Minimal phrase composition revealed by intracranial recordings

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Abstract

The ability to comprehend phrases is an essential component of language. Here we evaluate the neural processes that enable the transition from single word processing to a minimal compositional scheme using intracranial recordings. 19 patients implanted with penetrating depth or surface subdural intracranial electrodes heard auditory recordings of adjective-noun, pseudoword-noun and adjective-pseudoword phrases and judged whether the phrase matched a picture. Stimulus-dependent alterations in broadband gamma power activity (BGA), low frequency power or phase consistency, and phase-locking values across the compositional network were analyzed. The posterior superior temporal sulcus (pSTS) and temporo-occipital junction (TOJ) revealed a fine-structured cortical mosaic, with closely neighboring tissue displaying exclusive sensitivity to either lexicality or phrase structure, but not both. During phrase composition, greater functional connectivity was seen between pSTS-TOJ and both pars triangularis and temporal pole. These two regions also encode anticipation of composition in broadband low frequencies. These results implicate pSTS-TOJ as a crucial hub for the retrieval and computation of minimal phrases. Overall, this work reveals an interface of sparsely interwoven coding for lower and higher level linguistic features, coupled with large-scale network organization, with direct relevance to our understanding of cognitive networks in the human brain.

Keywords: composition, electrocorticography, semantics, posterior temporal lobe, anticipation, human, language

Introduction

How the brain integrates individual word meanings to comprehend the meaning of multi-word utterances is an issue that has vexed the cognitive neuroscience of language for decades. How the brain computes 'complex meaning' (Hagoort, 2020) from combinations of multiple lexical items is still largely a mystery. This linguistic compositional process – the combination of words into larger structures with new and complex meaning – is also referred to as "Merge" (Chomsky, 1995; Chomsky et al., 2019) or "Unification" (Hagoort, 2013).

The simplest form of studying complex meaning is by using minimal phrases such as in the *red-boat* paradigm, which focuses on simple combinations of two words (Bemis & Pylkkänen, 2011, 2013a; Bozic et al., 2015; Brennan & Pylkkänen, 2012; Flick et al., 2018; Flick & Pylkkänen, 2020; Pylkkänen, 2020; Westerlund et al., 2015; Westerlund & Pylkkänen, 2014), avoiding a range of confounds associated with more complex linguistic stimuli (Berwick, & Stabler, 2019). A "red boat" is interpreted as a boat which is red, and not a red object which hosts boat-related properties, with phrases delivering novel syntactic and conceptual formats (Leivada & Murphy, 2021; Murphy, 2015a; Pietroski, 2018). Experimental work using the *red-boat* paradigm implicates the left anterior temporal lobe (ATL), specifically the temporal pole (Antonucci et al., 2008; Bemis & Pylkkänen, 2011; Lambon Ralph et al., 2012; Pobric et al., 2010; Westerlund & Pylkkänen, 2014; Wilson et al., 2014; Zhang & Pylkkänen, 2018), and posterior temporal regions (Flick & Pylkkänen, 2020; Matchin & Hickok, 2020) as crucial nodes for phrase composition. *Red-boat* experiments isolate semantic composition, which in turn encompasses syntactic composition. These studies report responses that vary in timing (between 180–350ms post-composition) and duration (50–100ms). The left posterior temporal lobe and angular gyrus (AG) also show greater activity for sentences than word lists, and for phrases than words (Brennan et al., 2016; Matchin & Hickok, 2020), making them candidate regions for the retrieval of phrasal templates (Hagoort, 2003, 2017),

Phrase composition is a rapid process that is likely dependent on finely organized sets of distributed cortical substrates. Previous work in the *red-boat* paradigm has been limited by spatiotemporal resolution. Using recordings from intracranial electroencephalography (iEEG) with depth electrodes penetrating grey matter or electrodes located on the cortical surface, we conducted a study of minimal phrase composition with auditory presentations of adjective-noun phrases across a large patient cohort (n = 19).

We utilized grammatical noun phrases ("red boat") and pseudoword phrases with variable positions of the pseudoword ("bleeg boat", "red fulg") to isolate semantic compositional processing. An adjective-pseudoword condition ("red fulg") was included to isolate semantic compositionality and reduce predictability. Given the large number of patients in our study, we

were able to analyze not only regions of interest delineated by previous studies, but also a range of temporal, frontal and parietal cortices not previously implicated in models of phrase composition.

Studies using scalp electroencephalography and magnetoencephalography (MEG) were used to constrain our analytic space. iEEG provides uniquely high spatiotemporal resolution recordings and is less susceptible to artifacts (e.g., muscle movements) (Arya, 2019; Flinker et al., 2011). High frequency gamma changes (Conner et al., 2019; Forseth et al., 2018; Johnson et al., 2020; Leszczyński et al., 2020; Towle et al., 2008; Yi et al., 2019) typically index local cortical processing and are implicated in a range of cognitive processes (Buzsáki & Watson, 2012; Hovsepyan et al., 2020; Jensen et al., 2019; Marko et al., 2019; Packard et al., 2020; Prystauka & Lewis, 2019). An early anterior negative deflection immediately preceding the critical noun in combinatorial contexts (-50–100ms) (Neufeld et al., 2016) likely indexes syntactic prediction (Lau et al., 2006). Low frequency power increases have also been noted during the anticipatory window (Bastiaansen & Hagoort, 2015; Lewis et al., 2016; Segaert et al., 2018), during phrase composition (Segaert et al., 2018) and in a variety of auditory phrase and sentence processing paradigms (Ding et al., 2016; Keitel et al., 2018; Keitel et al., 2017; Mai et al., 2016). Therefore, we also evaluated the role of low frequencies during anticipatory composition. Lastly, our task required patients to determine whether the words they heard matched a subsequent image, enabling analyses related to phrase-matched and phrase-contrasted contexts.

Results

Patients were presented with auditory recordings grouped randomly into three conditions: Adjective-Noun, Pseudoword-Noun, Adjective-Pseudoword. A subsequent colored image was presented, and patients were tasked with responding, with a button press, to whether the image matched the phrase or not (Fig. 1A). Across the cohort, we had good coverage over lateral and medial temporal lobe, inferior parietal lobe and inferior frontal regions, with some coverage reaching into other portions of fronto-parietal regions (Fig. 1B). We saw activation in response to the auditory stimuli most prominently in superior and middle temporal regions (Fig. 1C). Below we report results pertaining to lexicality; phrase anticipation; phrase composition; and linguistic-visual unification.

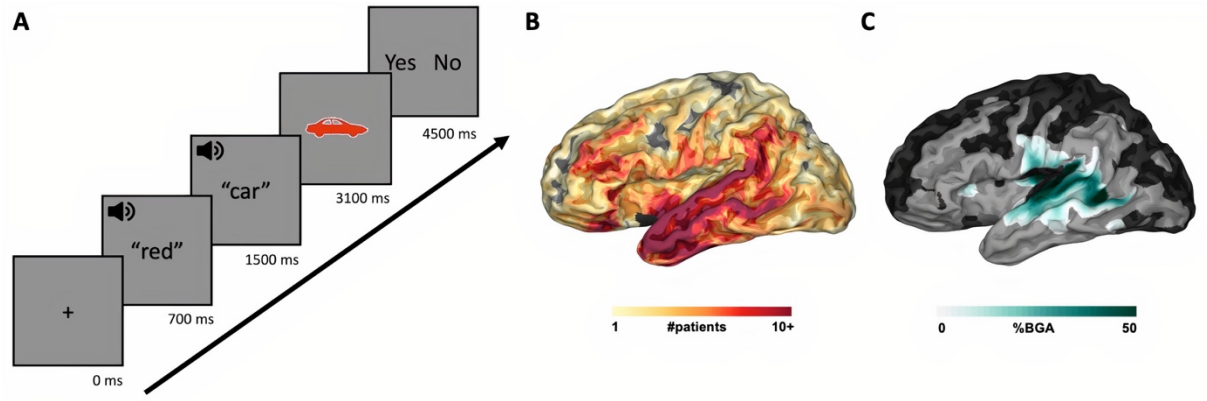


Figure 1: **Experimental paradigm with coverage and activation maps.** (A) Experimental design. Average stimuli length: adjectives (420 ± 39 ms; mean ± SD), nouns (450 ± 75 ms), pseudowords (430 ± 38 ms). (B) Group coverage map of included, left hemisphere electrodes, plotted on a semi-inflated standardised N27 surface. (C) Broadband gamma activity (BGA) increases from baseline (-500 to -100ms prior to first word) for all conditions from 100 to 400ms after onset of the first word (threshold: %BGA > 5%, t > 1.96, patient coverage ≥ 3; $p < 0.01$ corrected). Black surfaces fell below patient coverage threshold.

