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Modulation in Alpha Band Activity Reflects Syntax Composition: An MEG Study of Minimal Syntactic Binding

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Abstract

Successful sentence comprehension requires the binding, or composition, of multiple words into larger structures to establish meaning. Using magnetoencephalography (MEG), we investigated the neural mechanisms involved in binding of language at the level of syntax, in a task in which contributions from semantics were minimized. Participants were auditorily presented with minimal sentences that required binding (pronoun and pseudo-verb with the corresponding morphological inflection; *"she grushes"*) and wordlists that did not require binding (two pseudo-verbs; *"cugged grushes"*). Relative to the no binding wordlist condition, we found that syntactic binding in a minimal sentence structure was associated with a modulation in alpha band (8-12 Hz) activity in left-lateralized brain regions. First, in the sentence condition, we observed a significantly smaller increase in alpha power around the presentation of the target word (*"grushes"*) that required binding (-0.05s to 0.1s), which we suggest reflects an expectation of binding to occur. Second, following the presentation of the target word (around 0.15s to 0.25s), during syntactic binding we observed significantly decreased alpha phase-locking between the left inferior frontal gyrus and the left middle/inferior temporal cortex. We suggest that this results from alpha-driven cortical disinhibition serving to increase information transfer between these two brain regions and strengthen the syntax composition neural network. Together, our findings highlight that successful syntax composition is underscored by the rapid spatial-temporal activation and coordination of language-relevant brain regions, and that alpha band oscillations are critically important in controlling the allocation and transfer of the brain's resources during syntax composition.

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Significance statement

Essential to the power of human language is our ability to comprehend and bind together multiple words into larger sentence structures to establish meaning. In this study, we investigated the electrophysiological mechanisms of binding language at the level of syntax (i.e., relating to the grammatical features). Our MEG results reveal that syntactic binding, relative to no binding, is associated with modulation in alpha band activity (8-12 Hz), including less power increases and inter-regional phase-locking, within and among language-relevant brain regions in the left hemisphere. We suggest that these alpha oscillations help control the allocation of the brain's resources (in particular within the left inferior frontal gyrus and the left middle/inferior temporal cortex) to support syntactic binding in language comprehension.

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Introduction

The expressive power of human language is largely derived from our ability to combine multiple words into larger syntactic structures with more complex meaning. Such binding, or compositional, processes occur during the comprehension of even the most basic two-word phrases (e.g., *"she walks"*). Characterizing the neural processes involved in composition – also referred to as *Unification* (Hagoort, 2003) or *Merge* (Chomsky, 1995) – has been a central topic of research for many years (Hagoort, 2019; Matchin & Hickok, 2020; Pylkkänen, 2019). In the present study we provide novel insight into the neural mechanisms involved in syntax composition using a task in which syntactic binding is dissociable from semantic composition. We employ a minimal phrase paradigm involving pseudo-words (i.e., follow the rules of a language, but have no given meaning).

Sentential compositional processes predominantly occur within a left-lateralized network of brain regions, including the inferior frontal gyrus (IFG) and angular gyrus (Friederici et al., 2000; Humphries et al., 2006; Matchin et al., 2017; Pallier et al., 2011). Within this network, modulations in alpha and beta frequencies are thought to be crucial for higher-order linguistic functions (Bastiaansen et al., 2010; Meyer, 2018; Prystauka & Lewis, 2019). However, the precise neural mechanisms of syntax composition, relating to frequency modulations, remain elusive. This is because while some studies have found compositional processing to be associated with increased alpha and beta power (Meyer et al., 2013; Segaert et al., 2018), others have found sentence unification to be associated with a power *de*crease (Gastaldon et al., 2020; Lam et al., 2016; Wang et al., 2012). Moreover, it is unclear how functional connectivity (i.e., phase-locked) between the neural oscillations in different brain regions may contribute towards successful syntax composition. Current evidence suggests that functional connectivity between regions implicated in compositional processes, such as the left IFG, anterior temporal lobe (ATL) and posterior superior temporal gyrus, is beneficial

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for sentence comprehension (Lopopolo et al., 2021; Schoffelen et al., 2017; Vassileiou et al., 2018). However, the studies discussed thus far have typically used complex sentence structures – this means that other cognitive processes, such as working memory, are also involved in comprehending the sentence stimuli (Pylkkänen, 2019), thereby making it difficult to functionally isolate the neural processes involved in sentence composition alone. In this study, therefore, we aim to characterize the neural mechanisms of syntax composition, both in terms of power modulations and phase-locked connectivity, at its most basic two-word level.

A short two-word sentence (e.g., *"red boat"*) is a traceable linguistic unit which can be used to decompose the brain networks implicated in the processing of lengthier sentences (Pylkkänen, 2019). Research involving minimal sentences has identified a network of left-lateralized brain areas that underlie composition, most notably including the ATL (Bemis & Pylkkänen, 2011, 2013; Blanco-Elorrieta et al., 2018; Fyshe et al., 2019; Pylkkänen et al., 2014; Schell et al., 2017; Westerlund et al., 2015; Zaccarella et al., 2017; Zhang & Pylkkänen, 2015, 2018; Ziegler & Pylkkänen, 2016; but cf. Kochari et al., 2021). Importantly, in order to more precisely identify the neural processes involved in syntactic binding that are dissociable from semantics, one further approach is to use pseudo-words within a minimal phrase paradigm. Using fMRI, Zaccarella and Friederici (2015) found increased hemodynamic responses in the anterior part of the left pars opercularis (part of the IFG) during comprehension of determiner-noun phrases involving pseudo-nouns (*"this flirk"*) compared to wordlists involving one pseudo-noun (*"apple flirk"*). Using EEG, Segaert et al. (2018) found increased alpha and beta power (centralized over frontal-central electrodes) during comprehension of minimal phrases involving pseudo-verbs (*"she grushes"*) compared to wordlists of two pseudo-verbs (*"cugged grushes"*), which they interpreted as reflecting syntactic binding (see also Poulisse et al., 2020). We aim to build on

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these findings and use MEG to precisely characterize and localize the rapid temporal features and functional connectivity within a spatially distributed network of brain regions that support syntax composition independent of semantics.

