correct syntactic binding condition, the theta response shows a typical pattern, characterized by an event-related increase in theta power, followed by a return to baseline. Of relevance here is that the first word in the correct syntactic binding condition is a pronoun, i.e., a high frequency word. In contrast, the theta response in the no syntactic binding condition deviates from the typical pattern: power does not return to baseline until after the presentation of the second word. Here, the first word is a pseudoverb, i.e., a word with no representation in the mental lexicon. However, the fact that no mental representation exists for pseudoverbs does not mean that no lexical-semantic retrieval operations occur. In other words, the increased and prolonged theta power in the no syntactic binding condition may be indicative of maintained lexical-semantic processing. Note that neither the current study nor Segaert et al. (2018) found any condition differences in the theta band in younger adults. This suggests the prolonged lexical semantic processing in the no syntactic binding condition may be an age-related phenomenon. In other words, even though the minimal phrases carry limited meaning, older adults may nevertheless continue to recruit semantic resources to process the syntactic information, whereas younger adults more easily adapt to the greater emphasis on syntactic binding that the experimental manipulation exerts on the processing requirements of the stimuli. A study by Schneider et al. (2016) further supports this interpretation. Specifically, this study investigated the neural oscillations underlying grammatically correct and incorrect sentences in a group of young adults (aged 18–31). While the integration of semantic information associated with the presentation of each new word in the sentence was expected to elicit a theta increase (i.e., in accordance with Bastiaansen, van Berkum & Hagoort, 2002b and Bastiaansen et al., 2010), they observed a decrease in theta power following the critical verb in sentences containing a subject-verb agreement violation. Crucially, an explicit syntactic judgement task was used to assess comprehension performance. The authors speculate that the unexpected theta decrease may reflect that young adults minimized or stopped integrating semantic information after detecting a syntactic violation given that the syntactic error was the primary information required for making a subsequent grammaticality judgement. In other words, these findings tentatively suggest that semantic processing in young adults may halt, or minimize when they are required to explicitly focus on syntactic information. The experimental manipulation in the current study and Segaert et al. (2018) equally forced participants to focus on syntactic information to process the phrases. While the absence of any theta effects in young adults in both the current study

and Segaert et al. (2018) indeed suggests that semantic processing in young adults was minimal, we tentatively suggest that the theta effect in the older age group indicates involvement of semantic processing despite the minimal semantic information that could be retrieved. Supporting evidence for this idea comes from Beese et al. (2019b) who found that the use of syntactic constraints in sentence processing was compromised in older compared to young adults, while the benefit of semantic information was comparable across age groups. The authors propose that the increased reliance on semantic information in older adults may lead to a change in sentence processing strategies toward a semantic approach. The observed theta power differences in older adults in the current study might, therefore, reflect this processing change at the oscillatory level.

In the older age group, we also found a smaller increase in the correct syntactic binding relative to the no syntactic binding condition in the alpha (8–12 Hz) and low beta (15–20Hz) band in a time window surrounding the second word. In Segaert et al. (2018), modulations in the alpha and beta band were taken to reflect neural signatures for the expectation of binding and for binding taking place. However, while the general task-related increase in alpha and beta power is consistent with Segaert et al. (2018), findings from the current study suggest the relative power difference between conditions inverts between the two age groups. Specifically, the power difference associated with syntactic binding was *negative* in older adults (i.e., there was a *smaller* increase in alpha and beta power in correct relative to no syntactic binding). In contrast, results from the current work and Segaert et al. (2018) show a *positive* power difference in young adults (i.e., there was a *larger* increase in alpha and beta power in correct relative to no syntactic binding). The inverted response pattern cannot be readily reconciled with the proposed idea of increased reliance on semantic processing in older adults. Specifically, semantic (retrieval) processes are commonly associated with a suppression (i.e., a decrease) in alpha power (e.g., Klimesch et al., 1997; Klimesch, 1999; Mazaheri et al., 2018). Therefore, reasoning based on an age-related increase in semantic processing would predict a decrease in alpha power in sentences for which binding occurs and a stronger decrease in sentences for which no binding occurs. In contrast, we found an alpha increase that was overall stronger in sentences for which no syntactic binding occurs. Indeed, considering these two processes (i.e., lexical-semantic retrieval and syntactic binding operations) in isolation, one would expect the opposite synchronization pattern. However, the evaluation of the sentences in this study likely required both lexical-semantic retrieval as well as syntactic binding processing mechanisms. Different types of psycholinguistic information are, to a certain extent, processed in parallel (Pulvermüller et al., 2009). Consequently, these coexistent processes may generate oscillations that temporally overlap. From this viewpoint, the observed increase in alpha power may in fact be a summation of heterogeneous oscillatory mechanisms reflecting different, parallel processes. In support of this interpretation, the alpha power modulations were observed over a large cluster of left-frontal central and parietal regions and over a long time window lasting 0.45s. The exact source locations of the different oscillatory activities are difficult to compute due to the low spatial resolution of EEG. In future research, this issue could be clarified by using MEG instead of EEG.

