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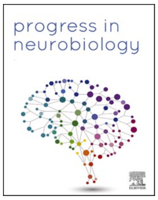

Multiple dimensions of syntactic structure are resolved earliest in posterior temporal cortex

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ABSTRACT

How we combine minimal linguistic units into larger structures remains an unresolved topic in neuroscience. Language processing involves the abstract construction of 'vertical' and 'horizontal' information simultaneously (e.g., phrase structure, morphological agreement), but previous paradigms have been constrained in isolating only one type of composition and have utilized poor spatiotemporal resolution. Using intracranial recordings, we report multiple experiments designed to separate phrase structure from morphosyntactic agreement. Epilepsy patients (n = 10) were presented with auditory two-word phrases grouped into pseudoword-verb ('trab run') and pronoun-verb either with or without Person agreement ('they run' vs. 'they runs'). Phrase composition and Person violations both resulted in significant increases in broadband high gamma activity approximately 300 ms after verb onset in posterior middle temporal gyrus (pMTG) and posterior superior temporal sulcus (pSTS), followed by inferior frontal cortex (IFC) at 500 ms. While sites sensitive to only morphosyntactic violations were distributed, those sensitive to both composition types were generally confined to pSTS/pMTG and IFC. These results indicate that posterior temporal cortex shows the earliest sensitivity for hierarchical linguistic structure across multiple dimensions, providing neural resources for distinct windows of composition. This region is comprised of sparsely interwoven heterogeneous constituents that afford cortical search spaces for dissociable syntactic relations.

1. Introduction

The neural mechanisms by which our brains assemble different linguistic components into larger structures is a critical question in contemporary neurobiology of language (Baggio, 2022; Murphy, 2024). An understanding of the processes that enable rapid composition of lexical, phrasal and morphological structures is essential for creating ecologically valid models of language and the generation of complex mental representations. Critically, linguistic meaning is rapidly inferred via multiple, interacting dimensions of information, such as hierarchical (vertical node structure) and horizontal (relational, linear) information, but previous research with intracranial recordings has only focused on discrete dimensions, e.g., the ramping of activity during hierarchical semantic composition (Desbordes et al., 2023; Woolnough et al., 2023) or morphological relational processing (Lee et al., 2018). An integrated measure of processing costs pertaining jointly to these vertical and horizontal dimensions can explain temporal lobe activity in fMRI (Li and Hale, 2019), pointing to the need for researchers to consider more than simply one isolated measure of linguistic structure and complexity (Murphy et al., 2024). Many open questions remain concerning the joint resolution of these dimensions of structure building. For example, is the composition of hierarchical phrase structure subserved by the same

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cortical networks as those subserving the functional relations between words? In our previous research we disentangled multiple types of semantic integration processes (Murphy et al., 2023), demonstrating the feasibility of resolving the spatiotemporal dynamics of overlapping but discrete operations over rapid time windows.

Recent studies have implicated the posterior temporal cortex in basic phrase and sentence processing (Pylkkänen, 2020; Murphy et al., 2022b; Woolnough et al., 2023), but there is no consensus concerning which specific aspects of language are responsible for these types of effects. Studies of lexical-phonological processing and morphology have often examined these in isolation from one another (Leminen et al., 2019) and have depended on techniques that lack adequate spatiotemporal resolution (Hardy et al., 2021; Stockbridge et al., 2023). Relative contributions from frontal, temporal and parietal regions to basic components of composition, and the precise timing of effects, remain debated (Prehn et al., 2018; Matchin and Hickok, 2020; Graessner et al., 2021; Desbordes et al., 2023). The left middle temporal gyrus is believed to be implicated in lexical access and processing (Indefrey and Levelt, 2004; Friederici, 2012; Hagoort and Indefrey, 2014), morphological decomposition (Pylkkänen et al., 2004, 2006; Fiorentino and Poeppel, 2007) and generative phonological processing (Gow et al., 2023), while the left inferior frontal cortex has been implicated in complex derivational morphology (Thompson et al., 2007; Carota et al., 2016; Neophytou et al., 2018; Leminen et al., 2019). However, the specific spatiotemporal mapping of sites engaged in these combinatorial processes remains incompletely addressed.

Prior research using intracranial recordings has probed activity related to individual words (Tanji et al., 2005; Canolty et al., 2007; Edwards et al., 2010; Kellis et al., 2010; Kojima et al., 2013) or complex sentences (Fedorenko et al., 2016; Nakai et al., 2017; Nelson et al., 2017). Yet, key compositional machinery at the intermediate, phrasal level (Marcolli et al., 2023) remains underexplored in high-resolution recordings. Recent intracranial research has revealed that the posterior superior temporal sulcus (pSTS) is engaged early in phrase composition and at a later time interval for non-composition involving pseudowords (Murphy et al., 2022b), implying layered reentrant activity in this region. However, this previous work used adjective-noun phrases, that are heavily centred on conceptual objecthood representations (Fyshe et al., 2019) – thus this compositional signature may not generalize to other structures. The experiments we report here utilize fundamental predicate-argument thematic relations involving pronouns and verbs.

We characterized the spatiotemporal dynamics of auditory phrase comprehension (Bemis and Pylkkänen, 2011; Westerlund et al., 2015; Blanco-Elorrieta and Pylkkänen, 2016; Blanco-Elorrieta et al., 2018; Flick et al., 2018; Flick and Pylkkänen, 2020; Pylkkänen, 2020) via a simple minimal phrase paradigm that targeted both hierarchical and horizontal linguistic information; namely, phrase composition (generating a basic hierarchical structure) and agreement (generating linear morphological agreement across multiple words). Across two experiments, we collected data using intracranial EEG (iEEG) with a combination of either penetrating depth electrodes or subdural electrode arrays, in native English-speaking participants being monitored for medically refractory epilepsy. In the first experiment, participants were randomly presented with auditory recordings of either pseudoword-verb pairs (e.g., 'pob send') or a pseudoword followed by an incomprehensible sound (i.e., pink noise) and made a forced choice as to whether or not they heard pink noise. In the second experiment, participants heard pronoun-verb pairs with either syntactic morphological agreement ('you send', 'he scours') or not ('you send', 'he scour') and made a forced choice concerning phrasal correctness (Fig. 1A). This design allowed us to separate the processing of linguistic constituents, from lexical items to morphosyntactic agreement (Fig. 1B) with the four trial types graded along a scale of increasing salience of linguistic meaning, from pseudoword–*noise*, to pseudoword–verb, to ungrammatical pronoun–verb, and finally to grammatical pronoun–verb. Relatively comprehensive frontotemporal and parietal coverage (Fig. 1C) allowed us to explore whether morphosyntactic violations are processed in brain regions that are distinct from or overlap with those indexing phrase composition and lexical-phonological processing, and whether these are resolved across similar time intervals or not (Brunellière et al., 2007; Maran et al., 2022). Recent research with fMRI has argued that posterior temporal cortex is sensitive to vertical phrase structure, while anterior temporal and inferior frontal cortices process relational dependencies (Lopopolo et al., 2021), yet intracranial recordings may unveil more subtle sensitivity profiles within these anatomical landmarks.