Materials and Methods

The methods, hypotheses and planned analyses of this study were pre-registered on the Open Science Framework prior to data collection (https://osf.io/ntszu).

Participants

We recruited 25 healthy participants: all were right-handed and native monolingual British-English speakers. One participant was excluded due to excessive movement artefacts during the MEG test session (> 50% trials removed), meaning that a sample of 24 participants was used in the time-frequency analyses (13 female / 11 male, *M* = 24.2yrs, *SD* = 4.1yrs). Anatomical T1 brain scans were acquired for 21 of the participants (two participants did not attend the MRI session, and another did not complete the MRI session due to unexpected discomfort). Further technical issues with MRI-MEG co-registration with two participants meant that a sample of 19 participants was used for the source localization and connectivity analyses (10 female / 9 male, *M* = 24.1yrs, *SD* = 4.2yrs). The study was approved by the University of Birmingham Ethical Review Committee. All participants provided written informed consent and were compensated monetarily.

Experimental Design and Stimuli

We employed a simple design of two experimental conditions: the sentence condition consisting of a minimal two-word phrase (pronoun plus pseudo-verb) for which syntactic

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binding occurred (e.g., *"she grushes"*); and the wordlist condition consisting of two pseudo-verbs for which no syntactic binding occurred (e.g., *"cugged grushes"*). Syntactic binding occurred in the sentence condition (but not the wordlist condition) because the correct morphological inflection (i.e., -es) cued binding with the corresponding pronoun. Behavioural evidence from previous use of this paradigm has shown that participants judge sentences with the incorrect morphological inflection to be syntactically unacceptable (e.g., *"she grush", "I grushes"*), but judge wordlists (e.g., *"cugged grushes"*) and sentences with the correct inflection to be acceptable (Poulisse et al., 2019, 2020; Segaert et al., 2018). This is evidence that listeners do not attempt to bind the two pseudo-words together in the wordlist condition as, if they did, it would be judged syntactically unacceptable. We are therefore confident that participants in our study were engaging in syntactic binding when a minimal sentence was presented, but not when a wordlist was presented.

To construct the experimental items, we used a set of 20 pseudo-verbs created by Ullman et al. (1997).[1] All pseudo-verbs were monosyllabic and could be inflected according to the grammatical rules of regular English verbs. We combined each pseudo-verb with three different morphological affixes (no affix; +s; +ed) to create 60 possible pseudo-verb-affix combinations. In English, only certain pronouns may be combined with certain affixes (e.g., *"she grushes"* is acceptable, but *"I grushes"* is not). Using a list of six pronouns (I, you, he, she, they, we), we created 120 sentence items by pairing each pseudo-verb-affix with two different pronouns that were syntactically appropriate for the corresponding affix, such that syntactic binding may plausibly occur (e.g., *"I dotch", "she grushes", "they cugged"*). To create the wordlist items, we paired together two different pseudo-verb-affix stimuli for which syntactic binding could not plausibly occur (e.g., *"cugged grushes", "dotch traffed"*).

[1] Pseudo-verbs (root form, un-inflected): brop, crog, cug, dotch, grush, plag, plam, pob, prap, prass, satch, scash, scur, slub, spuff, stoff, trab, traff, tunch, vask.

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Each pseudo-verb-affix stimulus occurred twice as the first word in a pair and twice as the second word in a pair, creating a total of 120 wordlist items. We ensured that the two words within each wordlist pair always consisted of a different pseudo-verb and a different affix.

We also created 120 filler items. Sixty of the fillers consisted of reversed speech and were included as a detection task for the participants. We reversed the speech of each of the 60 pseudo-verb-affix combinations and then paired each with either a non-reversed pseudo-verb-affix or pronoun (half as the first word of the pair and half as the second word). A further 60 filler items were included to minimize the possibility of participants forming expectations about when syntactic binding will occur based on the first word. Thirty such items consisted of two pronouns for which binding could not plausibly occur (e.g., *"she I"*). The other 30 items consisted of a pseudo-verb-affix stimulus followed by one of five possible adverbs (early, promptly, quickly, rarely, safely) for which syntactic binding could plausibly occur (e.g., *"cugged quickly"*). All auditory stimuli were spoken by a native English male speaker and normalised to 1db volume.

Experimental Procedure

The participants' task was to detect the reversed speech (which only occurred on filler trials). On each trial, participants were auditorily presented with a two-word phrase (**Figure 1**). Participants were instructed to press a button if part of the speech was reversed (half of the participants used their left index finger, and half used their right index finger), but to do nothing if the speech was not reversed. This ensured that participants paid close attention to the stimuli throughout the experiment, while also ensuring that there was no difference in response decision processes between the critical experimental conditions of interest (sentence vs. wordlist). Each participant completed 360 trials (consisting of 240 experimental trials and 120 filler trials) in a unique randomised order, divided into six blocks of 60 trials each.

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Before beginning the task, participants completed 23 practice trials that were similar to the experimental and filler items used in the main task.

As expected, participants were highly accurate at detecting the reverse speech on the filler trials (*M* = 94.6%, SD = 2.3%, *Range* = 82-98%), indicating that they were attentive during the task on both filler and experimental trials since they did not know when the reversed speech would be presented (i.e., randomized order of trials).

