A magnitude-independent neural code for linguistic information during sentence production

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Abstract

Humans are the only species with the ability to convey an unbounded number of novel thoughts by combining words into sentences. This process is guided by complex semantic and abstract syntactic representations. Despite their centrality to human cognition, the neural mechanisms underlying these systems remain obscured by inherent limitations of non-invasive brain measures and a near total focus on comprehension paradigms. Here, we address these limitations with high-resolution neurosurgical recordings (electrocorticography) and a controlled sentence production experiment. We uncover distinct cortical networks encoding word-level, semantic, and syntactic information. These networks are broadly distributed across traditional language areas, but with focal sensitivity to syntactic structure in middle and inferior frontal gyri. In contrast to previous findings from comprehension studies, these networks are largely non-overlapping, each specialized for just one of the three linguistic constructs we investigate. Most strikingly, our data reveal an unexpected property of higher-order linguistic information: it is encoded independent of neural activity levels. We propose that this "magnitude-independent coding" scheme represents a novel mechanism for encoding information, reserved for higher-order cognition more broadly.

Keywords: ECoG, language production, syntax, semantics, neural coding schemes

1 Introduction

Syntax, the abstract structure underlying uniquely human behaviors like language, music [1–5], and possibly logic and math [6, 7], is the evolutionary adaptation that sets our species' cognition apart. In language, syntactic representations take the form of abstract structural "rules" like *Sentence = Subject + Verb + Object*, which we use to communicate infinite meanings with finite words. Despite its centrality in human cognition, it continues to elude a satisfactory neural characterization, in large part due to a number of contradictory findings in the literature.

One area of disagreement is localization: where and how syntax is spatially encoded. Traditionally, syntax has been approached from a localizationist perspective. Consistent with this, certain anatomical regions are frequently associated with syntax, especially inferior frontal gyrus (IFG) [8–18] and posterior temporal lobe [8–15, 19–22]. However, a growing number of studies have identified syntactic processing throughout broad swaths of cortex outside these traditional hubs [17, 22–25], suggesting the localizationist view may be insufficient and pointing instead to a highly distributed code. Relatedly, there is significant disagreement regarding *selectivity*: the degree to which syntax overlaps in the brain with words and meaning, which has important theoretical implications (see [25, 26] for discussion). Findings of syntax-selective regions are abundant in the literature [11–13, 22, 27–34], although the precise locations and functions identified vary widely across studies. However, recent work using more advanced and targeted methods has reported extensive spatial overlap in these systems [22–25, 35–37].

These discrepancies likely reflect a number of factors. For one, different studies define syntax differently, and may in fact be studying different phenomena. While syntax is often treated as a monolith in neuroscience, it is in fact a complex system involving multiple types of representations (e.g., function words, hierarchical "tree" structures, word categories) and processes (e.g., agreement, sequencing, and binding). Some experimental designs target the depth of syntactic processing by manipulating the complexity of hierarchical structures [9, 17, 23]. Others have manipulated the presence or absence of syntactic structure by comparing sentences to unstructured lists of words [9, 35, 37–44], targeting the system as a whole. A second potential source of discrepancies are confounds, a potentially inevitable problem when studying an inherently abstract system [45]. For example, complexity manipulations vary working memory demand, and sentence-list comparisons vary combinatorial semantics. While creative solutions have been employed to mitigate these concerns, manipulations to syntax inevitably involve variation in some additional dimension in any study.

Here, we take a focused approach, aiming to understand the neural underpinnings of hierarchical structural representations rather than, e.g., syntactic processing as a whole. We draw inspiration from sensory neuroscience, where considerable advances have been made in mapping sensory cortices by contrasting particular representations like phonemes [46] and visual gradients [47, 48] rather than entire systems (e.g., conditions with vs. without syntax). Similarly, we compare two syntactic frames: active vs. passive. These structures can be used to express roughly the same meaning by arranging the same content words (e.g., Dracula, spray, chicken) in reverse orders (active: "Dracula sprayed the chicken"; passive: "The chicken was sprayed by Dracula"),