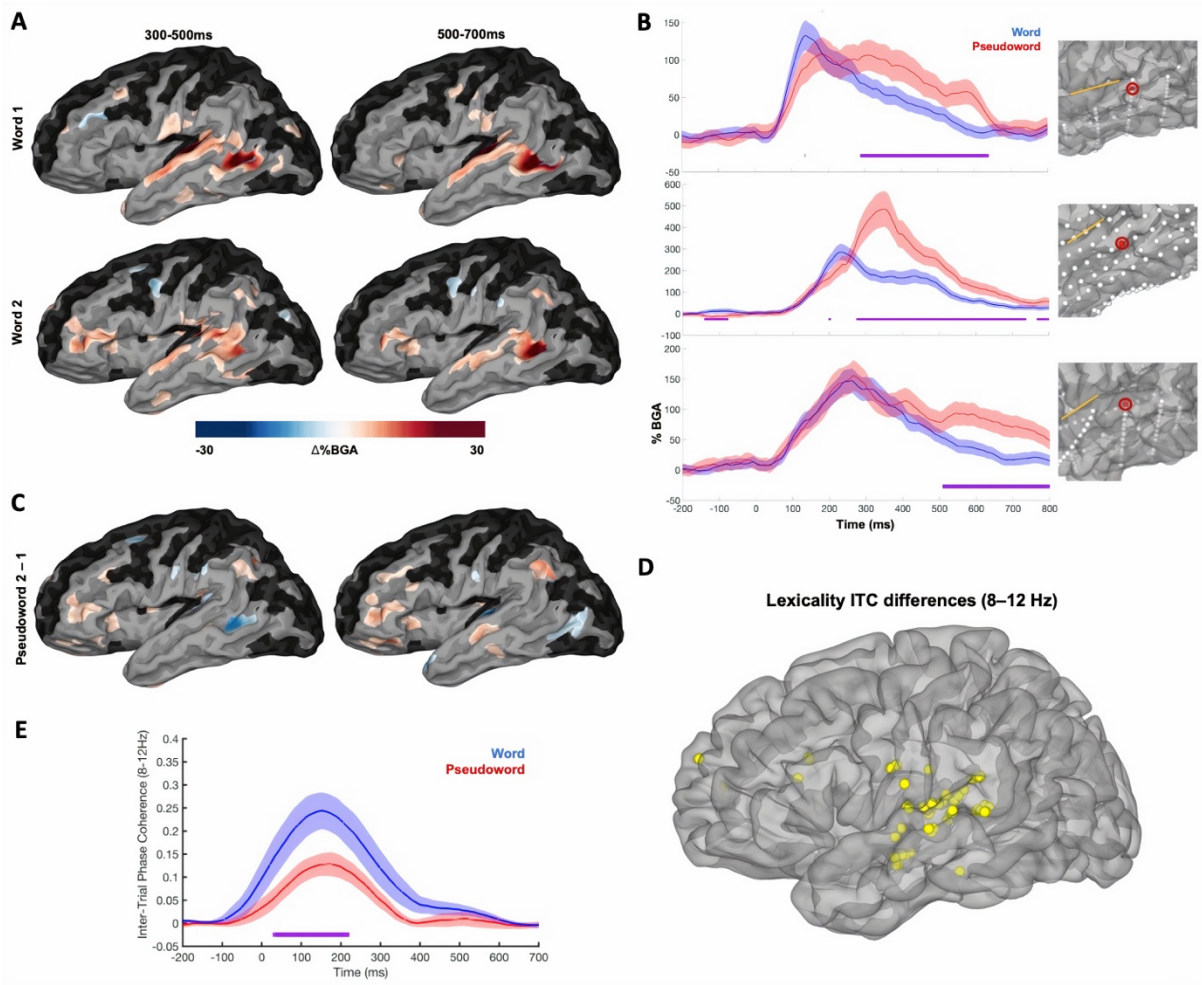
Behavioral performance

Performance in the image matching task was highly accurate 97 ± 3% (311 ± 11/320 trials) with an average response time of 1599 ± 539 ms. Only correct trials were analyzed further.

Effects of lexicality

To disentangle single word semantic effects from those of combinatorial semantics, we probed the difference in representation of words vs. pseudowords. We generated a surface-based, population-level map of cortical activity using a surface-based mixed-effects multi-level analysis (SB-MEMA) (Conner et al., 2011; Fischl et al., 1999; Kadipasaoglu et al., 2014; Kadipasaoglu et al., 2015), a method specifically designed to account for sampling variations in iEEG and minimize effects of outliers. An SB-MEMA contrasting adjectives vs. pseudowords in word position 1 and nouns vs. pseudowords in word position 2 (Fig. 2A) revealed significantly greater broadband gamma activity (BGA; 70–150 Hz) for pseudowords than words in posterior superior temporal gyrus (pSTG), posterior superior temporal sulcus (pSTS), temporo-occipital junction (TOJ) and pars triangularis 300–700ms after word onset, indexing the additional processing of unfamiliar word sounds in an attempt to derive potential lexicality. The greater BGA increase for pseudowords than words at position 2 than position 1 around

pars triangularis and surrounding frontal areas (Fig. 2C), suggests involvement of this region in effortful lexical processing (perhaps in phonological space) to facilitate semantic unification (Hagoort, 2005, 2013; Hagoort & Indefrey, 2014).



<u>Figure 2</u>: Grouped analysis for lexicality. (A) SB-MEMA comparing words vs pseudowords, red colors indexes greater BGA (70–150 Hz) for pseudowords and blue colors for words (threshold: %BGA > 5%, t > 1.96, patient coverage ≥ 3; $p < 0.01$ corrected). Top row: word position 1; bottom row: word position 2. (B) Exemplar electrodes for the words vs pseudowords analysis (red: pseudowords; blue: words). Error bars (colored shading) set at one standard error. Sylvian fissure is marked with a yellow line for reference on each surface. (C) SB-MEMA indicating BGA increases for pseudowords at the second word position relative to pseudowords at the first word position. (D) Electrodes with significant differences in inter-trial phase coherence (ITC) for words vs pseudowords, in posterior temporal cortex (9 patients). (E) ITC in alpha (8–12 Hz) at all electrodes in (D) for words (blue) and pseudowords (red) on the left. T0 = first word onset.

Additionally, to broaden our assessment of the contributions of lower frequencies, we computed inter-trial phase coherence (ITC) across regions and low frequencies. We found significantly greater ITC values for words relative to pseudowords in and around pSTG (Fig. 2D, E; Suppl. Fig. 1) in the alpha band (8–12 Hz). No other ROIs (ATL, pars triangularis, pars orbitalis, MTG, supramarginal gyrus: all FDR-corrected q-values >0.05) displayed such effects for this, or for phrase composition. Alpha phase coherence in pSTG may therefore encode information relevant to lexical interpretation.

Compositional anticipation

We next contrasted Adjective-Noun and Pseudoword-Noun conditions at the onset of second word presentation, with only the former condition licensing any phrasal anticipation. During the anticipatory window for phrase formation (from -200ms to 0ms prior to the second word onset), low frequency power (8–30 Hz) exhibited an anticipatory effect (Fig. 3). This anticipatory effect was found in IFG, pSTG and ATL, which all appear to be involved in syntactic-semantic prediction generation. In addition, these anticipatory effects were unrelated to BGA, and such widespread, regional effects were not found in delta or theta. For comparison, we also plot the anticipatory window in BGA for -100 to 0ms (Fig. 3B), which exhibited no relation with the lower frequency effects (compare also Fig. 3D with Fig. 3E).