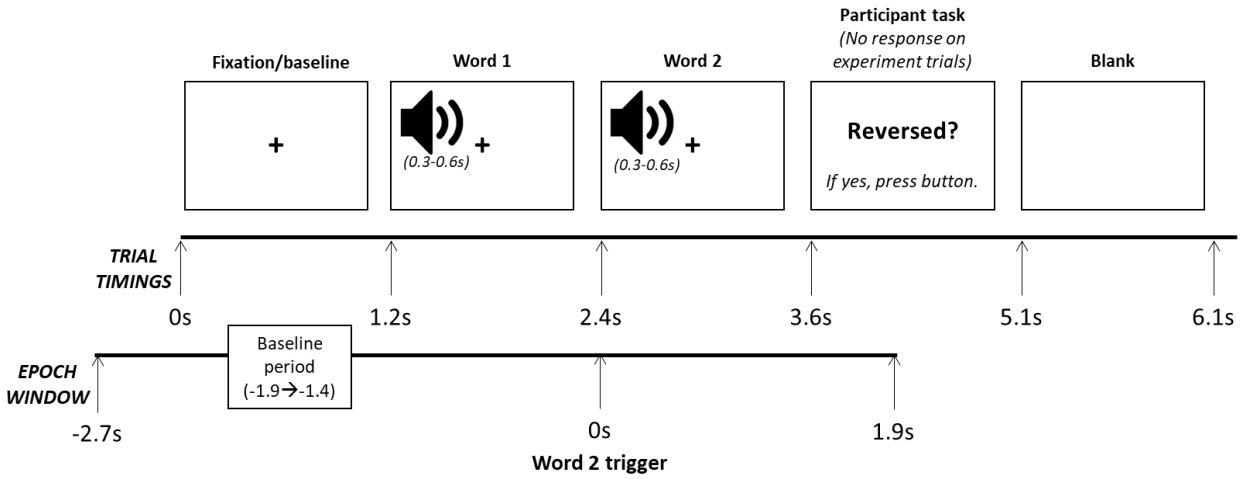

Figure 1. Stimuli presentation timings per trial and the related epoch window. Stimuli presentation and trigger signals were controlled using E-Prime (Schneider et al., 2002). Visual stimuli were presented using a PROPixx projector, and auditory stimuli were presented using the Elekta audio system and MEG-compatible ear plugs. Participants' motor responses were recorded using a NAtA button pad.

Data Acquisition

During the task, ongoing MEG data were recorded using the TRIUX™ system from *Elekta* (Elekta AB, Stockholm, Sweden). This system has 102 magnetometers and 204 planer gradiometers. These are placed at 306 locations, each having one magnetometer and a set of

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two orthogonal gradiometers. The data were collected using a sampling rate of 1000 Hz and was stored for offline analyses. Prior to sampling, a lowpass filter of ~250 Hz was applied. Scalp surface data were acquired using a Polhemus 3D digitiser to facilitate later co-registration with anatomical brain scans. Additional electrooculography (EOG) and electrocardiogram (ECG) data were collected using methods compatible with the TRIUX™ system.

Anatomical high-resolution T1 brain images were acquired for participants at a later session using a MAGNETOM Prisma 3T MRI system from *Siemens* (Siemens Healthcare, Erlangen, Germany). These images were used for the reconstruction of individual head shapes to create forward models for the source localization analyses.

MEG Pre-processing

The offline processing and analyses of the data were performed using functions from the Fieldtrip software package (Oostenveld et al., 2011) and custom scripts in the MATLAB environment. First, we applied a 0.1 Hz high-pass filter to the MEG data to remove slow frequency drift in the data. The data were segmented into epochs aligned to the onset of the auditory presentation of the second word from -2.7s to 1.9s (see **Figure 1**). We visually inspected the waveforms of each trial and removed trials that contained excessive signal artefacts (e.g., large sensor jumps or gross motor movement by the participant); on average, we removed 16% of trials (38.3/240) per participant (*Range* = 4-47%). We also removed any persistently poor channels that contained excessive noise or flatlined (*Mean* channels removed per participant = 2.46, *Range* = 0-9). We then used a spline interpolation weighted neighbourhood estimate to interpolate across the removed channels per participant. Ocular and cardiac artifacts were removed from the data using an independent component analysis (ICA) (*Mean* artifacts removed per participant = 1.75, *Range* = 1-3). We identified these

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components from their stereotypical topography and time course, as well as by comparisons with the recorded ECG and EOG time courses.

Lastly, we removed all filler trials as we were specifically interested in the difference in neural responses between the experimental sentence and wordlist conditions (i.e., our contrast of interest). We further removed trials for which the participant incorrectly responded with a button press (i.e., indicated that the speech was reversed when it was not) and trials during which the participant made an accidental button press before the response screen. Once all data pre-processing was complete, there was an average of 101 sentence trials and 100 wordlist trials per participant that were usable for the analyses (out of a maximal 120 per condition).

Statistical Analyses

Time-frequency

For the frequency range 1-30 Hz (1 Hz steps), we obtain time-frequency representations (TFRs) of power for each trial using sliding Hanning tapers with an adaptive time window of three cycles for each frequency ($\Delta T = 3/f$). This approach has also been used in a number of previous studies (e.g., Segaert et al., 2018; van Diepen & Mazaheri, 2017; Whitmarsh et al., 2011). For each participant, the data for the planar gradiometer pairs was added to create a 102-channel combined planar map in sensor space, and we baseline-corrected the data using the oscillatory activity in a 0.5s period of the fixation cross presentation (specifically, -1.9s to -1.4s in the epoch window). We calculated the TFRs separately per condition for each participant and then averaged across all participants.

We assessed the statistical differences in time-frequency power between the sentence and wordlist conditions across participants using a cluster-level randomization test (incorporated in the Fieldtrip software), which circumvents the type-1 error rate in a situation

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involving multiple comparisons (i.e., multiple channels and time-frequency points; Maris & Oostenveld, 2007). This approach first clusters the data in sensor space depending on whether the contrast between the two conditions exceeds a dependent samples *t*-test threshold of $p < .05$ (two-tailed). We used the following pre-defined frequency bands: alpha (8-12 Hz); low beta (15-20 Hz) and high beta (25-30 Hz). We considered a cluster to consist of at least two significant adjacent combined planar gradiometers. A Monte Carlo *p*-value of a cluster was then obtained by calculating the number of times the *t*-statistics in the shuffled distribution is higher than the original *t*-statistic obtained when contrasting conditions. We performed the analyses within the time window of interest, centred around the presentation of the second word (-0.5s to 1s of the epoch).