4.2. No evidence for a relationship between syntactic comprehension performance and the neural signatures associated with syntactic binding in healthy ageing

Having established that, at the group level, the neural signature of syntactic binding is different in older compared to young adults, a subsequent question is how these age-related changes in neural activity may contribute to successful behavioural performance in older age. Crucially, performance differences between the young and older adults were minimal: older adults were slower but equally accurate in detecting syntactic agreement errors. In the context of (near) equivalent behavioural performance between the two age groups, the observed differences in neural activity might reflect compensatory activity. The strongest evidence for compensation would be the existence of a direct relationship between the recruitment of neural resources and behavioural performance in older adults, but both the regression analysis predicting performance accuracy and response time generated inconclusive results. In this sense, our results are consistent with Tyler et al. (2010) and Peelle et al. (2009) who observed additional neural activity in older compared to younger adults in the absence of a relationship between the additional activity and behavioural performance. Nevertheless, a few important points should be made regarding the fact that we found no relationship.

Firstly, the absence of evidence is not equal to evidence of an absence. A possibility is that the age-related functional changes that we observed are not compensatory. Instead, they could reflect a general decline in neural efficiency, or dedifferentiation. Alternatively, as is always the case with null-findings, it is possible that a relation between behavioural performance and brain function exists for syntactic processing in healthy ageing, but that we were unable to detect such a relationship.

One possible reason why we may not have observed such a relationship is that our behavioural measure may not have been sensitive enough. However, even though the results of the models relating behavioural performance to the neural signatures were inconclusive, the dependent variables that were used to measure syntactic comprehension performance in this study were reliable measures. Specifically, both measures of syntactic comprehension (i.e., accuracy and RT) were found to have a high level of internal consistency.

Alternatively, it may be that the neural dynamics observed for older adults merely reflect generic properties of the neural signature of syntactic binding (i.e., properties that are present in all older individuals, but lacking the specificity to differentiate between sub groups). A critical remark in this connection is the fact that the alpha frequency in particular shows large age-related inter-individual differences (Klimesch, 1999). Consequently, it may be that the effect of age on the oscillatory dynamics of syntactic binding can only be observed by discarding fixed frequency bands. While using individual based alpha frequency bands would be a valuable direction for future ageing research on individual variability, it would not be a suitable approach in the current study, given that the changes in the EEG were not limited to modulations in the alpha band. When we did look at the individual peak-frequency of alpha activity, we found it to range between 9 and 11 Hz, which fell within the frequency bands we had previously used to define alpha activity in younger adults.

Lastly, the post-hoc power analyses using the effect sizes generated by the regression models and the desired power set to 0.8, revealed that a sample size of 73 and 70 is required to relate the neural signatures of syntactic processing to the accuracy and response time for syntactic judgements respectively. This suggests that if a relationship exists between syntactic comprehension performance and age-related functional neural changes, the relationship would be of a weak and complex nature, such that any study aimed at demonstrating a relationship unequivocally would require a very high number of participants.