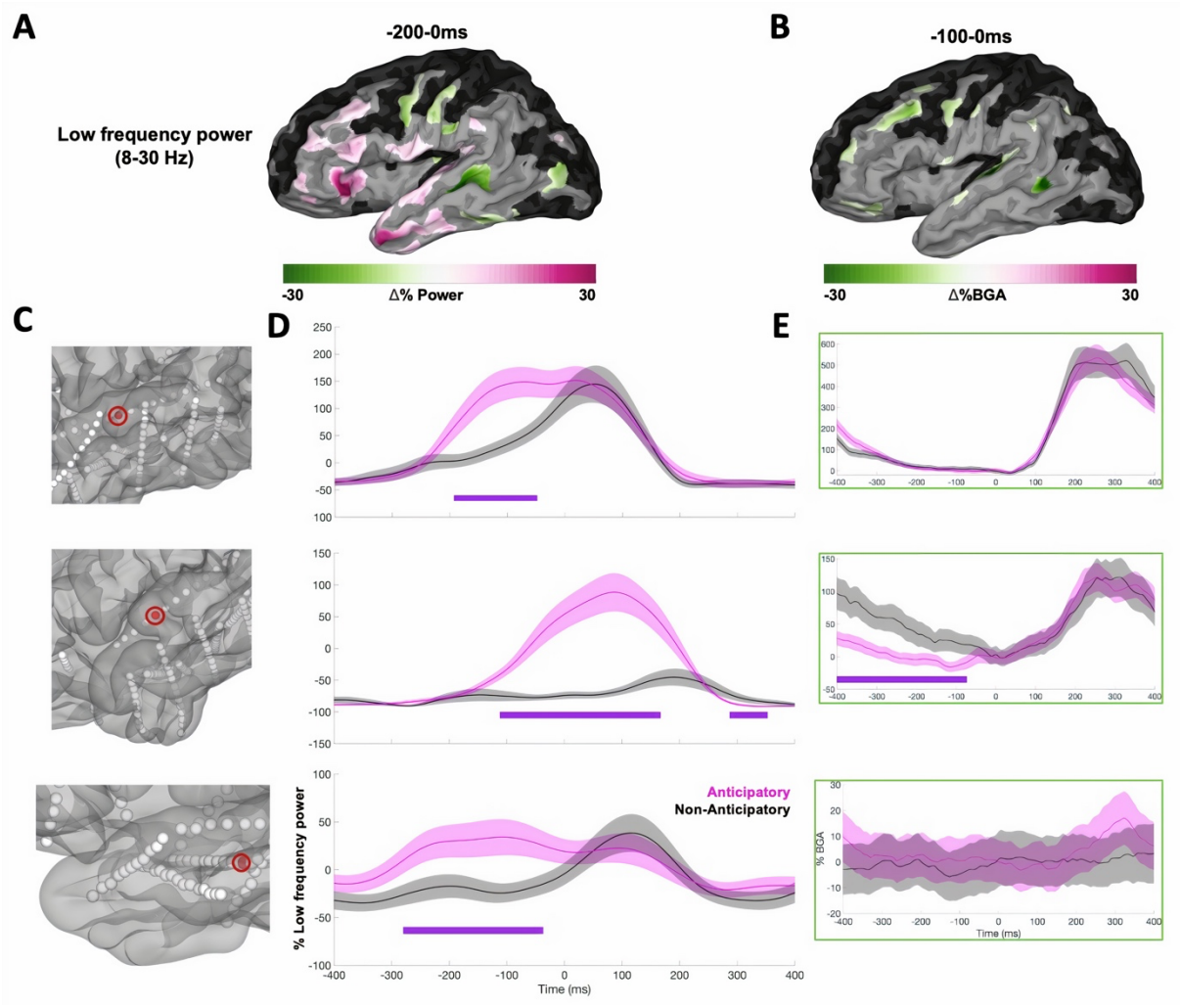


Figure 3: **Syntactic-semantic compositional anticipation.** (A) SB-MEMA for the anticipatory time window centred around second word onset (-200–0ms) for low frequency power. Pink: Greater power for composition anticipation. Green: Greater for no anticipation (i.e. after having heard a Pseudoword at first word position). (B) SB-MEMA for BGA for the same contrast for -100–0ms prior to second word onset. (C)-(E) Exemplar electrodes with location (C), low frequency power traces and (D) BGA traces in dashed green boxes (E), across three patients sorted by row.

Phrase composition

The full combinatorial contrast (Adjective-Noun vs [Adjective-Pseudoword + Pseudoword-Noun]), revealed greater BGA for portions of pSTS-TOJ during phrase composition than non-composition (Fig. 4A). The specific onset of this effect was around 210ms after noun onset, with peak BGA at around 300ms (Suppl. Fig. 3). The same region exhibited greater BGA for non-composition at later time points, implicating it in effortful phrase structure derivations.

Certain portions of pSTS-TOJ across patients displayed exclusive sensitivity to phrase composition, and not lexicality (Fig. 4B). Other regions – pSTG and inferior frontal gyrus (IFG) – did not show any significant BGA differences between these conditions (Suppl. Fig. 2). Since previous combinatorial effects in phrasal and sentential processing have also localized to anterior temporal pole, we also focused on this region (Suppl. Fig. 2, 4). These portions of left anterior temporal lobe (temporal pole) exhibited increased broadband low frequency activity in response to phrases from approximately 380–460ms and 700–900ms after noun presentation. This activity was unrelated to BGA, indicating that low frequency activity in ATL is an independent component of phrase structure comprehension; likely late-stage semantic processing. The ERPs were dissociable from BGA across the ROIs plotted (Suppl. Fig. 2): A late effect for Non-Composition was found in Broca's area, likely due to greater attempted lexical access for the pseudowords, while a late signature was detected in temporal pole for Composition, potentially related to late-stage conceptual access.

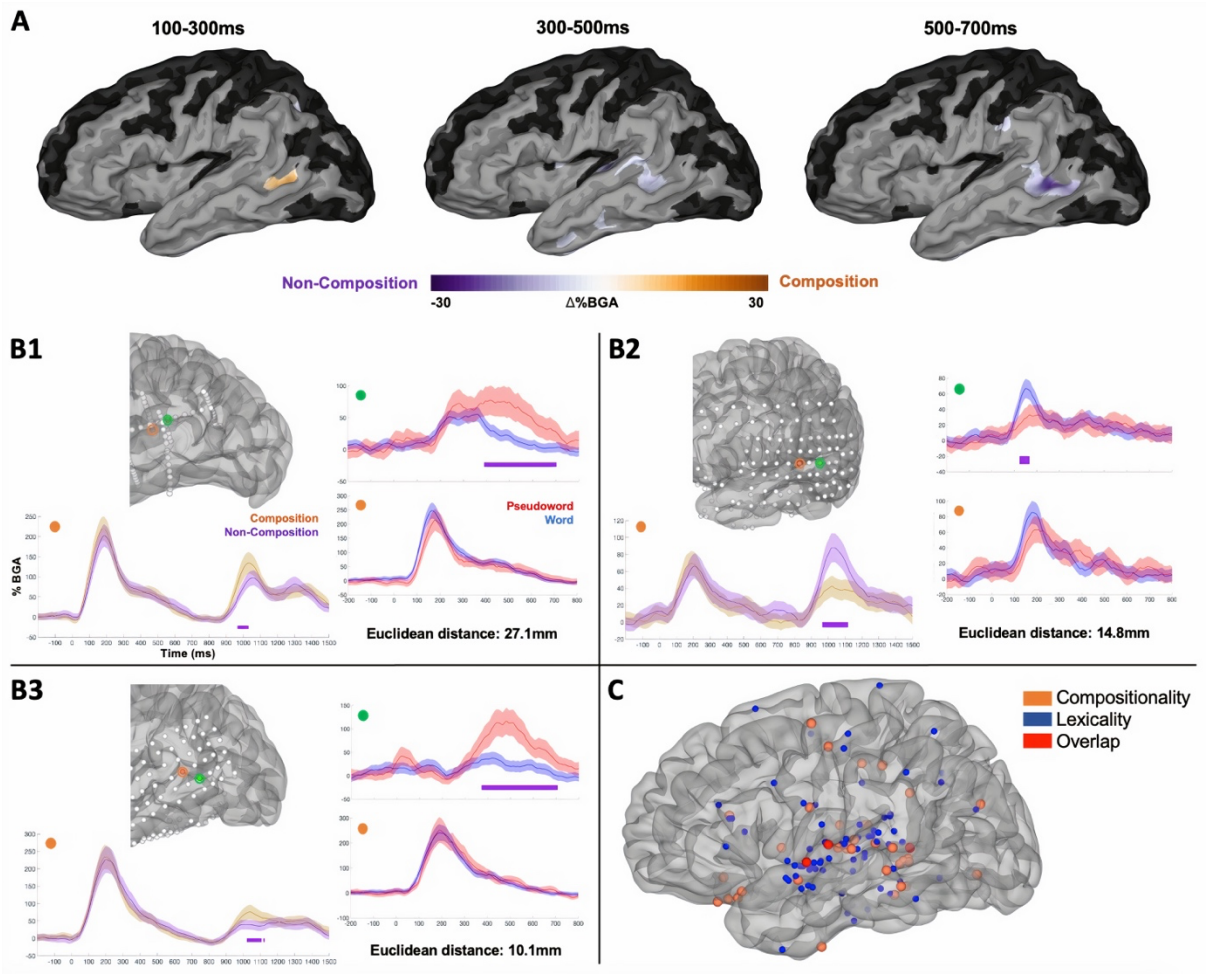


Figure 4: **Grouped analysis for phrase composition.** (A) SB-MEMAs for the phrase composition analysis for BGA. (B) Exemplar electrodes with FDR-corrected (one-tailed t-tests, q<0.05) significance bars in purple plotted in native patient space. Includes compositional

contrast and lexicality contrast, dissociating neighbouring portions of pSTS-TOJ that responded exclusively for phrase composition and not lexicality (orange dots = composition effect; green dots = lexicality effect). Error bars set at one standard error. Numbers denote distinct patients. (C) Electrodes exhibiting a significant BGA contrast between Compositional and Non-Compositional trials. 39 electrodes (orange) from 12 patients exhibited an FDR-significant contrast (one-tailed t-tests, $q<0.05$) for compositionality at some point between 0-1000ms after the second word; 97 electrodes across 17 patients for lexicality; 3 electrodes for both across 3 patients.