Source Localization

A realistically shaped description of each participant's brain was constructed using individual head models obtained using the Polhemus 3D digitiser and the acquired MRI anatomical brain scan (where available). Source estimation of the time-locked MEG data was performed using a frequency-domain beam-forming approach (dynamic imaging of coherent sources [DICS]; Gross et al., 2001), which uses adaptive spatial filters to localize power in the entire brain. The brain volume of each individual participant was discretized to a grid with a 0.8cm resolution and the lead field was calculated for each grid point. A common filter was calculated for the sentence and wordlist condition and then applied for the data separately for the individual conditions (Mazaheri et al., 2014; Whitmarsh et al., 2011). The source estimates of the individual participants' functional data along with the individual anatomical MRI images were warped into a standard Montreal Neurological Institute (MNI) standard brain (Quebec, Canada; http://www.bic.mni.mcgill.ca/brainweb) before averaging and statistics.

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We performed cluster-based randomization tests to identify the grid-points in which there was a significant difference in power between the two experimental conditions, guided by the findings of the time-frequency analyses (i.e., time-windows). We used these clusters to identify specific regions of interest (ROIs) of the condition difference. We derived anatomical labels of these regions from Brodmann's map and from the Automated Anatomical Labelling Atlas (Tzourio-Mazoyer et al., 2002).

Inter-regional Connectivity

We performed inter-regional connectivity analyses on four distinct ROIs identified as showing a significant condition difference in the source localization analyses. TFRs of the complex Fourier spectra for each trial at each ROI was obtained by using a sliding Hanning tapers with an adaptive time window of three cycles for each frequency ($\Delta T = 3/f$). We calculated the inter-regional phase-locked values of the oscillatory activity (1-30 Hz) between the four ROIs (creating six inter-regional connections) for the time period of interest (-0.5s to 1s of the epoch) separately for the sentence condition and wordlist condition (following Bastos & Schoffelen, 2016; Lachaux et al., 1999). We used the following formula to calculate the phase locking index (PLV):

$$PLV = \frac{1}{N}\left|\sum_{n=1}^{N} e^{i(\emptyset_{(n,t)} - \psi(n,t))}\right|$$

Applied to our study, the PLV reflects the consistency of the phase difference of oscillatory activity across trials between two ROIs. Here: N is the number of trials; $\emptyset_{(n,t)}$ is the phase (obtained from the complex spectra) at time t in trial n in one ROI; and $\psi_{(n,t)}$ is the phase at

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time *t* in trial *n* in the other ROI. A PLV of 0 indicates no phase locking between the activities of the two ROIs, whereas a PLV of 1 is indicative of perfect phase locking.

We then performed cluster-level randomization tests (Maris & Oostenveld, 2007) on the PLVs in order to identify the inter-regional connections in which there was a significant difference in phase-locked values between the two experimental conditions (for a similar statistical approach see, Schmidt et al., 2014). The use of a cluster-level randomization test, in which a Monte Carlo *p*-value is obtained, enables the control of multiple comparisons of different ROIs and time-frequency points. To correct for the multiple analyses performed across the six different inter-regional connections, we applied a Bonferroni correction (α / *n* comparisons) to our critical *p* value of interest (.05/6 = .0083). We used the same pre-defined frequency bands as for the oscillatory time-frequency analyses: alpha (8-12 Hz); low beta (15-20 Hz) and high beta (25-30 Hz).

Results

We compared participants' MEG activity during the comprehension of minimal sentences that required binding (a pronoun combined with a pseudo-verb with the corresponding morphological inflection; *"she grushes"*) to wordlists that did not require binding (two pseudo-verbs; *"cugged grushes"*). Our findings reveal two key mechanisms of syntactic binding.

Less alpha power in the left-lateralized brain network when syntactic binding occurs

The grand-average of the time-frequency representations (TFR) of power averaged across all sensors aligned to the onset of the second word are summarized in **Figure 2A** for the sentence condition in which syntactic binding occurred, and the wordlist condition in which no binding occurred. In both conditions, there are power increases in alpha and low

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beta surrounding the presentation of the second word (at 0s; *"grushes"*). Approximately 0.5s after the second word presentation, there is a slight decrease in alpha and low beta power in both conditions.

The statistical results of the cluster-based permutation tests (which controlled for multiple comparisons of different channels and time-frequency points) revealed that there was a significant condition difference in the alpha frequency range (8-12 Hz) surrounding the presentation of the second word where alpha power was lower in the sentence condition, compared to the wordlist condition (p = .021, see **Figure 2B-C**). This difference was maximal around the onset of the second word (-0.05s to 0.1) over a cluster of sensors predominantly in the left-frontal region (**Figure 2B**). Importantly, this oscillatory effect of alpha was distinct from the evoked fields as we did not observe any significant condition differences in the event-related fields during this time period (p > .05). We found no significant difference in oscillatory activity within the other analysed frequency bands: low beta (15-20 Hz) and high beta (25-30 Hz).

Source analyses co-registered on the participants' anatomical MRI brain scans indicated that the significant condition difference in alpha power (8-12 Hz, -0.05s to 0.1s) was localized to a network of left-lateralized brain regions which are typically associated with language function (**Figure 3A**). Within this network, we identified four brain areas (see **Figure 3B**) in which significant differences were found between the sentence condition and wordlist condition: the left inferior frontal gyrus (BA44; peak coordinates [-42 7 17]); the left angular gyrus (BA39; peak coordinates [-58 -48 29]); the left middle/inferior temporal cortex (BA21; peak coordinates [-60 -30 -18]); and the left anterior frontal gyrus (BA46; peak coordinates [-40 43 7]).