4.3. Limitations and future directions

A number of limitations to our approach deserve to be mentioned. Firstly, our approach to minimizing the contribution of semantics by using pseudoverbs comes with the constraint that the neural signatures in the time window between the first and the second word may reflect differences between processing an existing word (i.e., a pronoun) and a pseudoverb. However, this is not the most parsimonious explanation given the onset of these condition differences in relation to the first word. Specifically, compared to previous EEG findings on differences between real words and pseudowords (e.g., Münte et al., 1997; Shtyrov et al., 2005; Shtyrov and Lenzen, 2017), the observed effects in the

current study are relatively late (i.e., both the alpha and beta effects start 0.95s after the onset of word one).

The use of real verbs instead of (or perhaps in addition to) pseudoverbs could further elucidate the exact mechanism behind the observed signatures in the current study. This would be helpful in order to verify whether the observed age differences are indeed related to an increased reliance on semantic information with increasing age. Specifically, this account would lead us to predict that the neural signature associated with syntactic binding in older adults would show a closer resemblance to the neural signature in young adults for syntactic structures that are embedded in a semantically meaningful context. In line with this interpretation, our previous work showed that age-related decline in syntactic comprehension performance was reduced in real verb sentences compared to pseudoverb sentences (Poulisse et al., 2019).

Furthermore, the predictability of the conditions at the onset of the first word was not ideally controlled in the current design. Similar to our previous behavioural work (Poulisse et al., 2019), the inclusion of a condition in which a pseudoverb is paired with an adjective (e.g., "*cuggs slowly*") could address this issue in future work. Furthermore, counterbalancing the behavioural and the EEG task in future work would eliminate the potential influence of order effects on the EEG results.

Lastly, after taking into account inter-individual variability in our functional measure, it was evident that only half of the participants responded in a way that was in accordance with the group mean average. Research aimed at understanding what accounts for this inter-individual variability will be a critical direction for future research. Experiments specifically designed to allow for mixed effects model fits (i.e., accounting for individual by-subject variation) would be a particularly valuable future direction for estimating inter-individual variation in greater detail (Baayen et al., 2008).

4.4. General conclusions

This study provides novel evidence on age-related functional change associated with syntactic processing. We found that one of the most basic elements of syntactic processing, namely syntactic binding, is associated with a qualitatively and quantitatively different neural signature in healthy older, compared to young adults. Syntactic binding in older adults is associated with a *smaller* increase in theta (4–7 Hz), alpha (8–12 Hz) and beta (15–20 Hz) power for binding (compared to no binding) conditions, while young adults show the opposite pattern, that is, a *larger* increase in alpha power for binding (compared to no binding) conditions. We suggest that the observed functional neural differences between young and older adults are possibly related to an increased reliance on semantic processing with increasing age. However, we did not identify a relationship between behavioural performance and the neural signatures of syntactic binding in the older age group, leaving a functional interpretation of the observed neural change in terms of compensatory mechanisms an open question for future research.

Data availability

The stimulus materials are available in the OSF repository [https://osf.io/z5sk9/], and the data can be made available upon request to the corresponding author.

Declaration of competing interest

None.

CRediT authorship contribution statement

Charlotte Poulisse: Conceptualization, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. **Linda Wheeldon:** Conceptualization, Writing - review & editing. **Rupali Limachya:** Data curation, Writing - review & editing. **Ali Mazaheri:** Writing - review & editing. **Katrien Segaert:** Conceptualization, Writing - review & editing.

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Appendix A. Supplementary data

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References

Alatorre-Cruz, G.C., Silva-Pereyra, J., Fernández, T., Rodríguez-Camacho, M.A., Castro-Chavira, S.A., Sanchez-Lopez, J., 2018. Effects of age and working memory load on syntactic processing: an event-related potential study. Front. Hum. Neurosci. 12, 185.