Next, we isolated regions of interest to derive cortical functional connectivity during phrase composition. These were based either on results from our main analysis (pSTS-TOJ, temporal pole) or on composition effects described in the literature (inferior frontal regions). To characterize functional connectivity between these regions during phrase composition, we computed phase-locking values (PLV) for electrode pairs situated within pSTS-TOJ with either pars triangularis or anterior temporal lobe. We computed the generalized phase of the wideband filtered (3–50 Hz) signal that has previously been shown to be more effective than the use of narrowband alpha or theta filters (Davis et al., 2020).

Among patients with concurrent coverage in pSTS-TOJ and pars triangularis (n = 8, electrode pairs = 231), the majority (n = 5) exhibited significantly greater PLVs for Compositional than for Non-Compositional trials during the 0–500ms period after second word onset, averaging across PLV values for each pair. In patients with joint coverage in pSTS-TOJ and anterior temporal lobe (temporal pole) (n = 8, electrode pairs = 274), the majority (n = 6) showed greater PLVs for the same contrast during the same time window. We plot the magnitude of phase-locking values across these regions and in two exemplar patients (Fig. 5).

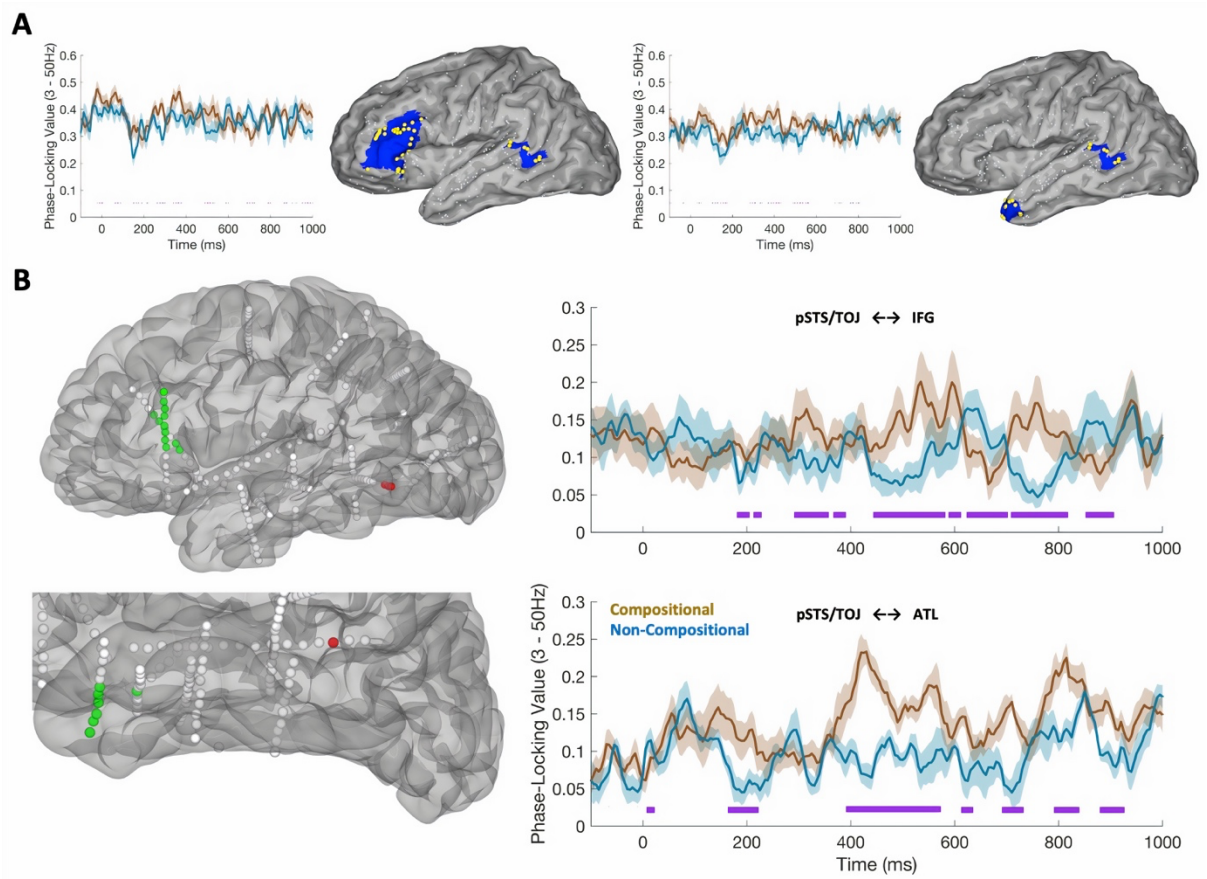
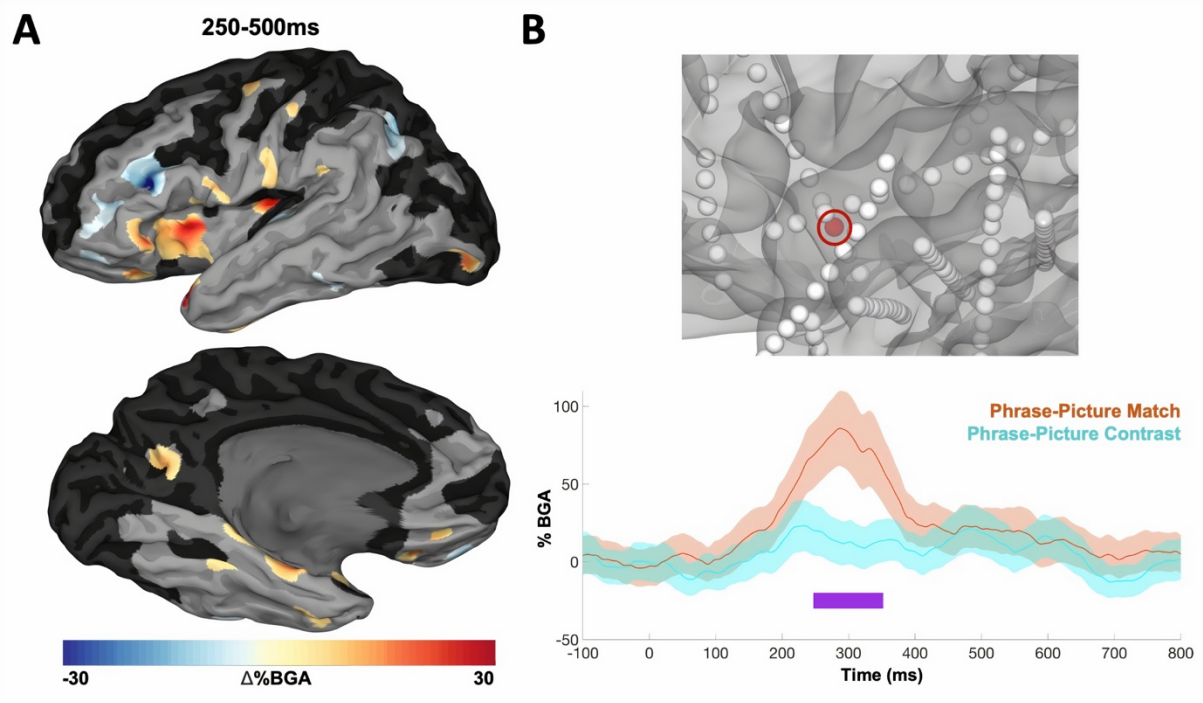


Figure 5: Phase-locking between semantic composition regions of interest. (A) Left: Average generalized phase-locking values (gPLV) for 5 patients showing greater gPLV for phrase composition relative to non-composition between pSTS-TOJ (HCP index: TPOJ1) and pars triangularis (HCP index: 45, IFSa, IFSp, 47l). Right: The same plot but for the 6 patients showing greater gPLV between pSTS-TOJ and temporal pole (HCP index: TGd). (B) Posterior temporal lobe (pSTS-TOJ) gPLVs with inferior frontal gyrus (specifically, pars triangularis) (Top) and anterior temporal lobe (specifically, temporal pole) (Bottom). Left plots show the localization in native space of electrodes significantly involved ($q < 0.05$) in inter-regional phase-locking (3–50 Hz). Right plots show average time courses (mean ± SEM) of phase-locking value changes from baseline in phrase composition (brown) and non-composition (blue) trials.

Integration of linguistic and visual information

Following each phrase, patients were presented with a matching or non-matching visual representation of the phrase. Comparing the Adjective-Noun trials which contained a matching picture, or a non-matching picture, during the 250–500ms post-picture window, SB-MEMAs revealed two notable effects (Fig. 6): Anterior insula exhibited greater BGA for phrase-picture

matches, while more dorsal frontal regions, centered around inferior frontal sulcus, exhibited greater BGA for phrase-picture non-matches. Thus, these regions appear to be implicated in linguistic-visual integration and monitoring, likely anchored around the semantic content denoted by both phrases and images and their successful association via some conjunction operator (i.e. [*red* ∧ *boat*], rather than a monadic adjectival or nominal representation). These two regions flank Broca's area, subserving distinct composition-related goals. Since activity of opercular regions can be misattributed to the insula (Woolnough et al., 2019), we ensured that these effects across patients specifically came from electrodes in insula proper, rather than operculum or Broca's area.