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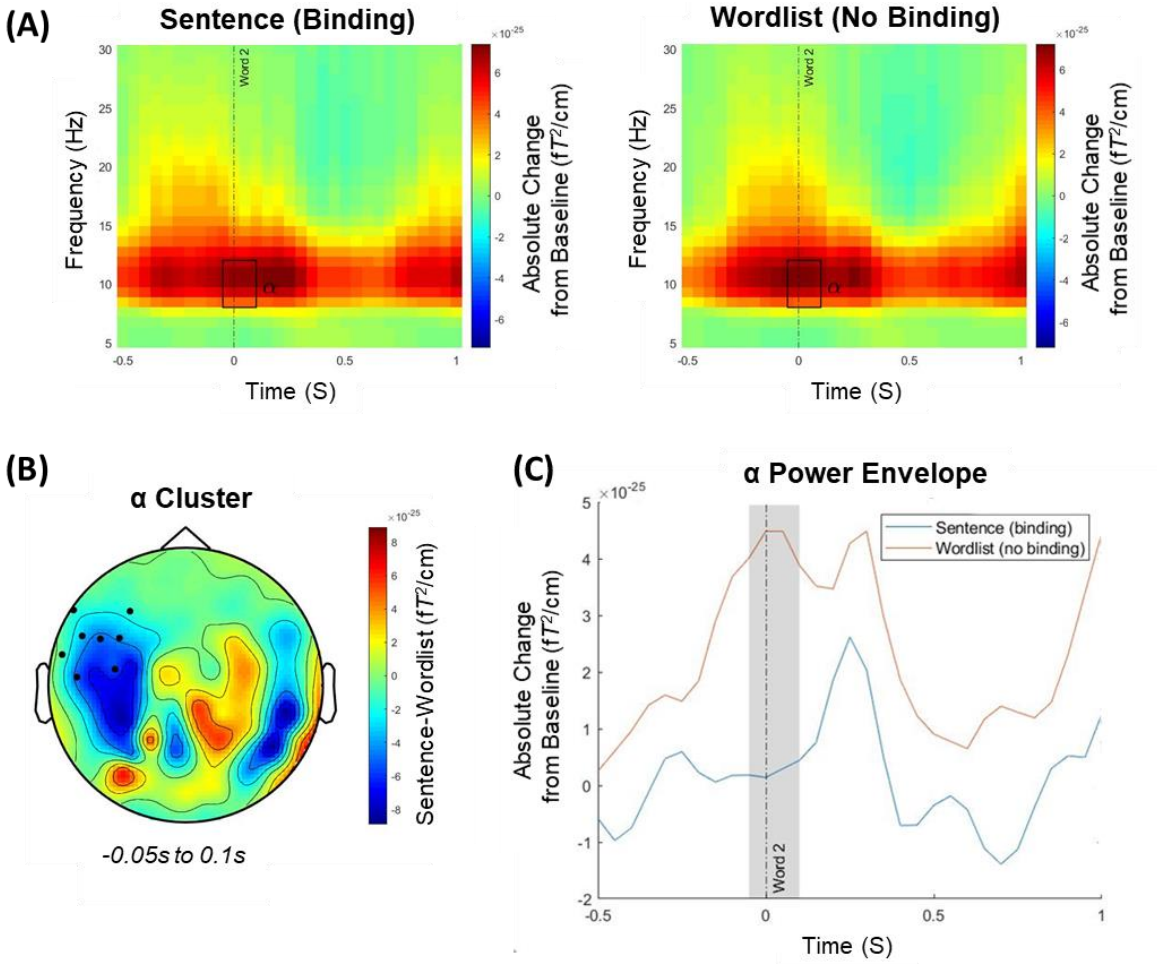

Figure 2. (A) Time-frequency representations of power averaged across all sensors, expressed as an absolute change from the baseline period (i.e., -1.9s to -1.4s before the onset of the second word) for the sentence condition [left panel] in which syntactic binding occurred (e.g., *"she grushes"*), and the wordlist condition [right panel] in which no binding occurred (e.g., *"cugged grushes"*). Time relates to the main time period of interest aligned to the onset of the second word (at 0s). The rectangle highlights the time period where we maximally observed the significant difference in alpha power (8-12 Hz) between the two conditions (-0.05s to 0.1s; p = .021). **(B)** The scalp topography of the condition contrast (sentence minus wordlist) of the averaged alpha power activity in the time window (-0.05s to 0.1s) where we maximally observed the significant difference in alpha power between the two conditions. The black dots illustrate where this effect was largest at the scalp level. For visualization purposes, the condition contrast of the non-baseline corrected data is shown. **(C)** The time course of the alpha power envelope for the sensors showing a significant difference in power between the sentence and wordlist conditions. The shaded grey area corresponds to the time window in which the difference between conditions is maximal centred around the presentation of the second word (-0.05s to 0.1s).