Despite the limitations of using two-word stimuli to tap into hierarchical linguistic processing (i.e., we are unable to track the ramping build-up of activity punctuated by specific moments of structural inference), we note that even at the level of bi-gram elements such as "he ran", linguists assume that some hierarchical 'projection' is represented which unifies words into a compositional interpretation. For example, the pronoun "he" and the verb "ran" would merge into a Verb Phrase (not a Determiner Phrase), which exhibits the distributional properties

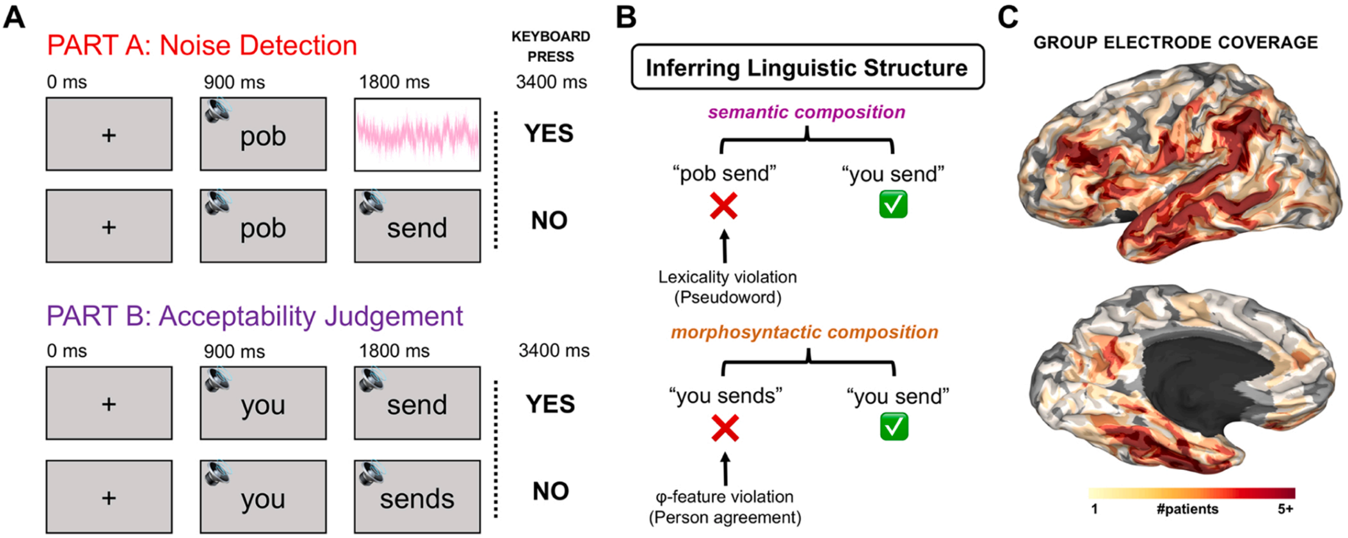

Fig. 1. : Task paradigm and patient electrode coverage. (A) Experimental paradigm for both parts of the task, involving pink noise detection and acceptability judgment tasks. (B) Representation of how the experimental paradigm isolates distinct compositional processes. (C) Group coverage map of left hemisphere electrodes included in analyses, plotted on a semi-inflated standardized N27 surface.

of verbs more generally, and the meaning of which is primarily driven by the ‘head’ of the phrase, the verb (Adger, 2003; Radford, 2004). Some researchers have argued that basic phrases involve ‘asymmetric’, hierarchical relations between elements (Dehaene et al., 2022), differentiating language from other domains that more readily tolerate symmetrical structures (e.g., music, mathematics). In addition, neural sensitivity to these minimally hierarchical units has been found in prior research (Segaert et al., 2018; Burroughs et al., 2021; Maran et al., 2022), with two-word phrases also triggering nested hierarchies of oscillatory behavior (Lu et al., 2022, 2023). Even though English requires pronoun-verb ordering, many other languages exhibit the reverse order, suggesting that with minimal structures there are syntactic inferences being made that pertain to aspects of hierarchical representation. The use of bi-gram elements to explore questions of hierarchical vs. horizontal linguistic information also mitigates problematic confounds that arise in standard sentence-level paradigms, such as working memory, attention and situation model construction processes.

2. Results

2.1. Behavioral performance

Task performance was mostly accurate both for pink noise detection (98 % ± 2 %) and for acceptability judgments (91.1 % ± 4.3 %). Average response times were 1030 ± 688 ms and 1125 ± 616 ms, respectively for the two tasks. Only correct trials were analyzed.

2.2. Lexical-phonological processing

A surface-based, population-level map of cortical activity was generated using a surface-based mixed-effects multi-level analysis (SB-MEMA) (Fischl et al., 1999; Conner et al., 2011; Kadipasaoglu et al., 2014, 2015), a method specifically designed to account for sampling variations in iEEG and minimize outlier effects. We used these maps to represent cortical responses for verbs (in Pseudoword-Verb trials) and pink noise (in Pseudoword-Noise trials). These contrast maps across the 100–900 ms period after the onset of the verb/noise revealed a number of regions sensitive to lexical-phonological processing. Significantly greater broadband gamma activity (BGA; 70–150 Hz) for verbs than for pink noise was found early (during the 100–300 ms post-onset window) in anterior superior temporal sulcus (aSTS), temporal pole (TP), anterior insula, mid-fusiform cortex (mFus) and inferior parietal cortex, and later (300–500 ms) in posterior superior temporal gyrus (pSTG), inferior frontal sulcus (IFS) and medial parietal cortex (MPC). Inferior frontal gyrus showed a late increase for pink noise over verbs (700–900 ms) (Table 1), which may partly be due to task-related engagement during this late period of decision-making and response, given the role of this region in executive control processes (Friedman and Robbins, 2022) and also given that stimuli presentation across all trial types was completed by the 600 ms mark. Effects across all participants are plotted alongside composition-sensitive sites (Figs. 3A, C, 4–5). Sites that were only sensitive to lexical-phonological processing were clustered mostly around pSTG and aSTG (Fig. 3A).

Table 1
Grouped statistics for SB-MEMA for earliest effects of lexical-phonological processing.

ROI	β(SD)	t-value	p-value
Anterior superior temporal sulcus (100–300 ms)	0.21 (.09)	2.66	.003
Temporal pole (100–300 ms)	0.13 (.05)	2.96	.001
Anterior insula (100–300 ms)	0.51 (.28)	2.79	.002
Mid-fusiform cortex (100–300 ms)	0.11 (.05)	2.76	.002
Inferior parietal cortex (100–300 ms)	0.10 (.04)	2.71	.003
Posterior superior temporal gyrus (300–500 ms)	0.24 (.09)	2.69	.003
Inferior frontal sulcus (300–500 ms)	0.21 (.09)	2.65	.003
Medial parietal cortex (300–500 ms)	0.24 (.10)	2.51	.005
Inferior frontal gyrus (700–900 ms)	0.14 (.07)	−2.54	.005

2.3. Phrase composition

To dissociate local cortical responses to lexicality from phrase composition, we probed differences in representation between pseudoword-verb trials and grammatical pronoun-verb trials. SB-MEMA analyses (Fig. 2) revealed significantly greater BGA for phrase composition in aSTS, posterior superior temporal sulcus (pSTS) and posterior middle temporal gyrus (pMTG), pSTG, IFS and anterior insula (Table 2). Earliest sensitivity to phrase composition was found in aSTS and pSTS/pMTG, with later effects in inferior frontal cortex (Figs. 3B, 5) and pSTG. Sites sensitive to both lexical-phonological processing and phrase composition were clustered around pSTG, pSTS and pMTG. Sites sensitive only to phrase composition were heavily clustered in inferior frontal cortex, inferior parietal cortex and posterior temporal cortex (Fig. 3A).