<u>Figure 6</u>: Grouped analysis for linguistic-visual integration. (A) SB-MEMA in BGA for phrase-picture match (orange) and phrase-picture contrast (turqoise) increases, 250–500ms after picture onset. (B) Exemplar insula electrode.

Discussion

We localized the neural signatures of combinatorial phrase structure comprehension using minimal adjective-noun phrases in a large patient cohort, with both penetrating depth and surface grid intracranial electrodes. We identified a broad portion of posterior temporal cortex as being sensitive to lexicality, and then isolated closely neighboring portions of pSTS-TOJ within patients that responded exclusively to phrase composition, and not lexicality, and vice versa. This computational contrast within a narrow strip of pSTS-TOJ provides a finely

organized cortical mosaic for the language system (Amunts & Zilles, 2015), going beyond more traditional, broader structure-function mappings for higher-order syntax-semantics. Our results can contribute to the development of a micro-map of pSTS-TOJ with respect to the demands of computational complexity; a necessary step towards understanding the organizational principles of the brain at distinct spatial scales, including ultimately cellular components.

Phrase composition was indexed by two main components: Greater BGA in portions of pSTS-TOJ at an early window (around 210-300ms); greater low frequency power in temporal pole at 380–460ms and 700–900ms after the presentation of a phrase-licensing nominal. Greater functional connectivity for phrase composition was found between these regions (pSTS-TOJ and temporal pole) and also between pSTS-TOJ and pars triangularis. pSTS-TOJ is initially active for phrase composition and subsequently shows greater local cortical activity for non-compositional stimuli, indicating its involvement in phrase-related processing. In addition, pSTS-TOJ and pSTG encode local processing of pseudowords, with pSTG likely coding speech signals into articulatory representations (Martin et al., 2019). Anterior portions of IFG exhibit greater BGA for pseudowords at the second word position, possibly indexing increased unification demands with the preceding adjective, compared to a real word (Hagoort, 2005, 2013; Hagoort & Indefrey, 2014). This effect may hence index the role of this region in the syntactic and semantic unification of more or less expected continuations, in agreement with earlier results in a sentence context (Hagoort, 2004).

In addition, STG, ATL and IFG index composition anticipation in low frequency power, consistent with a predictive neural mechanism for higher-order linguistic information (Bastiaansen & Hagoort, 2015; Benítez-Burraco & Murphy, 2019; Lewis et al., 2016; Murphy, 2015b; Prystauka & Lewis, 2019). These anticipatory effects were found in the context of our stimuli being controled for predictability (the addition of the Adjective-Pseudoword condition is the simplest way to achieve this). We additionally showed that alpha phase encodes lexical information exclusively in pSTG via ITC (and not phrase-relevant information).

Lastly, anterior insula and inferior frontal sulcus (IFS) subserve the integration of language input with the visual referent. Both of these regions have been argued to be the convergence zones of the ventral (anterior insula) and dorsal (IFS) attentional networks (Cazzoli et al., 2021), while task-evoked pupillary dynamics have been linked to the insula (Kucyi & Parvizi, 2020); given current task demands, these dynamics may also underscore our findings.

Lexicality

Our results replicate prior studies in which BGA localized to p/mSTG and pSTS tracks lexicality (Canolty et al., 2007; Humphries et al., 2006; Tanji et al., 2005). In addition, we show

recruitment of anterior IFG in this process. Further, pSTG alpha phase coherence may index the coordination of smaller-scale ensembles which may bundle sub-lexical features to yield coherent word-level interpretations of auditory stimuli, in accord with a recent neurocomputational model for lexical feature-set construction (Murphy, 2020).

Anticipatory response

According to a range of parsing models (Berwick et al., 2019), adjective-noun syntax is constructed predictively, in anticipation of the noun. Neural response differences in the period preceding the noun in combinatorial trials would likely reflect the generation of this structure. For instance, particular anticipatory amplitude increases have been isolated to the alpha (8–12 Hz) and beta (15–30 Hz) bands in fronto-central and fronto-temporal scalp EEG electrodes, and have been related to the pre-activation of linguistic structure/information (Gastaldon et al., 2020; Segaert et al., 2018). Based on our results, low frequency power in IFG and ATL may be preparing a syntactic slot to be filled by predicted upcoming nominal content, or initiating top-down local coordination of subsequent composition-indexing BGA in pSTS-TOJ. These low frequency dynamics might not even pertain to lexico-semantic prediction specifically, but rather anticipatory stages pertaining to phrasal initiation (Terporten et al., 2019). Our findings are also potentially in line with the notion that beta oscillations can index the construction and maintenance of sentence-level meaning (scaling up from minimal phrases) (Lewis et al., 2016), and the claims that beta can index aspects of syntactic anticipation and phrasal category generation (Benítez-Burraco & Murphy, 2019; Murphy, 2020).

Our results may relate to increased recruitment (Bonnefond & Jensen, 2013) of pSTS in late stage lexical processing effort (-200–0ms before the noun). The portion of temporal pole and MTG exhibiting low frequency increases during the anticipatory window could be also involved in late-stage lexico-conceptual processing of adjectival representations, although given the relatively late post-adjective window it is more likely to be related to anticipation. Given increasing evidence for IFG involvement in linear morpho-syntactic processing (Matchin & Hickok, 2020), it is also possible that effects in IFG index a form of lexical anticipation. Predictable word processing specifically pinpoints anterior IFG and ATL in preceding cortical activations (Pulvermüller & Grisoni, 2020). During basic semantic composition, anterior IFG activation has been shown to increase with the amount of lexical information being integrated into the structure (Schell et al., 2017), again pointing to a role for this region as a lexical memory buffer and/or the locus of higher-order predictions.

Minimal phrase composition

We found that neighbouring portions of pSTS-TOJ across patients can exclusively code either for lexicality or phrase composition, helping to isolate the core compositional operation in

phrase structure generation. While a large area of posterior and superior temporal cortex was sensitive to lexicality, a narrower portion was recruited exclusively to code for phrase structure, generating from simple lexical meanings the more computationally demanding structures of 'complex meaning' (Hagoort, 2020; Pietroski, 2018).

One of the main candidates for phrase composition from previous research, ATL, was implicated via low frequency activity (specifically, temporal pole activity). This may indicate that temporal pole is involved in compositional processing within a noun phrase, with low frequency activity possibly coordinating broader areas in the service of constructing a coherent semantic referent (Wang et al., 2020). Despite ATL being the "most consistent integrative node" (Pylkkänen & Brennan, 2020) in the syntax-semantics combinatorial network, the high spatiotemporal resolution of iEEG presented another candidate for composition: pSTS-TOJ. Increasing morpho-orthographic complexity in a similar minimal phrasal paradigm does not implicate ATL in early processing windows, but seems to delay ATL activity until after intra-word morphological composition (Flick et al., 2018). This suggests that there must be regions independent of semantic and orthographic processing that are common to all forms of (early) phrasal composition. Our findings suggest that pSTS-TOJ might be one such region, although since we only presented auditory stimuli we cannot make any stronger claims. Comparing the discovered composition effect in BGA (Fig. 4A) with the auditory stimuli activation map (Fig. 1C) suggests a clear overlap between sites of initial sensitivity to auditory stimuli and composition-sensitive sites. On the other hand, while there is indeed overlap, there is also a portion of posterior TOJ which seems uniquely active for composition but which is not prominently sensitive to audition, which may point to the involvement of a more modality-independent compositional process. Since MEG cannot detect high frequency activity deep in sulci (Irimia et al., 2012), our iEEG investigation was able to provide new insights here.

With respect to activation timings, we found greater BGA for phrase composition in pSTS-TOJ at 210ms, diminishing around 300ms, after which the majority of responses were greater for non-compositional trials. It is possible that composition-specific computations initiated earlier than this, and that it was only during these time windows that condition differences arose. The later, greater responses for non-composition could be due to more efficient encoding of phrases (hence lower BGA), or, more likely given the latency, late-stage compositional effort/evaluation. It is also possible that the low frequency responses we found to composition in ATL are responses to post-syntactic (pSTS-TOJ) processing, leading to conceptual integration. The timing of these late wrap-up effects might be due to the slow nature of these frequencies and could also be due to some form of traveling oscillatory component (Muller et al., 2018) from posterior temporal areas.