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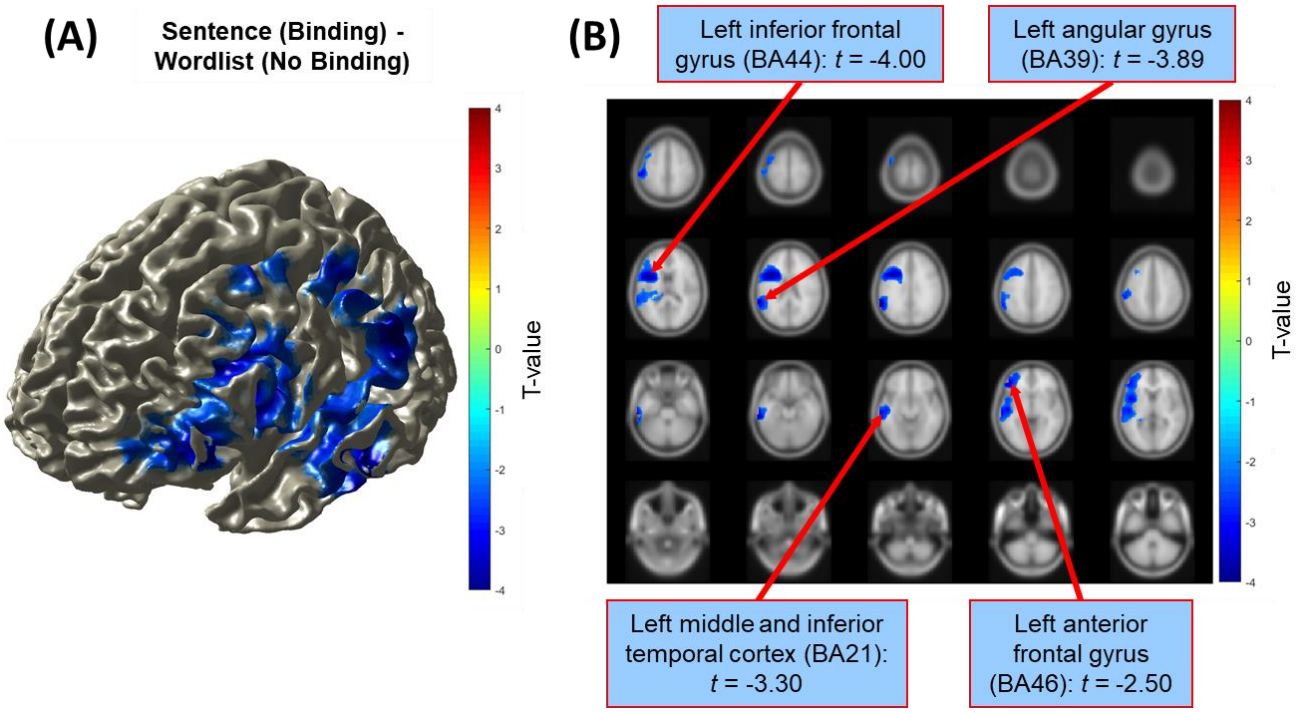

Figure 3. Source localization estimates of the condition difference in alpha power (8-12 Hz) of the sentence condition (e.g., *"she grushes"*) minus the wordlist condition (e.g., *"cugged grushes"*) surrounding the presentation of the target word (-0.15s to 0.15s) as shown for a surface **(A)** and sliced **(B)** view of the brain. The displays are masked for significant clusters only ($p < .05$). The condition difference was maximal over the left-frontal areas of the brain, with significant differences observed in the left inferior frontal gyrus, the left angular gyrus, the left middle/inferior temporal cortex, and the left anterior frontal gyrus.

During syntactic binding, there is decreased alpha phase-locking between the left inferior frontal gyrus and the left middle/inferior temporal cortex

We calculated the inter-regional phase-locked values between the peak coordinates of the four brain areas identified as displaying significant condition differences in the source localization analyses (**Figure 4A**). The statistical results of the cluster-based permutation tests (which controlled for multiple comparisons of different ROIs and time-frequency points) revealed a significant condition difference ($p = .005$) in inter-regional phase-locking

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in alpha activity (8-12 Hz) between the left inferior frontal gyrus (BA44) and the left middle/inferior temporal cortex (BA21) following the presentation of the second word that required binding (around 0.15s to 0.25s). During this time period, there was significantly less alpha phase-locking between these two brain regions in the sentence condition, compared to the wordlist condition (**Figure 4B**). While we are aware that amplitude may correlate with PLV (van Diepen & Mazaheri, 2018), we consider that it is unlikely that our observed condition difference in the PLVs is driven by amplitude differences alone because it occurred at a time interval when there was *not* the greatest amplitude difference between the two conditions, and because we only observed the effect between two specific ROIs, not the whole analysed left-lateralized brain network.

We did not find any other significant condition differences in inter-regional phase-locking in the other connections between our ROIs. Qualitatively though, across both conditions, inter-regional phase-locking does appear to be strongest between the left angular gyrus and the left middle/inferior temporal cortex, as well as within the alpha frequency range between the left anterior frontal gyrus and the left inferior frontal gyrus (**Figure 4C**).