2.4. Morphosyntactic composition

To probe responses to morphosyntax, we contrasted pronoun-verb phrases with or without Person-marked agreement on the verb. SB-MEMA analyses revealed significantly greater BGA for agreement violations (e.g., ‘they runs’) in pMTG (and the lower bank of pSTS), TP and IFS, and later in subcentral gyrus, middle STG and inferior supramarginal gyrus. Greater BGA for morphosyntactic agreement was found only in MPC (Table 3).

The earliest effects of agreement violations were found in pMTG and the lower bank of pSTS (100–300 ms), then in IFS (300–700 ms), and finally in inferior supramarginal gyrus and middle STG (700–900 ms). Sites sensitive to only morphosyntactic violations were much more widespread and were scattered across frontal, parietal and temporal cortices. Sites sensitive to both morphosyntax and phrase composition (but not lexical-phonological processing) were in inferior parietal and temporal cortex (Fig. 3A, C).

2.5. Topography of effects

We plot the topographical map of electrodes categorized by effect type (Fig. 3A), in addition to a number of individual participants who exhibited either widespread (Fig. 3C) effects or more focal effects in temporal (Fig. 4), frontal (Fig. 5) or parietal cortex (Fig. S2). Taking into account the above cartographic profile for lexical-phonological processing, phrase composition and morphosyntactic agreement, electrodes that were sensitive to all contrasts (Fig. 3A) were mostly tightly distributed along classical perisylvian frontotemporal language cortices in pSTS/pMTG and IFS/IFG. Along STG and pSTS/pMTG, electrodes sensitive to effects of both lexical-phonological processing and phrase composition were found. These effects were almost exclusive to these regions. We note that no electrodes exhibited an effect jointly of lexical-phonological processing and morphosyntax.

Specifically for participants with clear frontal and temporal composition effects, we note the structured tesselation of composition-sensitivity (Figs. 3C, 4, 5), in contrast with the more diffuse parietal responses (Fig. 3A, Fig. S2). Despite the lack of robust within- participant joint frontotemporal coverage and the relatively small patient population, there was nevertheless a clear spatiotemporal structure to the frontotemporal composition effects (Figs. 2, 3A, B). Electrodes that showed effects for both hierarchical and horizontal linguistic structure were exclusively found in posterior temporal and inferior frontal cortices. Effects of phrase composition were more widespread, although were mostly confined to posterior temporal, inferior parietal and inferior frontal cortices.

2.6. Low frequency effects of composition

Recent research has highlighted the importance of alpha power in

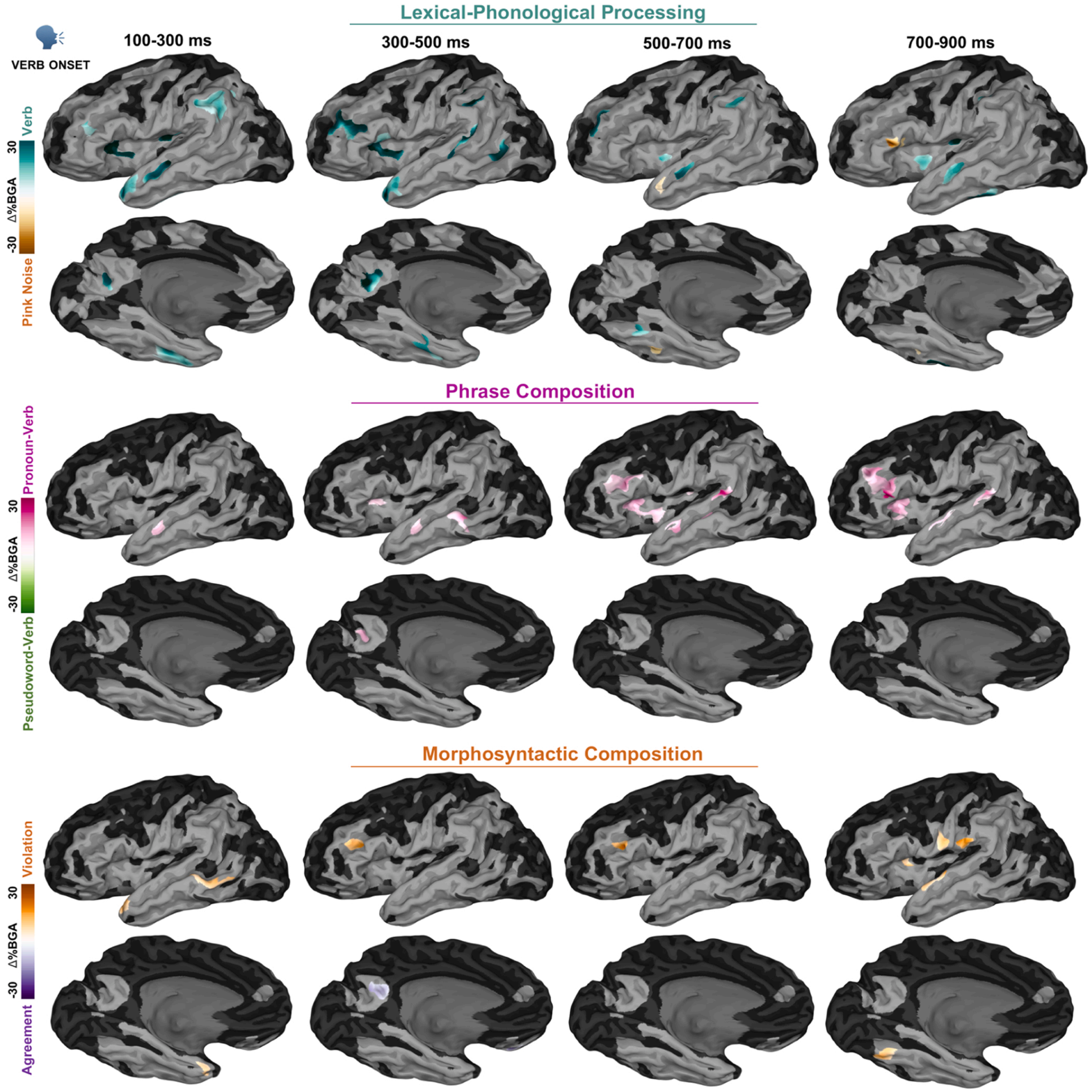

Fig. 2. : Grouped analysis for lexical-phonological processing, phrase composition and morphosyntactic composition. Top: SB-MEMA comparing lexical-phonological (verb) processing with pink noise processing and their broadband gamma activity (BGA; 70–150 Hz) time-locked to onset of the second word relative to baseline (pre-stimulus −500 to −100 ms). Middle: Phrase composition SB-MEMA comparing pseudoword-verb and pronoun-verb trials. Bottom: Morphosyntactic composition SB-MEMA comparing syntactic/acceptable pronoun-verb phrases with pronoun-verb phrases that exhibited an agreement violation. SB-MEMA thresholds: %BGA > 5 %, t > 2.5, patient coverage ≥ 2 (1 for Lexical-Phonological Processing); p < 0.01 corrected. Black surfaces fell below patient coverage threshold. Time 0 ms = onset of verb.