thereby varying syntax while holding meaning and lexical content largely constant. As with any approach to isolating abstract representations like syntax, this contrast entails certain confounds (see [45] for discussion), including differences in word count, prosody, discourse focus (though potentially less relevant in production), and processing difficulty [49]. These confounds mean the active/passive comparison should not be interpreted as uniquely identifying syntactic information, although we mitigate differences related to difficulty and articulation with signal processing and modeling techniques. Notably, while it may not be possible to disentangle which specific difference (e.g., syntax, prosody, processing difficulty) drives the response of an individual electrode sensitive to the active/passive manipulation, this ambiguity does not undermine our two most intriguing findings. Because these conclusions hold for nearly all electrodes sensitive to the active/passive contrast, they most likely hold for all of the constructs isolated by this manipulation, including hierarchical representations or prosodic planning.

We also address a number of other critical gaps in the literature. First, with few exceptions [21, 50–52], the vast majority of prior research has studied comprehension. However, comprehension as a modality introduces a number of complications for studying syntax. As comprehension is an ongoing process of building and assessing candidate syntactic structures, it is highly dynamic [11, 53, 54], meaning that reasonable temporal granularity is very hard to achieve for syntax, particularly when looking at individual representations whose activation may be relatively fleeting. Perhaps even more troublesome is that evidence suggests syntax can be ignored during comprehension in favor of less effortful strategies (e.g., context) [49, 55–57]. Consequently, the lack of selectivity reported by some studies may reflect a computational shortcut rather than anything inherent about syntax. Second, experimental paradigms comparing sentences and lists have become a dominant approach to studying syntax [9, 35, 37–44]. This design aims to isolate properties associated with sentences like syntax and combinatorial semantics, and typically controls for semantics with control conditions or modeling, as we do here. However, processing even single words engages syntax [58–60], calling into question the effectiveness of list conditions in "turninhg off" syntax. Finally, previous research has relied primarily on non-invasive neuroimaging and electrophysiology, which provide either high spatial or high temporal resolution, but not both [61, 62].

We address these gaps with a controlled sentence production experiment and by sampling neural data directly from cortex in ten neurosurgical patients. Electrocoticography (ECoG), which is virtually immune to motor artifacts, provides simultaneously high spatial and temporal resolution. In contrast to comprehension, the syntactic structure of an utterance is selected prior to speech onset in production and remains invariant over time [11, 54, 63–66]. In our stimuli, this is logically ensured by the fact that the first word of the sentence (i.e., the subject) depends on the choice of syntactic structure, making it impossible to begin speaking without a priori structure assignment. Together, these methods afford unparalleled resolution, and enable us to introduce a fine-grained manipulation, using the same images to elicit sentences with two syntactic structures involving the same content words but in reverse orders. We

directly contrast this manipulation with the traditional approach of comparing sentences and lists and show that the sentence-list comparison misses not just some, but the majority of electrodes that are sensitive to syntactic frame. We demonstrate that this derives from a striking and previously uncharacterized property of higher-level linguistic representations, which we term "magnitude-independent coding," whereby processing is independent of the overall degree of neural activity. The combination of ECoG, a production paradigm, and a controlled syntactic manipulation allow us to capture a number of important and previously unknown properties of this hallmark aspect of human cognition.

2 Results

Ten neurosurgical patients with electrode coverage of left peri-Sylvian cortex (Fig. 1A) performed a sentence production task and two control tasks: list production and picture naming (Fig. 1B). During sentence production, patients overtly described cartoon vignettes depicting transitive actions (e.g., poke, scare, etc.) in response to a preceding question. Questions were manipulated to use either active ("Who poked whom?") or passive syntax ("Who was poked by whom?"), implicitly priming patients to respond with the same structure ("The chicken poked Dracula" or "Dracula was poked by the chicken") [67]. This manipulation varied syntactic structure, while holding semantic and lexical content largely constant. During the list production control task, participants saw the same vignettes as in the sentence production trials, but preceded by an arrow indicating the direction in which participants should list the characters: left-to-right (e.g., "chicken Dracula") or right-to-left ("Dracula chicken"), mimicking the reverse order of nouns in active and passive sentences. We quantified neural activity as high gamma broadband activity ($70-150\,\mathrm{Hz}$), normalized (z-scored) to each trial's 200 ms pre-stimulus baseline, as this correlates with underlying spiking and BOLD signal [68, 69] and has been widely employed in the ECoG literature. Parallel analyses on beta-band activity, also associated with cognition [70, 71], appear in the supplemental information (see Supplemental Information A.2).