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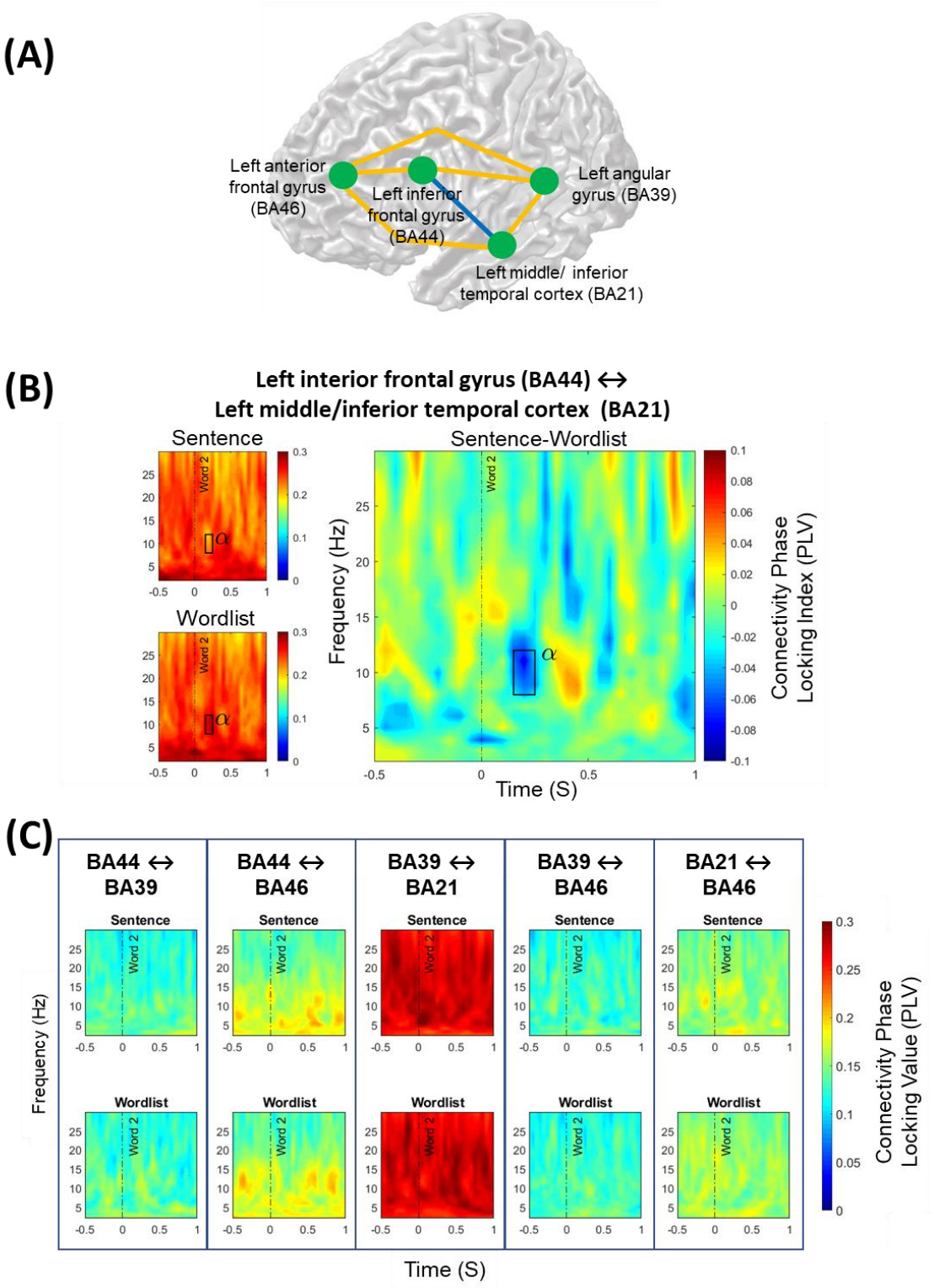

Figure 4. (A) Inter-regional phase-locking differences of oscillatory activity (2-30 Hz) were calculated between four brain areas in the left hemisphere for the time period of interest (-0.5s to 1s; second word presented at 0s). **(B)** A significant condition difference in inter-regional phase-locking was observed between the left inferior frontal gyrus (BA44) and the left middle/inferior temporal cortex (BA21) in the alpha frequency range (8-12 Hz). Time-

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frequency estimates of the phase-locking value are shown for the sentence condition (e.g., *"she grushes"*) [left upper panel], the wordlist condition (e.g., *"cugged grushes"*) [left lower panel] and the condition contrast (sentence minus wordlist) [right panel]. There was significantly greater phase-locking of alpha activity between BA44 and BA21 in the wordlist condition compared to the sentence condition when subjected to a cluster-randomisation analysis, maximally observed around 0.15s to 0.25s following the presentation of the target word (p = .005), as highlighted by the rectangle. **(C)** The inter-regional phase-locking values between the other brain regions of interest. Here, no other significant differences were found between the sentence and wordlist conditions.

Discussion

The findings of our MEG study suggest that minimal syntax composition is associated with distinct oscillatory changes in alpha band activity and the engagement of the left-lateralized language network of the brain. In the reported experiment we compared minimal pseudo-verb sentences for which syntactic binding may plausibly occur (e.g., *"she grushes"*) and wordlists for which no binding occurred (e.g., *"cugged grushes"*). We found that surrounding (-0.05s to 0.1s) the presentation of the target word (*"grushes"*), alpha power was significantly less in the sentence, compared to the wordlist, condition. The sources of this condition difference were localized to left-lateralized brain regions, including the inferior frontal gyrus (IFG), angular gyrus, middle/inferior temporal cortex, and anterior frontal gyrus. Moreover, following the presentation of the target word (0.15s to 0.25s), we observed decreased alpha phase-locking between the LIFG and the left middle/inferior temporal cortex in the sentence, compared to the wordlist, condition, indicating that syntactic binding is associated with a decoupling of alpha activity between these regions.

Modulation in alpha power in a network of left-lateralized language regions reflects an expectation of binding to occur

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Compared to baseline, we observed an increase in alpha power in both conditions during the comprehension of the second word, but critically this power increase was *less* when syntactic binding was required, compared to when no binding was required. This modulation in alpha power is consistent with existing evidence of alpha oscillatory activity in compositional processing (Gastaldon et al., 2020; Lam et al., 2016; Segaert et al., 2018) and the view that neural oscillations subserve the processing of syntactic information within language-relevant cortices (Meyer, 2018; Prystauka & Lewis, 2019). Our findings further demonstrate that alpha operates in auditory language processing in addition to its role in visual processing in occipital areas (Mazaheri et al., 2014; Zumer et al., 2014), supporting a varied functionality of alpha oscillations in multiple sensory systems in different cortical regions (Foxe & Snyder, 2011).

We suggest that, in our experiment, the observed lesser alpha power in the binding context around the presentation of the target word reflects an expectation of binding to occur. When comprehending linguistic input, we build expectations in order to predict upcoming words (Chang et al., 2006; Kuperberg & Jaeger, 2016). Thus, if the first word was a pronoun, as opposed to a pseudo-verb, the participant may reasonably expect that binding was likely to be required given their existing knowledge (based on language use in everyday life) about the properties and syntactic function of pronouns. This interpretation is consistent with studies that have found greater alpha suppression (i.e., decreased alpha power compared to baseline) when participants comprehend a highly predictive, compared to a less predictive, sentence (Piai et al., 2014; Rommers et al., 2017; Wang et al., 2017) and the proposed role of alpha power decreases in controlling the allocation of the brain's resources (Jensen & Mazaheri, 2010; Klimesch, 2012). Our finding of less alpha power around the presentation of the target word that required binding (compared to a no binding context) may therefore reflect the

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initiation of anticipatory binding processes, along with the increased engagement of brain regions involved in syntactic binding.