Antonenko, D., Brauer, J., Meinzer, M., Fengler, A., Kerti, L., Friederici, A.D., Flöel, A., 2013. Functional and structural syntax networks in aging. Neuroimage 83, 513–523. https://doi.org/10.1016/j.neuroimage.2013.07.018.

Baayen, R.H., Davidson, D.J., Bates, D.M., 2008. Mixed-effects modeling with crossed random effects for subjects and items. J. Mem. Lang. 59 (4), 390–412.

Baltes, P.B., Lindenberger, U., 1997. Emergence of a powerful connection between sensory and cognitive functions across the adult life span: a new window to the study of cognitive aging? Psychol. Aging 12 (1), 12.

Barnes, D.E., Yaffe, K., Satariano, W.A., Tager, I.B., 2003. A longitudinal study of cardiorespiratory fitness and cognitive function in healthy older adults. J. Am. Geriatr. Soc. 51 (4), 459–465.

Bastiaansen, M.C.M., van Berkum, J.J.A., Hagoort, P., 2002a. Syntactic processing modulates the theta rhythm of the human EEG. Neuroimage 17, 1479–1492. https://doi.org/10.1006/nimg.2002.1275.

Bastiaansen, M.C.M., Van Berkum, J.J.A., Hagoort, P., 2002b. Event-related theta power increases in the human EEG during online sentence processing. Neurosci. Lett. 323 (1), 13–16. https://doi.org/10.1016/S0304-3940(01)02535-6.

Bastiaansen, M., Hagoort, P., 2003. Event-induced theta responses as a window on the dynamics of memory. Cortex. https://doi.org/10.1016/S0010-9452 (08)70873-6.

Bastiaansen, M., Magyari, L., Hagoort, P., 2010. Syntactic unification operations are reflected in oscillatory dynamics during on-line sentence comprehension. J. Cognit. Neurosci. 22 (7), 1333–1347.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2014. Fitting linear mixed-effects models using lme4. J. Stat. Software 67 (1), 51. https://doi.org/10.18637/jss.v067.i01.

Beese, C., Vassileiou, B., Friederici, A.D., Meyer, L., 2019a. Age differences in encoding-related alpha power reflect sentence comprehension difficulties. Front. Aging Neurosci. 11, 183.

Beese, C., Werkle-Bergner, M., Lindenberger, U., Friederici, A.D., Meyer, L., 2019b. Adult age differences in the benefit of syntactic and semantic constraints for sentence processing. Psychol. Aging 34 (1), 43.

Bonhage, C.E., Meyer, L., Gruber, T., Friederici, A.D., Mueller, J.L., 2017. Oscillatory EEG dynamics underlying automatic chunking during sentence processing. Neuroimage 152, 647–657.

Cabeza, R., Albert, M., Belleville, S., Craik, F.I.M., Duarte, A., Grady, C.L., Rajah, M.N., 2018. Maintenance, reserve and compensation: the cognitive neuroscience of healthy ageing. Nat. Rev. Neurosci. https://doi.org/10.1038/s41583-018-0068-2.

Cabeza, R., Anderson, N.D., Locantore, J.K., McIntosh, A.R., 2002. Aging gracefully: compensatory brain activity in high-performing older adults. Neuroimage 17 (3), 1394–1402. https://doi.org/10.1006/nimg.2002.1280.

Campbell, K.L., Samu, D., Davis, S.W., Geerligs, L., Mustafa, A., Tyler, L.K., 2016. Robust resilience of the frontotemporal syntax system to aging. J. Neurosci. https://doi.org/10.1523/JNEUROSCI.4561-15.2016.

Caplan, D., Waters, G., 2005. The relationship between age, processing speed, working memory capacity, and language comprehension. Memory 13 (3–4), 403–413.