syntactic and semantic binding operations (Hardy et al., 2023), however there is no consensus about the precise cortical localization of alpha effects. Studies have also found contradictory effects of power increases (Segaert et al., 2018) but also decreases (Lam et al., 2016; Gastaldon et al., 2020) during phrase composition. These results may partially be due to previous designs not separating out distinct types of compositional processes. We therefore analyzed effects of phrase composition on alpha power (8–12 Hz; see Methods for further details) (Fig. S1). We discovered significant decreases in alpha power for phrase composition in pMTG (500–900 ms: $\beta = 0.16$ (SD 0.06), $t = 3.45$, $p = <.001$) and mid-fusiform gyrus (500–900 ms: $\beta = 0.16$ (SD 0.09), $t = 3.27$, $p = <.001$) exclusively in late windows (Fig. S1C, D). These effects began around the onset of the above BGA effects, but lasted around 500–600 ms. The alpha effect in pMTG was clearly dissociable from higher frequency dynamics, with no effects being found in BGA (Fig. S1B).

We next analyzed effects of morphosyntax on alpha power (8–12 Hz) (Fig. S1). We discovered significant decreases in alpha power for morphosyntactic violations in MTG (500–900 ms: $\beta = 0.16$ (SD 0.09), $t = 2.80$, $p =.002$) and subcentral gyrus (500–900 ms: $\beta = 0.13$ (SD 0.07), t

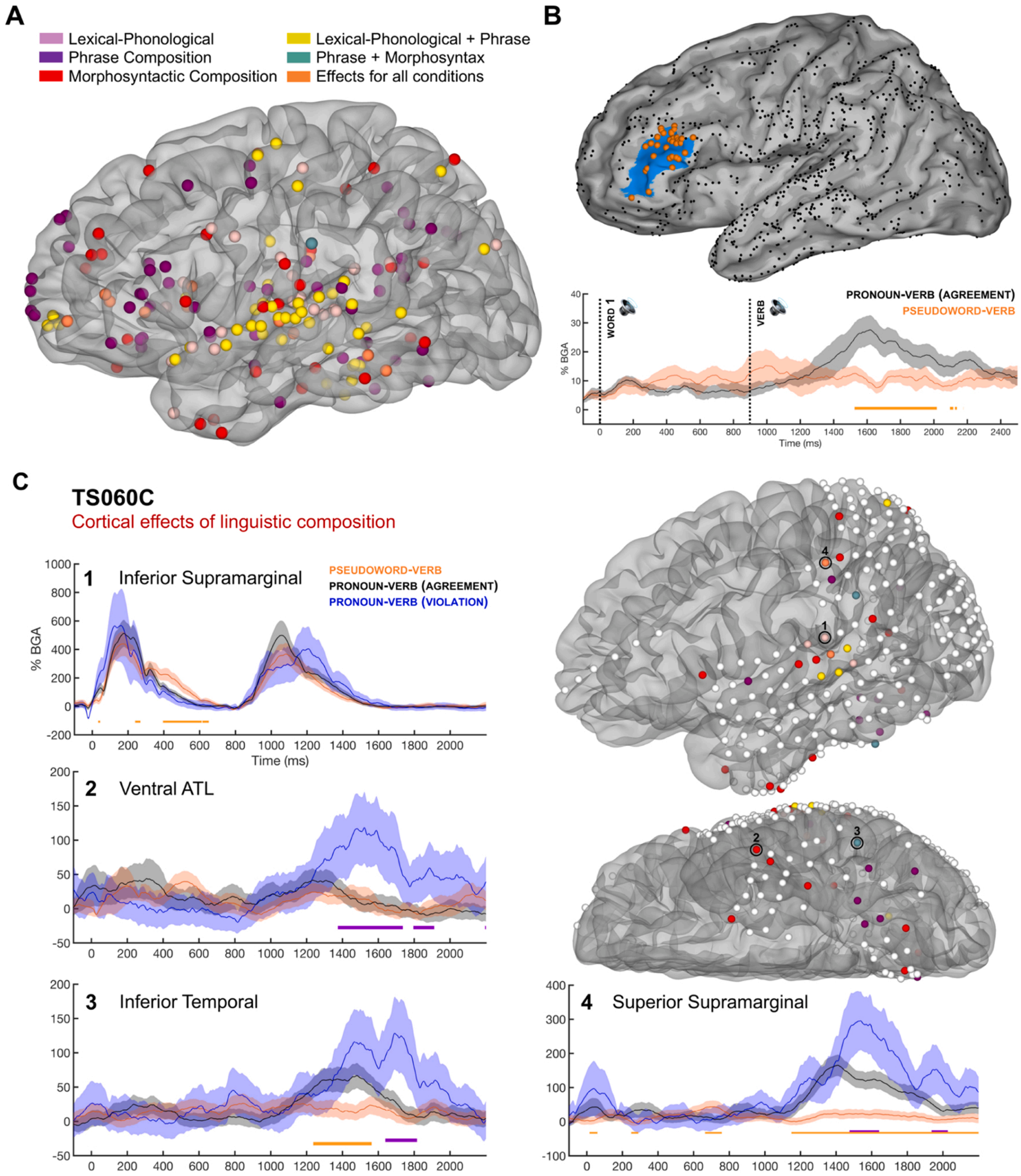

Fig. 3. : Response to distinct components of linguistic structure. (A) Topographic map of electrodes that exhibited a significant effect for specific linguistic structures, corrected for multiple comparisons (181 electrodes, 10 patients). Significant effects of lexical-phonological processing were determined by the 100–900ms window after word 1, and all other effects were determined by the 100–900ms window after word 2. (B) Grouped analysis for electrodes in inferior frontal sulcus and anterior inferior frontal gyrus, plotting the effect of phrase composition (36 electrodes, 8 patients). Horizontal colored lines depict periods of FDR-corrected significant differences in BGA between conditions. Error bars set at one standard error. (C) Exemplar patient with electrodes exhibiting either a morphosyntactic violation effect or phrase structure effect. Orange and purple bars underneath traces represent significant conditional differences, corrected for multiple comparisons (FDR-corrected, $q < 0.05$). Orange bars: pseudoword-verb and pronoun-verb (agreement) contrast (i.e., phrase structure effect). Purple bars: pronoun-verb (agreement) and pronoun-verb (violation) contrast (i.e., morphosyntax effect).

$= 3.04$, $p = .001$) exclusively in late windows (Fig. S1A, B). As with the effects of phrase composition, this alpha effect in MTG was clearly dissociable from higher frequency dynamics, with no effects being found in BGA (Fig. S1B).