We began by comparing neural activity between sentence production and the list production control. We looked for differences during the planning period – the time between the onset of the cartoon vignette and speech onset, when syntactic and semantic representations are selected [63, 64]. This identified 60 broadly distributed electrodes with significantly higher activity for sentences ($p < .05$ for 100 ms, Wilcoxon rank sum test), with sentences recruiting higher activity in the 200 to 400 ms post-stimulus window in posterior temporal areas and the inferior parietal lobule (IPL), and increasing in IFG and middle frontal gyrus (MFG) leading up to production (Fig. 1C). A region-of-interest (ROI) analysis (Fig. 1D) found four regions with significantly higher activity for sentences during the planning period: IFG, MFG, IPL, and middle temporal gyrus (MTG) ($p < .05$ for 100 ms, permutation test; see Methods Sec. 4.7).

While comparisons of sentences and lists are common, they differ in multiple processes [37–39, 41–43]. In order to specifically test for syntax, we looked for sensitivity to syntactic structure by comparing active and passive sentences. Because active and

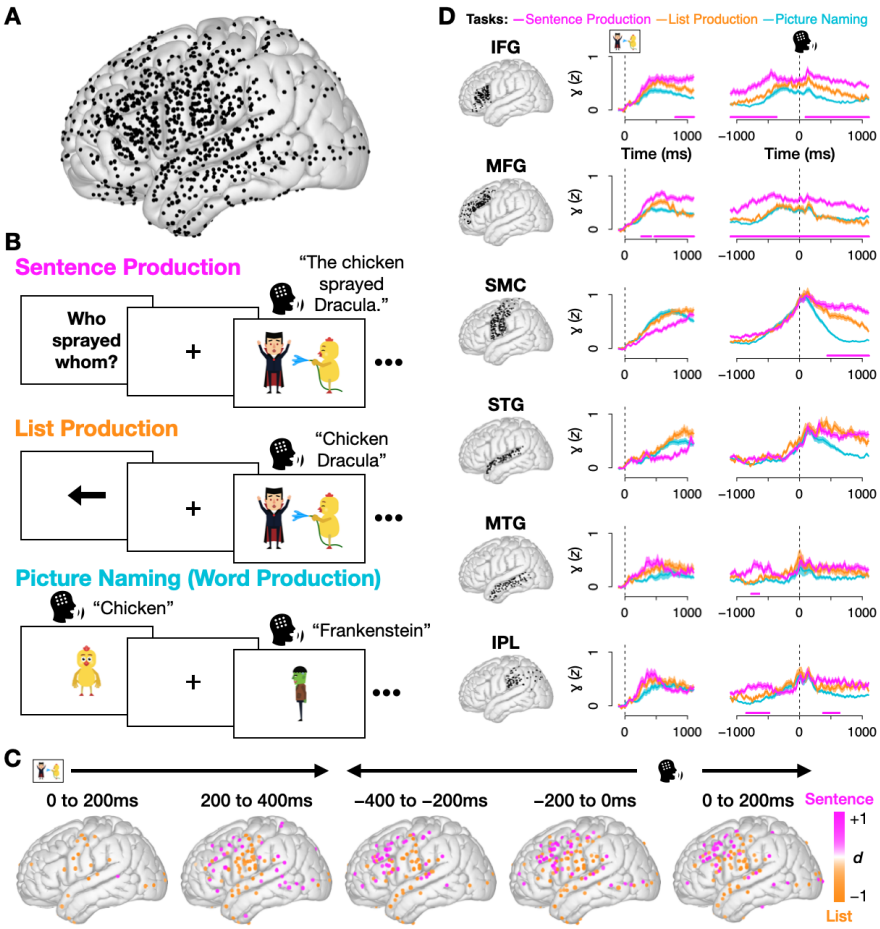

Fig. 1 (A) Coverage across all 10 patients (1256 electrodes after exclusions, see Methods Sec. 4.2). (B) Experimental design: Participants completed three overt production tasks. During Sentence Production trials, they produced sentences to respond to preceding questions. Questions appeared with either active ("Who sprayed whom?") or passive syntax ("Who was sprayed by whom?"), implicitly priming patients to respond with active ("The chicken sprayed Dracula") or passive syntax ("Dracula was sprayed by the chicken"). During List Production, a control task, participants saw the same stimuli from the Sentence Production block, but preceded by an arrow indicating the direction in which to order the two characters. During Picture Naming trials, they produced single words. (C) Magnitude of difference in neural activity (Cohen's d) for all electrodes with a significant difference between sentences and lists, in 200 ms bins ($p < .05$, FDR-corrected across electrodes, Wilcoxon rank sum test). (D) Mean and standard error of high gamma activity for all three tasks, by region, locked to stimulus (i.e., picture) onset (left column) and production onset (right column). Pink bar at bottom indicates times when sentences had significantly greater activity than lists ($p < .05$ for at least 100 ms; one-tailed Wilcoxon rank sum test). Region abbreviations: inferior frontal gyrus (IFG), middle frontal gyrus (MFG), sensorimotor cortex (SMC), superior temporal gyrus (STG), middle temporal gyrus (MTG), inferior parietal lobule (IPL).

passive trials had significantly different response times (see Sec. 4.8), we followed [72–74] and temporally warped the data to remove these differences, setting each trial's