Champely, S., Ekstrom, C., Dalgaard, P., Gill, J., Weibelzahl, S., Anandkumer, A., Ford, C., Volcic, R., De Rosario, H., 2018. Basic Functions for Power Analyses. Retrieved from. https://CRAN.R-project.org/package=pwr.

Chiang, A.K.I., Rennie, C.J., Robinson, P.A., Van Albada, S.J., Kerr, C.C., 2011. Age trends and sex differences of alpha rhythms including split alpha peaks. Clin. Neurophysiol. 122 (8), 1505–1517.

Chomsky, N., 1995. The Minimalist Program. The MIT Press, Cambridge, Massachussets.

Colcombe, S.J., Kramer, A.F., Erickson, K.I., Scalf, P., McAuley, E., Cohen, N.J., Elavsky, S., 2004. Cardiovascular fitness, cortical plasticity, and aging. Proc. Natl. Acad. Sci. U. S. A. 101 (9), 3316–3321. https://doi.org/10.1073/pnas.0400266101.
Davidson, D.J., Indefrey, P., 2007. An inverse relation between event-related and time–frequency violation responses in sentence processing. Brain Res. 1158, 81–92.
Davis, S.W., Dennis, N.A., Daselaar, S.M., Fleck, M.S., Cabeza, R., 2008. Que PASA? The posterior–anterior shift in aging. Cerebr. Cortex 18 (5), 1201–1209.
Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J. Neurosci. Methods 134 (1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009.
Federmeier, K.D., McLennan, D.B., De Ochoa, E., Kutas, M., 2002. The impact of semantic memory organization and sentence context information on spoken language processing by younger and older adults: an ERP study. Psychophysiology 39, 133–146. https://doi.org/10.1017/s0048577202001373.
Federmeier, K.D., Kutas, M., 2005. Aging in context: age-related changes in context use during language comprehension. Psychophysiology 42, 133–141.
Fjell, A.M., Walhovd, K.B., 2010. Structural brain changes in aging: courses, causes and cognitive consequences. Rev. Neurosci. 21 (3), 187–222.
Friederici, A.D., 2004. Event-related brain potential studies in language. Curr. Neurol. Neurosci. Rep. 4 (6), 466–470.
Grady, C., 2012. Trends in neurocognitive aging. Nat. Rev. Neurosci. 13 (7), 491.
Grandy, T.H., Werkle-Bergner, M., Chicherio, C., Lövdén, M., Schmiedek, F., Lindenberger, U., 2013a. Individual alpha peak frequency is related to latent factors of general cognitive abilities. Neuroimage 79, 10–18.
Grandy, T.H., Werkle-Bergner, M., Chicherio, C., Schmiedek, F., Lövdén, M., Lindenberger, U., 2013b. Peak individual alpha frequency qualifies as a stable neurophysiological trait marker in healthy younger and older adults. Psychophysiology 50 (6), 570–582.
Grossman, M., Cooke, A., DeVita, C., Alsop, D., Detre, J., Chen, W., Gee, J., 2002. Age-related changes in working memory during sentence comprehension: an fMRI study. Neuroimage 15 (2), 302–317. https://doi.org/10.1006/nimg.2001.0971.
Hagoort, P., 2005. On Broca, brain, and binding: a new framework. Trends Cognit. Sci. 9, 416–423.
Hagoort, P., 2009. Reflections on the neurobiology of syntax. In: Bickerton, D., Szathmary, E. (Eds.), Biological Foundations and Origin of Syntax. MIT Press, Cambridge, MA.
Hagoort, P., 2016. A model on the neurobiology of language beyond single word processing. In: Hickok, G., Small, S. (Eds.), Neurobiology of Language. Elsevier, Amsterdam, pp. 339–347.
Jackson, L.T., Rothmann, S., Van de Vijver, F.J., 2006. A model of work-related well-being for educators in South Africa. *Stress and Health*. J. Int. Soc. Invest. Stress 22 (4), 263–274.
Johnson, M.K., 1996. Feature memory and binding in young and older adults. Mem. Cognit. 24 (4), 403–416.
Kemmer, L., Coulson, S., De Ochoa, E., Kutas, M., 2004. Syntactic processing with aging: an event-related potential study. Psychophysiology 41 (3), 372–384.
Kemtes, K.A., Kemper, S., 1997. Younger and older adults' on-line processing of syntactically ambiguous sentences. Psychol. Aging 12 (2), 362.
Klimesch, W., Doppelmayr, M., Pachinger, T., Russegger, H., 1997. Event-related desynchronization in the alpha band and the processing of semantic information. Cognit. Brain Res. 6 (2), 83–94.