Our findings are in line with recent models implicating these posterior portions of temporal lobe in phrase structure building (Flick & Pylkkänen, 2020; Law & Pylkkänen, 2021; Matar et al., 2021; Matchin & Hickok, 2020; Murphy, 2018, 2020); a recent meta-analysis of sign language implicating TOJ and pMTG/pSTS in comprehension (Trettenbrein et al., 2020); and the finding that cross-linguistic (French and Chinese) reading competence is linked to pSTS (Feng et al., 2020), contributing to the neural localization of complex composition (Chomsky et al., 2019; Pietroski, 2018). In particular, evidence from neuroimaging and lesion-deficit mapping indicates a role for pMTG in syntactic comprehension and production (Matchin & Hickok, 2020), while pSTS has been implicated via iEEG in hierarchical syntactic computations (Nelson et al., 2017). Data from brain stimulation implicate postero-middle temporal areas in syntactic processing (Duffau et al., 2014), and a recent *red-boat* study in fMRI implicated a broad portion of pMTG in meaningful phrase composition (Graessner et al., 2021). Impairments in grammaticality judgments have primarily been linked to posterior temporal lobe damage (Wilson & Saygin, 2004). Lastly, widespread monotonic fronto-temporal language network gamma power increases over the course of sentence reading have been documented in iEEG (Fedorenko et al., 2016); our findings isolate a more specific site in the network responsible for the core compositional operator underlying sentence comprehension.

We also discovered greater functional connectivity between pSTS-TOJ and both temporal pole and pars triangularis after the presentation of the phrase-licensing nominal (Fig. 5). White matter atlas consultation reveals that the subcortical distribution of responses to semantic stimuli reflects the continuous and homogenous ventral course of functional information in the deep white matter of the temporal lobe, from TOJ, ascending to white matter underneath the posterior two-thirds of IFG (Sarubbo et al., 2020). These ventral workflow pathways subserve our regions of interest (temporal pole; TOJ; IFG). In addition, arcuate fasciculus is classically implicated in connectivity between pSTS-TOJ and pars triangularis (Figley et al., 2017; Glasser & Rilling, 2008). In relation to current findings and frameworks, it is possible that the formation of phrase structure in pSTS-TOJ feeds categorial information (e.g. phrase type) to interpretation interfaces in ATL and memory/control interfaces in pars triangularis (a form of "spell-out"). One such piece of information encoded via PLV would be the phrase category/label (Adger, 2012; Murphy, 2015a; Murphy & Shim, 2020). These results may point to a degree of top-down control from pars triangularis on initial phrase construction in pSTS-TOJ (Hagoort et al., 2009). The more precise computational role of such connectivity metrics requires further empirical, and conceptual, advances.

Inhibition of a portion of left posterior temporal lobe (pSTS, pSTG and temporo-parietal junction) selectively impairs the ability to produce appropriate functional morphemes for

383 particular hierarchical relations, but does not effect any other sub-linguistic process such as
384 semantic or lexical retrieval (Lee et al., 2018). Our data are compatible with the idea that in
385 connection with other areas, such as IFG (Baggio & Hagoort, 2011; Zaccarella et al., 2021),
386 pSTS-TOJ contributes to both morphological and phrasal unification (Jackendoff & Audring,
387 2020; Rizzi, 2016). Our results are concordant with a division between sensitivity to non-local
388 dependency structure (in left anterior temporal pole and IFG) and sensitivity to phrase
389 structure (in left pSTG) (Lopopolo et al., 2021). Data from sEEG comparing noun phrases and
390 acoustically-matched, identical words acting as verb phrases (with the latter demanding richer
391 syntactic structure) reveals greater high gamma activity in MTG and STG in the coding of
392 complex syntax (Artoni et al., 2020). This points to partial spatial overlap with our composition
393 effects, in compliance with the idea that the re-application of recursive hierarchical structure
394 generation calls upon the same basic compositional operator (i.e., that the computation
395 implicated in forming verb phrases is the same operation that forms "red boat").

396 While we did not find composition effects in inferior parietal lobule (in particular, angular gyrus),
397 and had good electrode coverage here, this may be due to this region's role in higher-order
398 semantic processing (e.g. thematic role assignment, discourse structure) and event structure
399 (Boylan et al., 2015). For instance, there is a range of evidence, including from intracranial
400 recordings, that taxonomic conceptual relationships are encoded in ATL, while thematic
401 relationships are encoded in angular gyrus (Davis & Yee, 2019; Thye et al., 2021).

402 Given the nature of our stimuli, we can make direct claims about semantic composition, and
403 we suspect that portions of pSTS-TOJ are also implicated in minimal syntax, however the
404 dynamics of the syntax network may differ from that of the semantic compositional network.
405 Overall, our results contribute to isolating the neural signatures of basic phrase structure
406 composition, an elementary computational procedure of natural language and potentially a
407 species-defining property (Friederici et al., 2017; Murphy, 2019; Murphy et al., 2021), and we
408 hope that future intracranial research can expand on our findings.

409

410 **Materials and Methods**

411 *Participants*: 19 patients (10 male, 18-41 years, IQ 97 ± 12, 2 left-handed) participated in the
412 experiment after written informed consent was obtained. All were native English speakers. All
413 experimental procedures were reviewed and approved by the Committee for the Protection of
414 Human Subjects (CPHS) of the University of Texas Health Science Center at Houston as
415 Protocol Number HSC-MS-06-0385.

Electrode Implantation and Data Recording: Data were acquired from either subdural grid electrodes (SDEs; 6 patients) or stereotactically placed depth electrodes (sEEGs; 12 patients) (Fig. 1B). SDEs were subdural platinum-iridium electrodes embedded in a silicone elastomer sheet (PMT Corporation; top-hat design; 3mm diameter cortical contact), and were surgically implanted via a craniotomy (Conner et al., 2011; Pieters et al., 2013; Tandon, 2012; Tong et al., 2020). sEEGs were implanted using a Robotic Surgical Assistant (ROSA; Medtech, Montpellier, France) (Rollo et al., 2020; Tandon et al., 2019). Each sEEG probe (PMT corporation, Chanhassen, Minnesota) was 0.8mm in diameter and had 8-16 electrode contacts. Each contact was a platinum-iridium cylinder, 2.0mm in length and separated from the adjacent contact by 1.5-2.43mm. Each patient had 12-20 such probes implanted. Following surgical implantation, electrodes were localized by co-registration of pre-operative anatomical 3T MRI and post-operative CT scans in AFNI (Cox, 1996). Electrode positions were projected onto a cortical surface model generated in FreeSurfer (Dale et al., 1999), and displayed on the cortical surface model for visualization (Pieters et al., 2013). Intracranial data were collected during research experiments starting on the first day after electrode implantation for sEEGs and two days after implantation for SDEs. Data were digitized at 2 kHz using the NeuroPort recording system (Blackrock Microsystems, Salt Lake City, Utah), imported into Matlab, initially referenced to the white matter channel used as a reference for the clinical acquisition system and visually inspected for line noise, artifacts and epileptic activity. Electrodes with excessive line noise or localized to sites of seizure onset were excluded. Each electrode was re-referenced to the common average of the remaining channels. Trials contaminated by inter-ictal epileptic spikes, saccade artefacts and trials in which participants responded incorrectly were discarded.

Stimuli and Experimental Design: Participants were presented with two-word auditory phrases, grouped by three conditions: Adjective-Noun ("red boat"), Adjective-Pseudoword ("red neub"), Pseudoword-Noun ("zuik boat"). Since these pseudoword phrases include phonologically viable nonwords, differences in the second position of the phrase between these items and the grammatical noun phrases are likely a result of compositional processing. While most previous studies have presented a licensable noun, our inclusion of the Adjective-Pseudoword condition further isolates composition and reduces predictability. To ensure attention was maintained, after each trial participants were shown a colored drawing and asked to press a button indicating whether the picture matched the phrase they had just heard. Participants were told to respond positively only when the picture fully matched the phrase (e.g. the phrase "red boat" followed by a picture of a red car, or a blue boat, would be negative). Auditory and visual stimuli were recruited from previous *red-boat* experiments (Bemis & Pylkkänen, 2013b).

A fixation cross was presented in the centre of the screen for 700ms followed by the first word and 800ms later the second word was presented. 1600ms after the onset of the second word the picture was presented, and 1400ms after picture presentation participants were prompted to respond (Fig. 1A). Following their response, a blank screen was shown for 1500ms. Stimuli were presented in a pseudorandom order, with no repetition amongst items. The number of trials per block across the full experiment was as follows: Adjective-Noun (80), Pseudoword-Noun (40), Adjective-Pseudoword (40). All patients undertook 2 blocks. Half of the Adjective-Noun trials matched the picture presented (i.e. “red boat” was heard by the patient, and a picture of a red boat was then presented), and the other half did not match. 6 adjectives were used: black, blue, brown, green, pink, red (length M: 4.3, SD: 0.7; SUBTLEXus log-frequency 3.64). 20 nouns were used: bag, bell, boat, bone, cane, cross, cup, disc, flag, fork, hand, heart, house, key, lamp, leaf, lock, plane, shoe, star (length M: 4.0, SD: 0.6; log-frequency 3.38) (Brysbaert, New, & Keuleers, 2012). 6 pseudowords were used: beeg, cresp, kleg, nar, neub, zuik (length M: 4.0, SD: 0.6). Average stimuli length: Adjectives (420 ms), Nouns (450 ms), Pseudowords (430ms).

Stimuli were presented using Psychtoolbox (Kleiner et al., 2007) on a 15.4” LCD screen positioned at eye-level, 2-3’ from the patient. Auditory stimuli were presented using stereo speakers (44.1 kHz, MacBook Pro 2015).