response time to the median for that task (see Supplementary Fig. S1). Critically, this did not change the pattern of results in Fig. 1 (see Supplementary Fig. S2 for a replication using the warped data), and demonstrably increased the signal-to-noise ratio in the sentence and list production data (Supplementary Fig. S3). Figure 2A shows the sentence-list and active-passive comparisons for three sample electrodes. Electrodes E1 and E2 showed patterns assumed in the literature: E1 had significantly higher activity for sentences than lists (top plot; $p < .05$ for 100 ms, Wilcoxon rank sum test) and corresponding differences between active and passive syntax in the same time windows (bottom; $p < .05$ for 100 ms, Wilcoxon rank sum test). Electrode E2 also had significantly higher sentence activity ($p < .05$ for 100 ms, Wilcoxon rank sum task), but showed no syntax sensitivity, suggesting involvement in some other process that differs between sentences and lists such as combinatorial semantics.

However, the most prevalent pattern we observed among significant electrodes, exemplified by Electrodes E3 and E4, was unexpected. Despite no significant increase in sentence activity relative to lists, these electrodes showed significant differences between active and passive trials. These differences could in principle be due to any feature that differs between actives and passives, including syntax but also complexity, prosody, length, and discourse focus. However, regardless of which of these drives the effect, we would expect sentences to have higher activity than lists, as sentences involve all of these features to a higher degree than lists. This combination of sensitivity to syntactic frame without elevated sentence activity violates a fundamental assumption in the field: that information processing corresponds to increased neural activity. Indeed, while 125 electrodes were sensitive to syntax, only 6 of these (fewer than 5%) were identified by comparing sentences to lists (Fig. 2B). Thus, whatever properties our syntactic manipulation isolates are not well characterized by "increased neural activity." In order to quantify and isolate sources of variance, we leveraged an analytical technique that combines Representational Similarity Analysis (RSA) and multiple regression (Fig. 2C; Methods Sec. 4.9) [75–78]. We modeled neural dissimilarity as a linear combination of syntactic (active vs. passive), event-semantic (GPT-2 sentence embeddings [79]), (sub)lexical (same vs. different sentence-initial word), and response time dissimilarity. The (sub)lexical term accounts for variance associated with surface differences between active and passive sentences such as the presence of the word "by" – although these differences did not appear until the third or fourth word of the sentences (relatively late compared to the period prior to sentence onset, where we concentrated our analyses). We also included response time as a covariate in the model to further account for potential differences in the frequency and/or difficulty of actives and passives. We derived *Representational Similarity Indices* (RSIs) from the model coefficients to approximate the amount of evidence for syntactic, event semantic, and (sub)lexical information in each electrode (shown for the three sample electrodes in Fig. 2D). The syntax RSI accurately captured the presence of syntactic information in E1, E3, and E4, and verified that E2's higher activity for sentences than lists corresponded to the presence of event semantics ($p < .05$ for 100 ms, permutation test, for all three tests). Across electrodes with any significant RSIs, the majority of electrodes processed only one of the three types of information (Fig. 2E), contradicting claims of a fully interwoven system [24, 35, 36].