Klimesch, W., Schimke, H., Pfurtscheller, G., 1993. Alpha frequency, cognitive load and memory performance. Brain Topogr. 5 (3), 241–251.
Klimesch, W., 1999. EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. Brain Res. Rev. 29 (2–3), 169–195.
Lam, N.H., Schoffelen, J.M., Uddén, J., Hultén, A., Hagoort, P., 2016. Neural activity during sentence processing as reflected in theta, alpha, beta, and gamma oscillations. Neuroimage 142, 43–54.
Lara, J., Cooper, R., Nissan, J., Ginty, A.T., Khaw, K.-T., Deary, I.J., Mathers, J.C., 2015. A proposed panel of biomarkers of healthy ageing. BMC Med. 13 (1), 222. https://doi.org/10.1186/s12916-015-0470-9.
Leckey, M., Federmeier, K.D., 2017. Age-related shifts in hemispheric dominance for syntactic processing. Psychophysiology 54 (12), 1929–1939.
Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. J. Neurosci. Methods 164 (1), 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024.
Mazaheri, A., Jensen, O., 2008. Asymmetric amplitude modulations of brain oscillations generate slow evoked responses. J. Neurosci. 28 (31), 7781–7787.
Mazaheri, A., Picton, T.W., 2005. EEG spectral dynamics during discrimination of auditory and visual targets. Cognit. Brain Res. 24 (1), 81–96.
Mazaheri, A., Segaert, K., Olichney, J., Yang, J.C., Niu, Y.Q., Shapiro, K., Bowman, H., 2018. EEG oscillations during word processing predict MCI conversion to Alzheimer's disease. Neuroimage: Clinical 17, 188–197.
Meyer, L., Obleser, J., Friederici, A.D., 2013. Left parietal alpha enhancement during working memory-intensive sentence processing. Cortex 49 (3), 711–721.
Meyer, L., 2018. The neural oscillations of speech processing and language comprehension: state of the art and emerging mechanisms. Eur. J. Neurosci. 48 (7), 2609–2621.
Mitchell, K.J., Johnson, M.K., Raye, C.L., Mather, M., D'Esposito, M., 2000. Aging and reflective processes of working memory: binding and test load deficits. Psychol. Aging 15 (3), 527.
Münte, T.F., Matzke, M., Johannes, S., 1997. Brain activity associated with syntactic incongruencies in words and pseudo-words. J. Cognit. Neurosci. 9 (3), 318–329.
Nikulin, V.V., Linkenkaer-Hansen, K., Nolte, G., Lemm, S., Müller, K.R., Ilmoniemi, R.J., Curio, G., 2007. A novel mechanism for evoked responses in the human brain. Eur. J. Neurosci. 25 (10), 3146–3154.
Obler, L.K., Fein, D., Nicholas, M., Albert, M.L., 1991. Auditory comprehension and aging: decline in syntactic processing. Appl. Psycholinguist. https://doi.org/10.1017/S0142716400005865.
Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.-M., 2011. FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Comput. Intell. Neurosci. 156869. https://doi.org/10.1155/2011/156869, 2011.
Peelle, J.E., 2019. Language and Aging. The Oxford handbook of neurolinguistics, 295-216.
Peelle, J.E., Troiani, V., Wingfield, A., Grossman, M., 2009. Neural processing during older adults' comprehension of spoken sentences: age differences in resource allocation and connectivity. Cerebr. Cortex 20 (4), 773–782.
Poulisse, C., Wheeldon, L., Segaert, K., 2019. Evidence against preserved syntactic comprehension in healthy aging. J. Exp. Psychol. Learn. Mem. Cognit. https://doi.org/10.1101/299883 (in press).
Prystauka, Y., Lewis, A.G., 2019. The Power of Neural Oscillations to Inform Sentence Comprehension: A Linguistic Perspective. Language and Linguistics Compass, e12347.
Pulvermüller, F., Shtyrov, Y., Hauk, O., 2009. Understanding in an instant: neurophysiological evidence for mechanistic language circuits in the brain. Brain Lang. 110 (2), 81–94.
R Core Team, 2015. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from. https://www.r-project.org/.
Raz, N., 2009. Decline and compensation in aging brain and cognition: promises and constraints. Preface. *Neuropsychology Review* 19 (4), 411–414. https://doi.org/10.1007/s11065-009-9122-1.