Signal Analysis: A total of 3458 electrode contacts were implanted in these patients; 2135 of these were included for analysis after excluding channels proximal to the seizure onset zone or exhibiting excessive inter-ictal spikes or line noise. Analyses were performed by first bandpass filtering the raw data of each electrode into broadband gamma activity (BGA; 70–150 Hz) following removal of line noise and its harmonics (zero-phase 2nd order Butterworth band-stop filters). Electrodes were also visually inspected for saccade artefacts. A frequency domain bandpass Hilbert transform (paired sigmoid flanks with half-width 1.5 Hz) was applied and the analytic amplitude was smoothed (Savitzky-Golay FIR, 3rd order, frame length of 251ms; Matlab 2019b, Mathworks, Natick, MA). BGA was defined as percentage change from baseline level; -500 to -100ms before the presentation of the first word in each trial. Periods of significant activation were tested using a one-tailed t-test at each time point and were corrected for multiple comparisons with a Benjamini-Hochberg false detection rate (FDR) threshold of $q<0.05$. For the grouped analysis, all electrodes were averaged within each subject and then the between-subject averages were used.

To provide statistically robust and topologically precise estimates of BGA, and to account for variations in sampling density, population-level representations were created using surface-based mixed-effects multilevel analysis (SB-MEMA) (Conner et al., 2011; Fischl et al., 1999;

Kadipasaoglu et al., 2014; Kadipasaoglu et al., 2015). This method accounts for sparse sampling, outlier inferences, as well as intra- and inter-subject variability to produce population maps of cortical activity. A geodesic Gaussian smoothing filter (3mm full-width at half-maximum) was applied. Significance levels were computed at a corrected alpha-level of 0.01 using family-wise error rate corrections for multiple comparisons. The minimum criterion for the family-wise error rate was determined by white-noise clustering analysis (Monte Carlo simulations, 5000 iterations) of data with the same dimension and smoothness as that analyzed (Kadipasaoglu et al., 2014). Results were further restricted to regions with at least three patients contributing to coverage and BGA percent change exceeding 5%.

Anatomical groups of electrodes were delineated, firstly, through indexing electrodes to the closest node on the standardized cortical surface (Saad & Reynolds, 2012), and secondly, through grouping channels into parcellations determined by Human Connectome Project (HCP) space (Glasser et al., 2016). Parametric statistics were used since HCP regions of interest contained >30 electrodes. When contrasting experimental conditions, two-sided paired t-tests were evaluated at each time point for each region and significance levels were computed at $q<0.01$ using an FDR correction for multiple comparisons.

To generate event-related potentials (ERPs), the raw data were band pass filtered (0.1–50 Hz). Trials were averaged together and the resultant waveform was smoothed (Savitzky-Golay FIR, third-order, frame length of 251ms). To account for differences in polarity between electrodes, ERPs were converted to root mean square (RMS), using a 50ms sliding window. All electrodes were averaged within each subject, within ROI, and then the between subject averages were used.

There is increasing evidence that the phase of activation across distributed neural populations correlates with distinct underlying neural processes from the amplitude (Buzsáki, 2019; Fries, 2015; Sauseng & Klimesch, 2008). We investigated the influence of lexicality and phrase construction on inter-trial phase coherence (ITC). Phase information was extracted from the band-pass filtered data (zero-phase 3rd order Butterworth band-pass filter) using a Hilbert transform. ITC was calculated as the circular mean (absolute vector length) of instantaneous phase of stimulus-aligned trials computed as the median value of 10 iterations of a random 50% of trials.

To explore the functional connectivity between regions of interest, we used a generalized phase-locking analysis to estimate the dominant spatio-temporal distributions of field activity, and the strength of the coupling between them. Phase information was extracted from the down-sampled (200 Hz) and wide band-pass filtered data (3–50 Hz; zero-phase 8th order Butterworth band-pass filter) using the ‘generalized phase’ method (Davis et al., 2020) with a

522 single-sided Fourier transform approach (Marple, 1999). This method captures the phase of
523 the predominant fluctuations in the wideband signal and minimizes filter-related distortion of
524 the waveform. PLV was calculated as the circular mean (absolute vector length) of the
525 instantaneous phase difference between each electrode pair at each time point and baselined
526 to the period -500 to -100 ms before onset of the first word. Statistics were calculated using
527 the mean PLV of correctly answered trials between 0 to 500ms after second word onset,
528 comparing against a null distribution generated by randomly re-pairing trial recordings across
529 the electrode pairs 500 times. Significant PLV was accepted at a threshold of $p<0.05$.

530

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540 0385.

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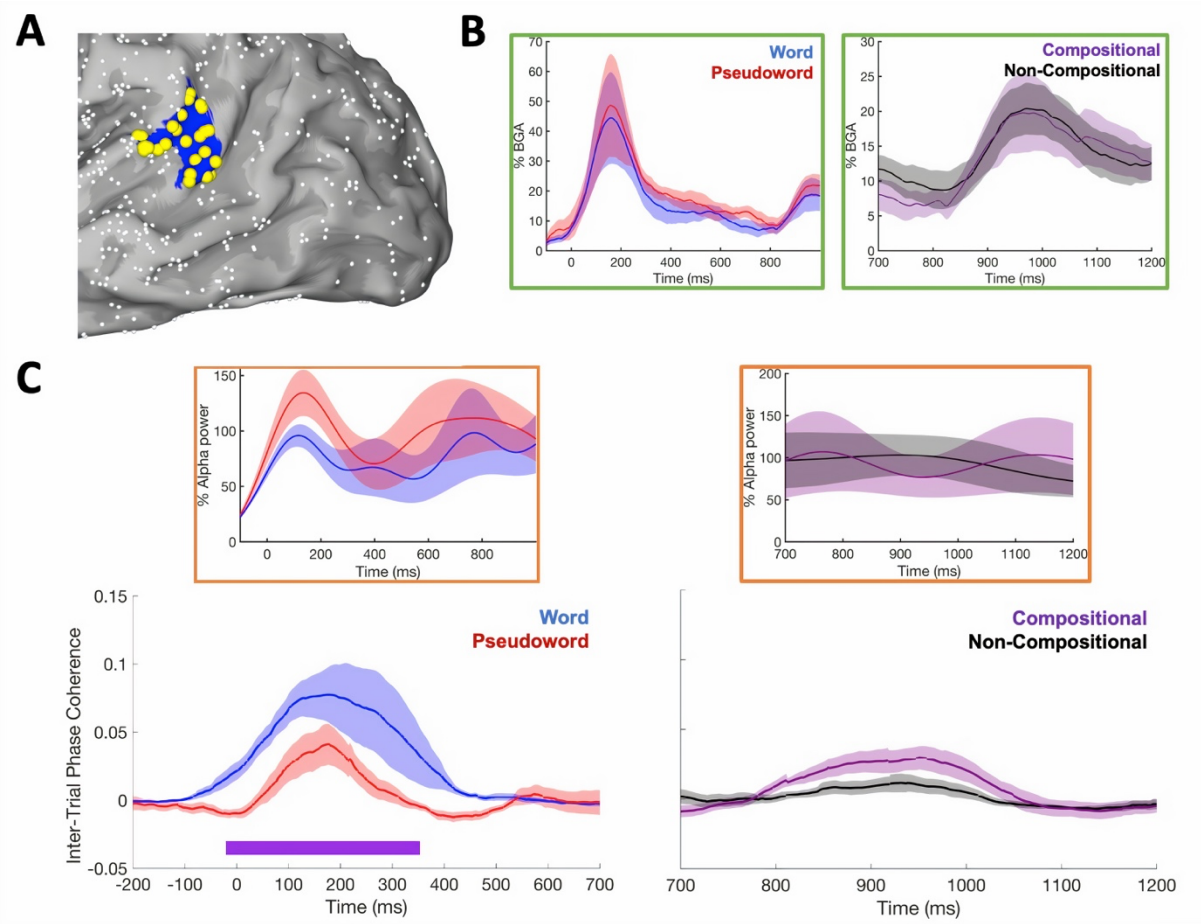
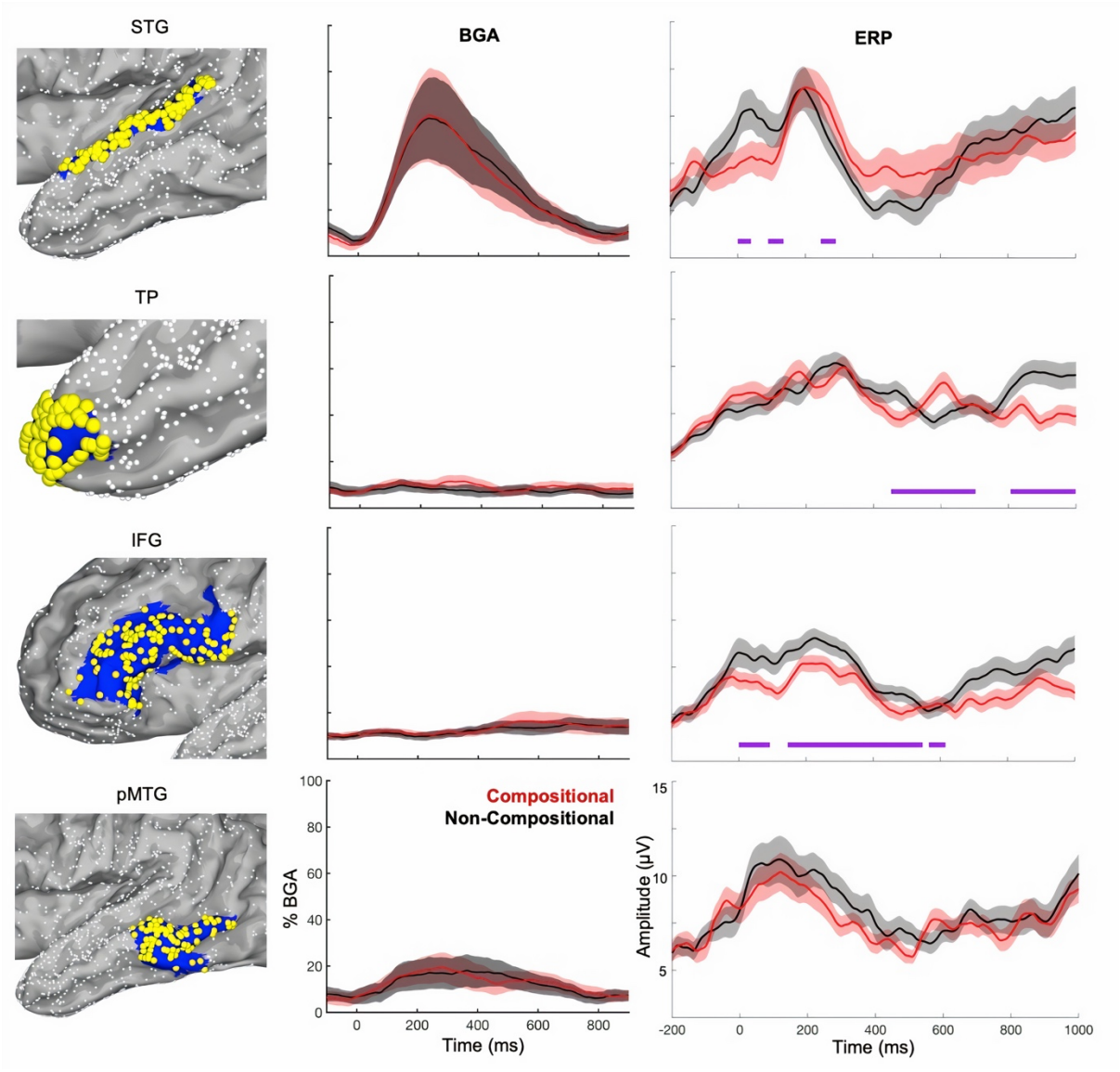
Supplementary Figures