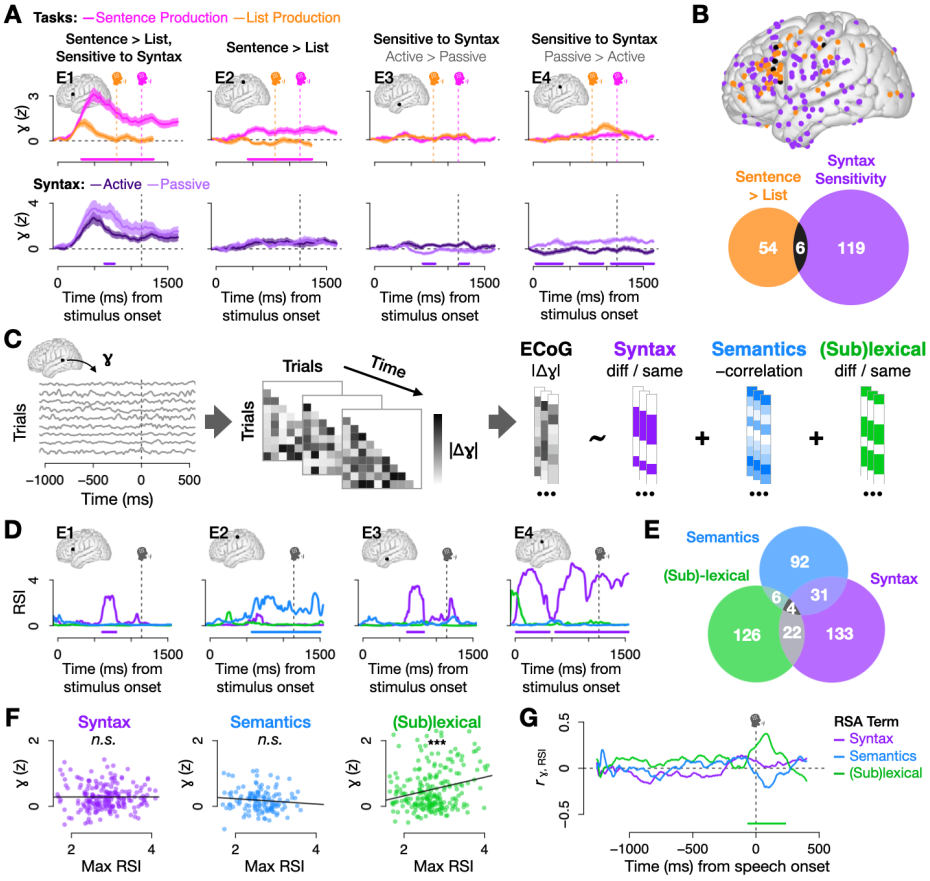

Fig. 2 (A) Four sample electrodes. Top: mean and standard error of high gamma activity by task. Pink bars denote where sentences were significantly higher than lists ($p < .05$ for 100 ms, Wilcoxon rank sum test). Bottom: mean and standard error of sentence trials split by syntax condition; bars denote significant differences between active vs. passive trials ($p < .05$ for 100 ms, Wilcoxon rank sum test). (B) 60 electrodes had significantly higher activity for sentences than lists ($p < .05$ for 100 ms, Wilcoxon rank sum test) and 125 electrodes had significant differences between active and passive trials ($p < .05$ for 100 ms, Wilcoxon rank sum test). Only 6 electrodes ($< 5\%$) had both. (C) RSA analysis pipeline: For each electrode at each time sample, we modeled the magnitude of differences in high gamma activity for each pair of sentence trials as a function of differences in syntax, event semantics, and (sub)lexical content. (D) *Representational Similarity Indices* (RSIs; derived from model coefficients) for the same four sample electrodes show evidence for syntax in E1, E3, and E4 and event semantics in E2 (all $p < .05$ for 100 ms; one-tailed permutation tests). (E) Significant electrodes ($p < .05$ for 100 ms, permutation test) by RSA term. Most significant electrodes were selective for just one representation. (G-H) Two approaches to assessing the relationship between high gamma activity and RSIs for significant electrodes. In both, syntax and semantics were not significantly related to high gamma, but (sub)lexical processing was. (F) Regressing activity over RSIs at the electrode- and RSI- specific time sample when RSIs peaked (syntax: $p = .987$, semantics: $p = .248$, (sub)lexical: $p < .001$, linear regression). (G) Correlating across electrodes at each time sample (significant (sub)lexical RSI: $p < .05$ for 100 ms, Spearman correlation).

Next, to investigate the relationship between degree of neural activity and syntactic processing (or lack of such a relationship, as in Electrodes E3 and E4), we performed a series of analyses comparing each RSI to high gamma. Note that while RSIs index differences in high gamma activity in an electrode, such differences do not require that the electrode exhibit a high degree of activity. This, however, is the general assumption, and predicts that RSIs should be positively correlated with the magnitude of high gamma activity. However, in two analyses we found no evidence that either event semantics or whatever differences are captured by