3. Discussion

Using high spatiotemporal resolution intracranial recordings, we investigated the direct cortical substrates of two distinct types of elementary structure composition that covered both hierarchical and horizontal dimensions of linguistic information. We discovered that sensitivity to morphosyntactic violations occurred in sites mostly separable from those sensitive to phrase composition in posterior temporal and inferior frontal cortices. However, a small number of closely neighboring sites were sensitive to both types of composition, indicating dissociable roles for specific sites within frontotemporal cortex. Posterior temporal sites exhibited the earliest sensitivity to both phrase composition and morphosyntax. Averaging these effects across participants (Fig. 2), as in many neuroimaging studies, ultimately serves to disguise the underlying functional topology of specific sub-portions of

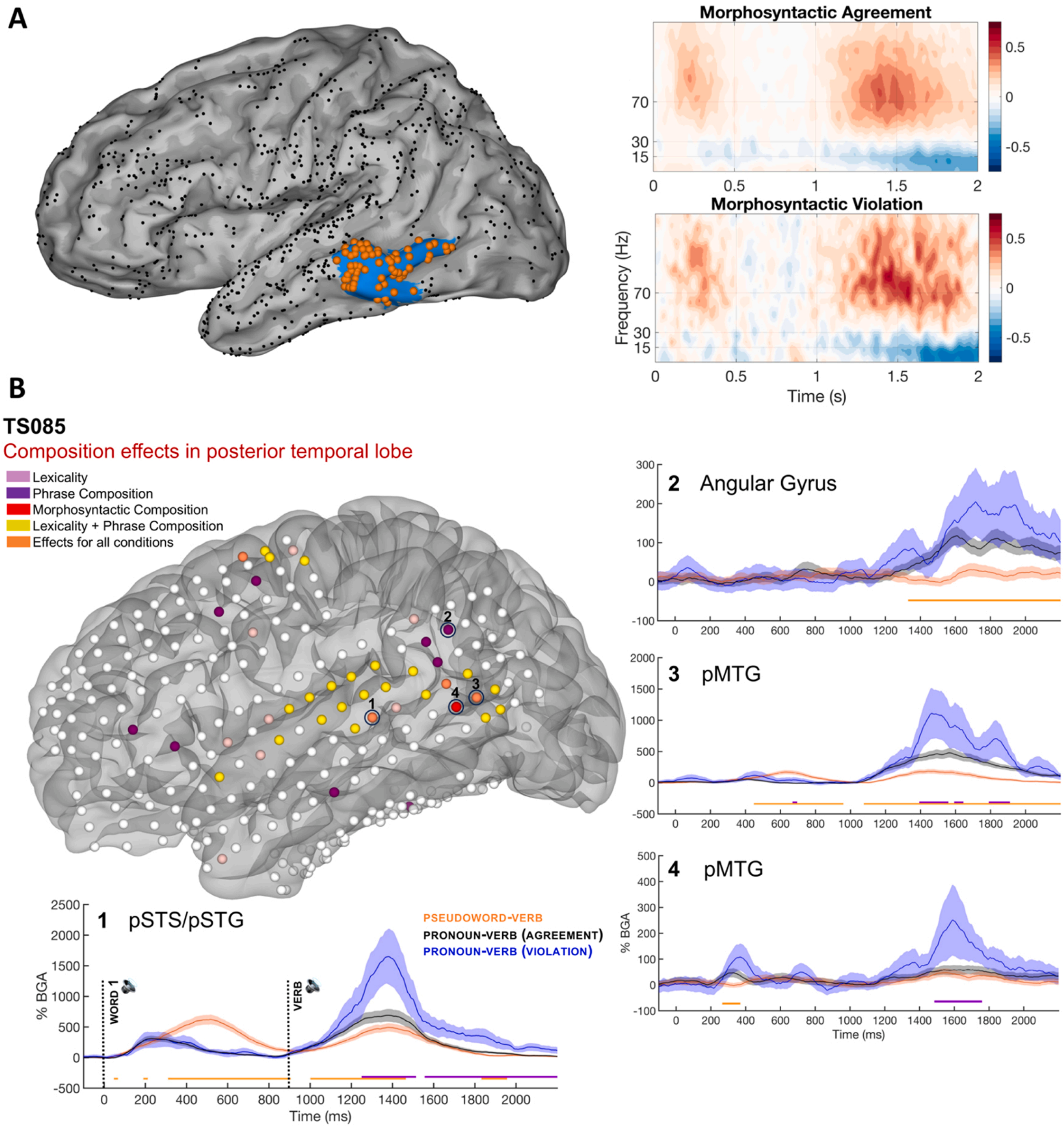

Fig. 4. : Effects of composition in temporal cortex. (A) Grouped analysis for electrodes in posterior middle temporal gyrus and posterior superior temporal sulcus, plotting the effect of morphosyntactic composition (51 electrodes, 9 patients). Spectrograms depict percentage power change from baseline (0.5 = 50 %). (B) Participant with heterogeneous responses to linguistic structure in posterior temporal and inferior partietal cortex (number of channels: 254; channels with effects: 43). Orange and purple bars underneath traces represent significant conditional differences, corrected for multiple comparisons (FDR-corrected, $q < 0.05$). Orange bars: pseudoword-verb and pronoun-verb (agreement) contrast. Purple bars: pronoun-verb (agreement) and pronoun-verb (violation) contrast.

pSTS/pMTG and IFS/IFG (Fig. 3-6).

The existence of limited shared sites for both phrasal and morphosyntactic composition, that are closely localized within posterior temporal and inferior frontal language sites, supports the notion of a basic compositional structure-building operation (Harley, 2014; Bobaljik, 2017; Bruening, 2018; Jackendoff and Audring, 2020; Krauska and Lau, 2023), which varies in timing across distinct types of constituents (Siddiqi, 2009). Posterior temporal engagement was markedly earlier than inferior frontal engagement. This might indicate that posterior temporal regions are responsible for building basic syntactic representations (specifically, hierarchical phrase structures and minimal morphosyntactic relations), and during later windows (i.e., 500–900 ms) inferior frontal cortex maintains these representations (Schell et al., 2017) either for linearization of morphosyntactic information during production (Matchin and Hickok, 2020) or for semantic integration (Wang et al., 2021). More technically, we assume here that syntactic representations are labeled set-theoretic structures and non-intentional abstractions of brain states that interface with various cognitive and sensorimotor systems. Building off proposals of other researchers (Matchin and Hickok, 2020), we assume that inferior frontal cortex is responsible for parsing elements of morphosyntactic information, which is only possible once posterior temporal regions have established the initial, minimal syntactic representation. Examining the effect durations in our study, we also note that the effects we document in posterior temporal cortex for both phrasal and morphosyntactic composition were shorter than the effects in inferior frontal cortex (e.g., Figs. 2–4), potentially supporting this framework of initial, rapid structure-generation in pSTS/pMTG being followed by a more semantically demanding interpretation process in IFS/IFG. Other recent work provides causal evidence for the role of pMTG as a hub in syntactic comprehension (Yu et al., 2022), while IFG appears to be an amodal center for linear sequence processing but is *not* an amodal core syntax