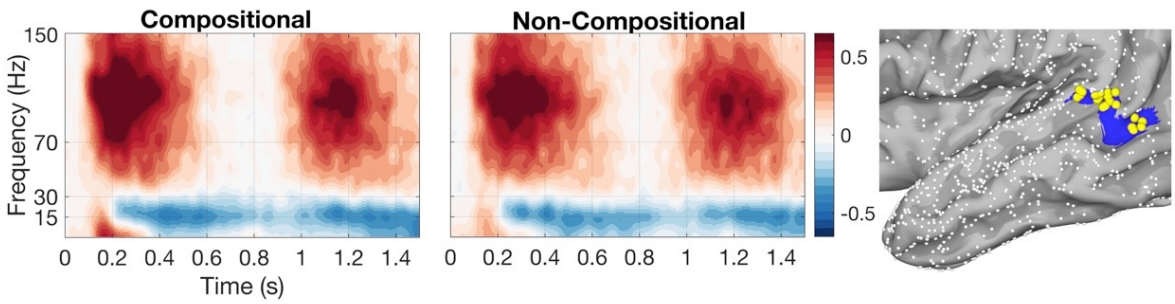


<u>Supplementary Figure 1</u>: Inter-trial phase coherence and lexicality.

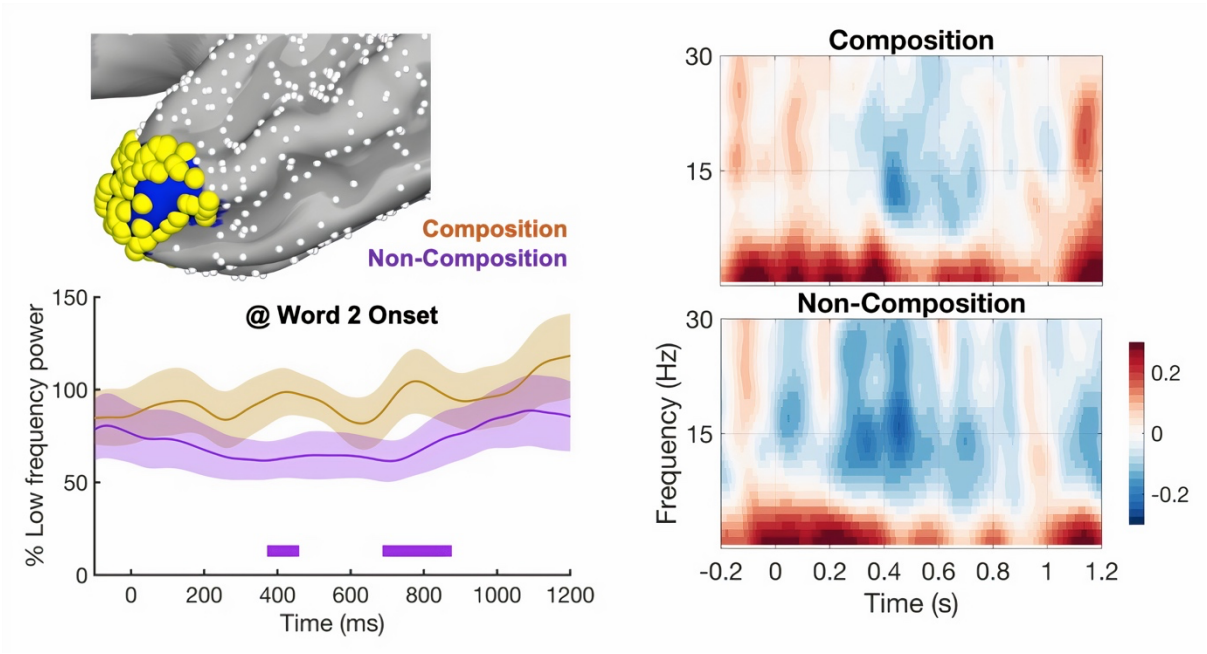
(A) Electrodes with significant differences in ITC for words vs pseudowords, in a portion of posterior temporal cortex with a high concentration of electrodes exhibiting significant differences (9 patients); HCP index: area STV (Glasser et al., 2016). (B) Gamma traces (green dashed box) for electrodes in (A) for words vs. pseudowords and compositional vs. non-compositional trials (C) ITC in alpha (8-12Hz) for all electrodes in (A) for words (blue) and pseudowords (red) on the left, with alpha (orange dashed box) amplitude traces, and for phrase composition (purple) and non-composition (black) on the right isolated around the onset of the second word (no significant effect for composition contrast). T0 = first word onset.



<u>Supplementary Figure 2</u>: Regions of interest and their BGA/ERP signatures. Regional broadband gamma amplitude (middle column) with event-related potentials (right column). Red: Compositional. Black: Non-Compositional. HCP index from top-down: posterior superior temporal gyrus (pSTG) = [A4]; temporal pole = [TGd]; inferior frontal gyrus (IFG) = [FOP4, 44, 45, IFSp, p47r, IFSa, 47l]; posterior middle temporal gyrus (pMTG) = [PHT, TE1p]. BGA traces are thresholded by $p<0.05$ significantly active from baseline (first word onset, -500 to -100ms) with a minimum of 10% BGA amplitude increase during the 100-400ms post-second word onset period. ERPs were computed across the four ROIs plotted on the left column, with significant condition differences being computed across 0-1000ms in the same (FDR-corrected) manner as the BGA plots (see Methods).



<u>Supplementary Figure 3</u>: pSTS-TOJ regional spectrograms. Spectrograms and electrodes in pSTS-TOJ for all active channels (HCP index: TPOJ1; electrodes = 23, patients = 10). Second word onset was at 800ms.



<u>Supplementary Figure 4</u>: Temporal pole effects. Low frequency (2–15Hz) temporal pole trace with FDR-significant bars for the Compositional (brown) vs Non-Compositional (purple) contrast (HCP index: TGd) with spectrograms, thresholded at 10% increased activity from baseline; T0 = second word onset. For BGA, see Suppl. Fig. 2.