The observed condition difference in alpha power was localized to a left-lateralized network of brain regions, consistent with established neurobiological models of linguistic processing (Friederici, 2011; Hagoort, 2003; Tyler & Marslen-Wilson, 2008). The implication of the LIFG (BA44) is expected given the region's proposed role in managing the combination of words into a coherent syntactic structure (Hagoort, 2005; Segaert et al., 2012; Snijders et al., 2008; Uddén et al., 2019) and in computing dependency structures (Lopopolo et al., 2021). Indeed, the LIFG has been identified in previous studies of minimal syntactic binding (Zaccarella et al., 2017; Zaccarella & Friederici, 2015) and top-down predictive processing (Matchin et al., 2017; Strijkers et al., 2019). The other three left-lateralized regions we identified – angular gyrus (BA39), anterior frontal gyrus (BA46), and middle/inferior temporal cortex (BA21) – have also been found to contribute towards syntactic processing (Giraud et al., 2004; Humphries et al., 2006; Matchin et al., 2017; Menenti et al., 2011; Segaert et al., 2012). Our findings therefore suggest that successful composition of the syntactic properties between words in a sentence is driven by the engagement of a distributed network of left-lateralized regions (including the frontal gyri, temporal cortex and angular gyrus), and critically their coordination (as we discuss in more detail in the next section). Moreover, given that we did not observe any effect of compositionality in the anterior temporal lobe (ATL) in our task in which contributions from semantics were minimized, our findings further add to the current evidence that the functional role of the ATL relates primarily to semantic, not syntactic, composition (Del Prato & Pylkkänen, 2014; Kim & Pylkkänen, 2019; Pylkkänen, 2019; Wilson et al., 2014).

Nevertheless, our findings of alpha power decrease is somewhat at odds with Segaert et al. (2018) who, using a similar paradigm but with EEG, found syntactic binding to be

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associated with alpha power increases. An explanation for this difference most likely reflects MEG vs. EEG differences in spatial coherence and sensitivity to deeper brain tissues that can lead to differences in detectable power (Bénar et al., 2019; Lopes da Silva, 2013). In particular, MEG and EEG differ in their sensitivity to the radical and tangential components of the dipolar sources in the brain, which can lead to the two producing diverging estimates for the same cognitive process (Dehghani et al., 2010; Edgar et al., 2003; Fonteneau et al., 2015; Ross et al., 2020). Our findings should therefore not be considered as opposing, but instead reflective of the different components of the wider neural processes involved in syntax composition (which are differently detected by MEG and EEG), and the more general functionality of alpha oscillations in syntax processing (Meyer, 2018; Prystauka & Lewis, 2019).

Alpha band decoupling in the language network reflects strengthened network communication required for successful syntactic binding

Inter-regional connectivity analyses revealed that syntactic binding was associated with a decoupling of alpha between the LIFG and the left middle/inferior temporal cortex: we found *less* alpha phase-locking in the sentence, compared to the wordlist, condition following the presentation of the target word (0.15s to 0.25s). The time window of the effect, after the auditory processing of the target word (which typically occurs within the first 0.1s; Zouridakis et al., 1998), suggests that it reflects the underlying syntax composition mechanisms taking place as opposed to an expectation of binding to occur. Our finding is consistent with evidence that alpha band decoupling, or desynchronisation, between relevant brain regions is beneficial for language comprehension and can predict successful sentence encoding (Becker et al., 2013; Magazzini et al., 2016; Vassileiou et al., 2018). This functional connectivity reflects the dynamic interaction among distributed brain regions that are

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subserved by deep white matter pathways and which communicate through frequency-specific networks (Sarubbo et al., 2020; Schoffelen et al., 2017; White et al., 2018). This communication may operate through top-down mechanisms of cortical disinhibition, such that alpha band desynchronisation serves to functionally disinhibit the cortex to enable information to be transferred from and to specific areas for processing (Jensen & Mazaheri, 2010; Klimesch, 2012).

We suggest that similar mechanisms of frequency-specific communication and alpha-driven disinhibition were operating in our task when participants comprehended sentences that needed binding (*"she grushes"*). In order to bind the two words together into a minimal syntactic structure, increased information, such as the labels of syntactic components (Murphy, 2015), needed to be transferred between the LIFG and the middle/inferior temporal cortex. Thus, the less alpha band synchronisation between these two regions, the greater the cortical disinhibition; this, in turn, strengthens the communication within the cortical and oscillatory network involved in syntax composition, thereby enhancing participants' processing. This interpretation fits with the wider understanding of the role of alpha oscillations in controlling the access, transfer and storage of information within the brain (Bonnefond et al., 2017; Klimesch, 2012).

Summary

In sum, when comparing minimal pseudo-verb sentences that required binding (*"she grushes"*) to no binding wordlists (*"cugged grushes"*), we first found evidence of less alpha power in left-lateralized brain regions which we suggest reflects an expectation of binding to occur. Second, we found that during syntactic binding there was decreased alpha phase-locking between the LIFG and the left middle/inferior temporal cortex; we suggest that this results from increased information transfer and the strengthening of the neural network

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involved in syntax composition. The observed oscillatory modulations (including power decreases and decoupling) occurred in brain regions in the left hemisphere known to be relevant for language processing. These regions are not uniquely selective for syntactic processing; rather, we suggest that each region plays a contributing role in syntax composition mechanisms, and that coordination between these regions (particularly the LIFG and left middle/inferior temporal cortex) is critical for successful syntactic binding. Together, our findings contribute to the wider understanding of the rapid spatial-temporal dynamics of syntactic processing in the brain that occur independently of semantic processing.

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