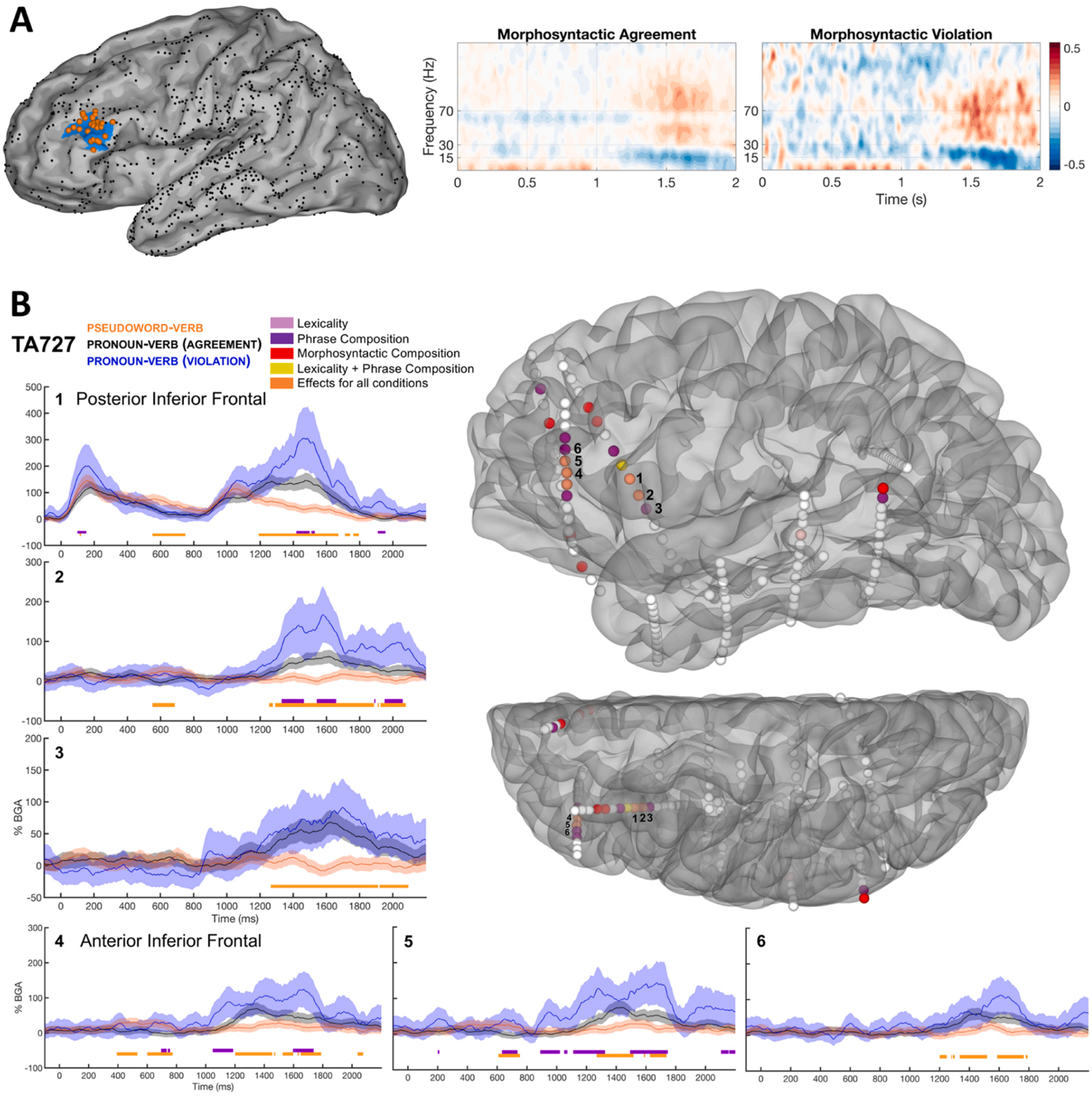

Fig. 5. : Effects of composition in frontal cortex. (A) Grouped analysis for electrodes in inferior frontal sulcus, plotting the effect of morphosyntactic composition (31 electrodes, 8 patients). Spectrogram depicts percentage power change from baseline (0.5 = 50 %). (B) Patient with effects in frontal cortex, either to all effects or to phrase composition. TA727: 154 channels, 20 with effects. Orange and purple bars underneath traces represent significant conditional differences, corrected for multiple comparisons (FDR-corrected, $q < 0.05$). Orange bars: pseudoword-verb and pronoun-verb (agreement) contrast. Purple bars: pronoun-verb (agreement) and pronoun-verb (violation) contrast.

Table 2

Grouped statistics for SB-MEMA for earliest effects of phrase composition.

ROI	*β(SD)*	*t-value*	*p-value*
Anterior superior temporal sulcus (100–500 ms)	0.08 (.02)	2.72	.003
Posterior middle temporal gyrus (300–500 ms)	0.09 (.06)	2.51	.006
Posterior superior temporal gyrus (500–700 ms)	0.16 (.09)	2.58	.004
Inferior frontal sulcus (500–700 ms)	0.09 (.04)	2.56	.005
Anterior insula (500–700 ms)	0.11 (.05)	2.70	.003

region (Fahey et al., 2024) and is involved in mapping morphological features onto syntactic structures (Planton and Dehaene, 2021). Thus, instead of concluding that left IFG is the major hub in the network responsible for processing morphological composition and agreement relations (Leminen et al., 2019; Maran et al., 2022), our results highlight the centrality of posterior temporal cortex across all types of composition, and across both high- and low-frequency activity; concordant with recent lesion-symptom mapping analyses (Fahey et al., 2024).

Table 3

Grouped statistics for SB-MEMA for earliest effects of morphosyntactic violations.

ROI	*β(SD)*	*t-value*	*p-value*
Posterior middle temporal gyrus (100–300 ms)	0.08 (.03)	2.87	.002
Temporal pole (100–300 ms)	0.11 (.05)	2.84	.002
Inferior frontal sulcus (300–500 ms)	0.11 (.03)	2.84	.002
Medial parietal cortex (300–500 ms)	0.09 (.02)	−3.23	.001
Subcentral gyrus (700–900 ms)	0.09 (.02)	2.91	.001
Middle superior temporal gyrus (700–900 ms)	0.08 (.02)	2.84	.002
Inferior supramarginal gyrus (700–900 ms)	0.14 (.05)	2.61	.004

Our results are compatible with models implicating inferior frontal gyrus in inflectional morphology (Marslen-Wilson and Tyler, 2007; Hagoort and Levelt, 2009; Sahin et al., 2009; Whiting et al., 2014). The time course of the morphosyntactic violation effects are in line with P600 ERP effects in Number and Gender agreement (morpho)syntactic violations (Osterhout and Holcomb, 1992; Hagoort et al., 1993; Hagoort, 2003), and they also appear to have the same latencies. The early effects of two-word morphosyntax that we report in both lateral and medial anterior temporal lobe, and the later effects in inferior frontal sulcus, are within similar regions to the effects of more complex, sentential syntactic dependencies documented in the literature (Westerlund et al., 2015; Lopopolo et al., 2021). Interestingly, this literature examined non-local dependencies (as opposed to our basic word-word agreement relations), pointing to the possibility of shared sites involved in abstract dependencies as well as local agreement relations; i.e., a shared cortical resource for 'Agree' computations (Smith et al., 2019).