Rentzsch, J., Jockers-Scherübl, M.C., Boutros, N.N., Gallinat, J., 2008. Test–retest reliability of P50, N100 and P200 auditory sensory gating in healthy subjects. Int. J. Psychophysiol. 67 (2), 81–90.
Salthouse, T.A., 1996. The processing-speed theory of adult age differences in cognition. Psychol. Rev. 103 (3), 403–428. Retrieved from. http://www.ncbi.nlm.nih.gov/pubmed/8759042.
Sanchez-Lopez, J., Silva-Pereyra, J., Fernández, T., Alatorre-Cruz, G.C., Castro-Chavira, S.A., González-López, M., Sánchez-Moguel, S.M., 2018. High levels of incidental physical activity are positively associated with cognition and EEG activity in aging. PloS One 13 (1).
Sander, M.C., Werkle-Bergner, M., Lindenberger, U., 2011. Binding and strategic selection in working memory: a lifespan dissociation. Psychol. Aging 26 (3), 612.
Schneider, J.M., Abel, A.D., Ogiela, D.A., Middleton, A.E., Maguire, M.J., 2016. Developmental differences in beta and theta power during sentence processing. Developmental Cognitive Neuroscience 19, 19–30.
Segaert, K., Lucas, S.J.E., Burley, C.V., Segaert, P., Milner, A.E., Ryan, M., Wheeldon, L., 2018b. Fit to Speak - Physical Fitness Is Associated with Reduced Language Decline in Healthy Ageing. Retrieved from. http://arxiv.org/abs/1801.01441.
Segaert, K., Mazaheri, A., Hagoort, P., 2018. Binding language: structuring sentences through precisely timed oscillatory mechanisms. Eur. J. Neurosci. 48 (7), 2651–2662.
Shafto, M.A., Tyler, L.K., 2014. Language in the aging brain: the network dynamics of cognitive decline and preservation. Science (New York, N.Y.) 346 (6209), 583–587. https://doi.org/10.1126/science.1254404.
Shafto, M.A., Henson, R.N., Matthews, F.E., Taylor, J.R., Emery, T., Erzinclioglu, S., Hanley, C., Rowe, J.B., Cusack, R., Calder, A.J., Marslen-Wilson, W.D., Duncan, J., Dagleish, T., Brayne, C., Tyler, L.K., 2019. Cognitive diversity in a healthy aging cohort: cross-domain cognition in the cam-CAN project. J. Aging Health, 0898264319878095.
Shtyrov, Y., Lenzen, M., 2017. First-pass neocortical processing of spoken language takes only 30 msec: electrophysiological evidence. Cognit. Neurosci. 8 (1), 24–38.
Shtyrov, Y., Pihko, E., Pulvermüller, F., 2005. Determinants of dominance: is language laterality explained by physical or linguistic features of speech? Neuroimage 27 (1), 37–47.
Tyler, L.K., Shafto, M.A., Randall, B., Wright, P., Marslen-Wilson, W.D., Stamatakis, E.A., 2010. Preserving syntactic processing across the adult life span: the modulation of the frontotemporal language system in the context of age-related atrophy. Cerebr. Cortex 20 (2), 352–364. https://doi.org/10.1093/cercor/bhp105.
Ullman, M.T., Corkin, S., Coppola, M., Hickok, G., Growdon, J.H., Koroshetz, W.J., Pinker, S., 1997. A neural dissocation within language: evidence that the mental dictionary is part of declarative memory, and that grammatical rules are processed by the procedural system. J. Cognit. Neurosci. 9 (2), 266–276. https://doi.org/10.1162/jocn.1997.9.2.266.
Vassileiou, B., Meyer, L., Beese, C., Friederici, A.D., 2018. Alignment of alpha-band desynchronization with syntactic structure predicts successful sentence comprehension. Neuroimage 175, 286–296.
van Diepen, R.M., Cohen, M.X., Denys, D., Mazaheri, A., 2015. Attention and temporal expectations modulate power, not phase, of ongoing alpha oscillations. J. Cognit. Neurosci. 27 (8), 1573–1586. https://doi.org/10.1162/jocn_a_00803.
van Diepen, R.M., Mazaheri, A., 2017. Cross-sensory modulation of alpha oscillatory activity: suppression, idling, and default resource allocation. Eur. J. Neurosci. 45 (11), 1431–1438. https://doi.org/10.1111/ejn.13570.
van Diepen, R.M., Miller, L.M., Mazaheri, A., Geng, J.J., 2016. The role of alpha activity in spatial and feature-based attention. eNeuro 3 (5). https://doi.org/10.1523/ENEURO.0204-16.2016.
Waters, G.S., Caplan, D., 2001. Age, working memory and on-line syntactic processing in sentence comprehension. Psychol. Aging 16 (1), 128–144. https://doi.org/10.1037/0882-7974.16.1.128.