Our findings complement previous cortical stimulation and focal lesion evaluations indicating a causal role for specific portions of pSTS and pSTG specifically in the production of functional morphemes but not in the evaluation of semantic or lexical information (Lee et al., 2018). While much neuroimaging work in comprehension has implicated similar frontotemporal sites in lexico-semantic and combinatorial processing (Rodd et al., 2015; Hagoort, 2017), our results indicate that while some sites in pSTS and IFS overlap in this respect, there are also a number of frontotemporal sites that selectively respond to distinct types of compositional operations, somewhat complicating the search for a "core language network" defined purely by sentence-level processing dynamics that do not strictly mitigate effects of working memory, attention, situation model construction, and so forth (Fedorenko et al., 2024; Murphy and Woolnough, 2024). Indeed, effects of lexical-phonological (verb) processing were most salient within STS and inferior parietal cortex, in sites mostly independent of effects in higher-order computations. As with prior intracranial work (Murphy et al., 2022b), our effects of phrase composition in STS fell within a larger area sensitive to lexical-phonological processing.

Integrating the present findings with prior intracranial research, we suggest that pSTS is the critical node in the language network that drives basic compositional processing in language. Other intracranial research has shown that pSTG is sensitive to syntactic complexity pertaining to phrasal embedding depth (McCarty et al., 2023), and pSTS is sensitive to lexico-semantic search demands (Murphy et al., 2023), indicating a closely interwoven lateral posterior temporal network of syntactic compositionality and hierarchical complexity, which is crucially engaged for both elementary types of hierarchical and horizontal linguistic structures. A comparison with prior extracranial research indicates that the timings and locations of our effects overlap with the posterior temporal LANm event-related field component (documented around 200–250 ms) for auditory comprehension of morphology (Leminen et al., 2019). Given the clear overlap in the timing of frontotemporal composition effects, our results align well with claims that inflection is a grammatical operation with robust correlates in MTG and IFG (Ullman, 2004).

With respect to low frequency dynamics, our results suggest a more complex picture than present proposals in the literature. Instead of linguistic composition yielding either power increases (Meyer, 2018) or decreases (Lam et al., 2016), we found that this dynamic depends on the specific compositional process in question. As with prior MEG research (Hardy et al., 2023), we found lower alpha power when phrase binding occurred relative to no binding, however for morphosyntactic violations we found alpha power decreases relative to successful Person agreement. We also discovered that alpha power in MTG was actively increasing during successful morphosyntactic agreement. In order to reconcile the apparent divide between our composition-related alpha increases/decreases (Fig. S1), we note that the pseudoword-verb trials were taken from the oddball detection task, where intensive compositional demands may have been less salient, while the pronoun-verb trials were taken from an explicit acceptability judgment task. As such, it appears that the trials in both contrasts that yielded alpha decreases (Fig. S1) (i.e., morphosyntactic violations and successful phrase composition) demanded some form of active attempt at compositional processing. Alpha has been proposed to be involved in the allocation of global neuronal resources (Jensen et al., 2014; Van Diepen et al., 2019; Alavash et al., 2021), and we suggest that alpha increases in MTG may index maintenance of compositional information via the regulation of inhibition in regions associated with structure-building computations, following a recent neurocomputational model of syntax (Murphy, 2020, 2024).

Our results also support a more general picture of syntactic licensing occurring before semantic composition, in line with major psycholinguistic models (Ferreira and Qiu, 2021), with posterior temporal regions exhibiting earlier sensitivity to morphosyntactic violations than to phrase composition (Fig. 2; compare 100–300ms and 300–500ms windows). Widespread effects of morphosyntactic sensitivity were found in early windows across pSTS/pMTG, most likely responding first to an asyntactic absence of 's' person-marking in shorter verbs (e.g., 'he run') and slightly later to the presence of asyntactic person-marking (e.g., 'they runs'), while phrase composition effects were found early in aSTS and pMTG/pSTS but later in frontal regions. Meanwhile, our STG morphosyntax effects may be due to speech segmentation prediction violations; perhaps even post-composition evaluation processes, following a recent psycholinguistic model (Gwilliams, 2020).

Lastly, comprehensive reviews of the cortical basis of syntax (Hagoort and Indefrey, 2014; Heard and Lee, 2020; Matchin and Hickok, 2020) have highlighted the role of posterior temporal regions in hierarchical structure-building in language. One review used an activation likelihood estimate to implicate pSTS, pMTG, pars triangularis and anterior STG in structural computations (Heard and Lee, 2020). For syntactic reanalysis (e.g., re-parsing structures) pSTS, pSTG and broad portions of IFG were implicated. Some of these results appear to be concordant with our study. While our design has strictly isolated phrase composition and morphosyntax, we note that some linguists maintain that basic morphological generalizations can be accounted for in terms of syntactic operations and principles (Jackendoff and Audring, 2020; Collins and Kayne, 2023).

4. Limitations

We acknowledge that our limited survey of pronoun-verb structures prevents immediate generalizability to other English manipulations of hierarchical vs. horizontal syntactic information, and future research should compare distinct types of minimal compositional schemes, potentially along dimensions of semantic complexity. Nevertheless, we also note that pronoun-verb structures minimally encode truth-evaluable claims (in contrast to adjective-noun phrases), and our documented spatiotemporal dynamics may be tapping into the encoding of more general linguistic inferences. Relatedly, we also note that our effects of lexical-phonological processing (Fig. 2) are likely not specific purely to lexicality but are more general in scope. Given that two major sites of our lexical-phonological processing analysis are mid-fusiform cortex and inferior frontal cortex – considered to be major lexico-semantic hubs (Forseth et al., 2018; Murphy et al., 2023) – some of these effects are still likely to be due to lexical processing.

Another limitation of our study pertains to the observation of a reviewer that morphosyntactic agreement is possibly a precondition for successful phrase composition. Given that our task required explicit acceptability judgments (either for lexicality or syntactic acceptability), we expect that participants initially successfully parsed the phrase structure (e.g., [D [V]]), as in phrases such as 'you sends', and later recognized a morphosyntactic violation, hence generating a VP inference. In many current syntactic theories, ungrammatical structures are certainly possible to generate, even if they lead to interpretation conflicts. We do not believe that the morphosyntactic violation completely blocks any initial phrase structure parsing, partly due to evidence for the typically later effects of morpho-semantic violations occurring after lexico-semantic real-time processing (Beyersmann et al., 2014), with a related 'meaning before grammar' framework recently emerging at the developmental level (Morgan et al., 2020). However, we do acknowledge that our paradigm does not cleanly carve out these two processes, and other recent research points to an interactive model of parsing, deviating from any syntax-first or semantics-first models (Yang et al., 2021). We note that our stimuli exhibited an increasing scale of salient meaning: from a single lexical item to a pseudoword and a word, to two words without agreement, and finally to two words with agreement. Given all of the above, we expect that phrase composition occurred in morphosyntactic violation conditions, although we acknowledge that future paradigms should more sharply establish this boundary between possible and impossible compositional processing.

5. Conclusion

Our results point towards a coordinated neural code for multiple dimensions of linguistic structure, that appears to be driven by compositional processing in posterior temporal cortex being fed into a wider network including inferior frontal (Maran et al., 2022; Riva et al., 2022; Liu et al., 2023) and anterior temporal sites. Future research utilizing acute recordings could explore speech production paradigms, potentially in naturalistic contexts, with a more extensive range of morphological and compositional manipulations, to explore common signatures of composition across both comprehension and production. An additional route to explore is to elaborate how these posterior temporal dynamics relate not just to other cortical sites, but also to subcortical structures (Murphy et al., 2022a), furnishing a more global map of the neural infrastructure for elementary dimensions of syntactic structure.