Waters, G.S., Caplan, D., 2003. The reliability and stability of verbal working memory measures. Behav. Res. Methods Instrum. Comput. 35 (4), 550–564. https://doi.org/10.3758/BF03195534.
Whitmarsh, S., Nieuwenhuis, I.L., Barendregt, H., Jensen, O., 2011. Sensorimotor alpha activity is modulated in response to the observation of pain in others. Front. Hum. Neurosci. 5, 91.
Wingfield, A., Grossman, M., 2006. Language and the aging brain: patterns of neural compensation revealed by functional brain imaging. J. Neurophysiol. 96 (6), 2830–2839. https://doi.org/10.1152/jn.00628.2006.
Wingfield, A., McCoy, S.L., Peelle, J.E., Tun, P.A., Cox, C.L., 2006. Effects of adult aging and hearing loss on comprehension of rapid speech varying in syntactic complexity. J. Am. Acad. Audiol. https://doi.org/10.3766/jaaa.17.7.
Wingfield, A., Peelle, J.E., Grossman, M., 2003. Speech rate and syntactic complexity as multiplicative factors in speech comprehension by young and older adults. Aging Neuropsychol. Cognit. 10 (4), 310–322. https://doi.org/10.1076/anec.10.4.310.28974.
Wlotko, E.W., Federmeier, K.D., Kutas, M., 2012. To predict or not to predict: age-related differences in the use of sentential context. Psychol. Aging 27 (4), 975.
Wlotko, E.W., Federmeier, K.D., 2012. Age-related changes in the impact of contextual strength on multiple aspects of sentence comprehension. Psychophysiology 49 (6), 770–785.
Wlotko, E.W., Lee, C.L., Federmeier, K.D., 2010. Language of the aging brain: event-related potential studies of comprehension in older adults. Language and linguistics compass 4 (8), 623–638.
Zaccarella, E., Friederici, A.D., 2015. Merge in the human brain: a sub-region based functional investigation in the left pars opercularis. Front. Psychol. 6, 1818.