6. Methods

6.1. Participants

10 patients (7 male, 21–51 years, IQ 97.8 ± 13.6) participated in the experiment after written informed consent was obtained. All were native English speakers. All experimental procedures were reviewed and approved by the Committee for the Protection of Human Subjects (CPHS) of the University of Texas Health Science Center at Houston as Protocol Number HSC-MS-06–0385. Experiments were performed in strict adherence with institutional guidelines and extensive care was taken to ensure that experimental participation did not perturb any aspect of ongoing clinical care.

6.2. Electrode implantation and data recording

Data were acquired from either subdural grid electrodes (SDEs; 4 patients) or stereotactically placed depth electrodes (sEEGs; 6 patients) (Fig. 1C). SDEs were subdural platinum-iridium electrodes embedded in a silicone elastomer sheet (PMT Corporation; top-hat design; 3 mm diameter cortical contact), and were surgically implanted via a craniotomy (Conner et al., 2011; Pieters et al., 2013; Tong et al., 2020; Kohlhase et al., 2021). sEEGs were implanted using a Robotic Surgical Assistant (ROSA; Medtech, Montpellier, France) (Rollo et al., 2020; McCarty et al., 2021). Each sEEG probe (PMT corporation, Chanhassen, Minnesota) was 0.8 mm in diameter and had 8–16 electrode contacts. Each contact was a platinum-iridium cylinder, 2.0 mm in length and separated from the adjacent contact by 1.5–2.43 mm. SDE patients had a number of cortical arrays implanted (mean ± SD: 8.8 ± 0.4) with a mean of 186.7 electrodes (SD ± 51.8). sEEG patients had penetrating depth probes (mean 13.7 ± 2.1) with a mean of 180.1 electrodes (SD ± 23.2). The total number of electrodes implanted was 1801 and the number of clean electrodes that entered into analysis was 1045. Typical coverage was fronto-temporal, dictated by location of the epilepsy in the antero-mesial temporal lobe in the majority, with parietal and occipital coverage in a number of patients. Following surgical implantation, electrodes were localized by co-registration of pre-operative anatomical 3 T 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. iEEG provides uniquely high spatiotemporal resolution recordings and is less susceptible to artifacts (e.g., muscle movements) (Flinker et al., 2011; Arya, 2019). 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. Electrodes contributing to regions of interest were taken from both SDE and sEEG participants; for instance, we follow previous intracranial work that has included subdural contacts in monitoring activity from posterior temporal sulcus (Uno et al., 2015).

6.3. Stimuli and experimental design

Grammatical verb phrases (‘they run’), ungrammatical verb phrases (‘they runs’), pseudoword phrases (‘pob run’) and pseudowords followed by pink noise (‘pob *noise*’) were used to isolate phrasal and morphosyntactic compositional processing. We focused on high frequency gamma changes (Forseth et al., 2018; Conner et al., 2019; Johnson et al., 2020; Leszczyński et al., 2020) that typically index local cortical processing and are implicated in a range of cognitive processes (Buzsáki and Watson, 2012; Hovsepyan et al., 2020; Packard et al., 2020). Analyses were restricted to language-dominant left hemisphere electrode coverage.

The experiment was split into two parts: Part 1 involved word detection (pseudoword phrases vs pseudoword-*noise* pairs), involving a Yes-No forced choice. Average pseudoword duration was 580 ms, and average verb duration was 530 ms. Pink noise is characterized by a falloff in spectral power inversely proportional to the frequency, and exclusively was presented in word position 2 (duration: 500 ms). Part 2 involved an acceptability judgement (grammatical vs ungrammatical verb phrases), with the same forced choice (Fig. 1). Average pronoun duration was 430 ms, and average verb duration was 560 ms. Each word consisted of an individual audio file, and within each file the onset of the word began at precisely 0 s. Across both Parts 1 and 2, 280 trials were presented in total (pseudword-verb: 120; syntactic pronoun-verb: 120; asyntactic pronoun-verb: 20; pseudoword-*noise*: 20). Morphemes marking (un)grammaticality were always at the end of verbs (‘-s’), and 25 % of the ungrammatical trials were marked by the absence of the morpheme (e.g., ‘he run’), and 75 % were marked by the presence (‘they runs’). Distinct tensed versions of each verb were presented (e.g., ‘bit’, ‘bite’, ‘bites’). All participants conducted both parts of the experiment.

A fixation cross was presented in the centre of the screen for 900 ms followed by the auditory recording of the first word, and 900 ms later (i.e., at 1800 ms after fixation onset) the second word was presented. At 3400 ms after fixation onset, participants were prompted to respond with a keyboard press (Fig. 1A). Following their response, a blank screen was shown for 1500 ms. Stimuli were presented in a pseudorandom order, with no repetition amongst items.

6 pronouns were used: I, you, he, she, we, they (length M: 2.5, SD: 0.9; SUBTLEXus log-frequency 5.74). Including all of their morphological instantiations, 117 verbs were used (length M: 5.02, SD: 1.14; log-frequency M: 2.66, SD: 1.10) (Brysbaert et al., 2012). 66 pseudowords were used (length M: 5.5, SD: 1.31).

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

6.4. Statistical analysis

A total of 1801 electrode contacts were implanted in these patients; 1045 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 251 ms; MATLAB 2020b, Mathworks, Natick, MA). BGA was defined as percentage change from baseline level; −500 to −100 ms 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) (Fischl et al., 1999; Conner et al., 2011; Kadipasaoglu et al., 2014, 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 (3 mm 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 two participants contributing to coverage and BGA percent change exceeding 5 %, and t-values exceeding 2.5.

We also conducted SB-MEMA analyses of regions of interest in the alpha band. Recent research documents effects in this range for both broad (Grant et al., 2022; León-Cabrera et al., 2022; Wang et al., 2022; Zioga et al., 2023) and narrow (Hardy et al., 2023; Lago et al., 2023) aspects of language comprehension (and also production (Zioga et al., 2024)), from general measures of spoken and written comprehension to specific syntactic binding and semantic congruency effects. Theoretical models have also pointed to alpha dynamics as being related to the generation and storage of syntactic phrases (Murphy, 2015; Meyer, 2018), and we sought to differentiate our high frequency power effects from some domain of low frequency power; the alpha band is the most promising based on the above studies and also prior intracranial research (Murphy et al., 2022b).

Anatomical groups of electrodes were delineated, firstly, through indexing electrodes to the closest node on the standardized cortical surface (Saad and 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.

CRediT authorship contribution statement

Elliot Murphy: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Nitin Tandon:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Conceptualization. **Katrien Segaert:** Writing – review & editing, Validation, Supervision, Conceptualization. **Peter Hagoort:** Writing – review & editing, Supervision, Conceptualization. **Patrick S Rollo:** Data curation.

Declaration of Competing Interest

The authors declare no conflict of interest.

Data Availability

Data will be made available on request.

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Code availability

The datasets generated from this research are not publicly available due to their containing information non-compliant with HIPAA, and the human participants from whom the data were collected have not consented to their public release. However, they are available on request from the corresponding author. The custom code that supports the findings of this study is available from the corresponding author on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.nanoen.2024.109639.

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