our syntactic frame manipulation were related to neural activity in this way: not across electrodes at the time when each electrode's RSI reaches its maximum (Fig. 2F), nor across electrodes at each time sample (Fig. 2G). In contrast, (sub)lexical processing showed the expected result in both analyses: a positive relationship with degree of high gamma activity at the times when the (sub)lexical RSI peaked ($p < .001$, linear regression), as well as at each time sample ($p < .05$ for 100 ms, Spearman correlation). Thus, intriguingly, the independence from the magnitude of neural activity appears to correspond specifically to higher-order linguistic constructs.

A traditional region-of-interest approach showed limited representational specificity for the active/passive contrast across IFG and MFG and event-semantics in MTG and IPL (Fig. 3A), as well as (sub)lexical information in SMC and STG ($p < .05$ for 100 ms, permutation test). However, testing within each electrode revealed that these representations were widely distributed across cortex (see Fig. 3B and Supplementary Fig. S6 for beta band activity). Given that our findings were not confined to particular cortical hubs, we aimed to characterize these networks without imposing anatomical assumptions on the neural data. We took a data-driven approach and used an unsupervised machine learning technique, Non-negative Matrix Factorization (NMF, see Methods 4.10), to cluster electrodes according to prototypical patterns in the combined high gamma and RSI dataset (Fig. 3C). This identified five major clusters (Fig. 3D).

The first three clusters were characterized by high information content (RSI) accompanied by very low high gamma activity (Clusters 1-3 in Fig. 3D), replicating the dissociation between syntactic (and other structure-dependent) information and neural activity found at the electrode level (see Fig. 2B). Each of these three clusters was spatially distributed and contained significant information about a single representation type – syntax, event semantics, or (sub)lexical information ($p < .05$ for 100 ms, permutation test). Temporally, these profiles aligned with theoretical and computational models of sentence production, according to which semantics is processed first, then syntax, and finally (sub)lexical representations [63, 64, 80] (see Fig. 3D, bottom).

In contrast, the last two clusters were characterized by robust high gamma activity and high regional specificity, despite the fact that our unsupervised approach did not have access to electrode locations. Cluster 4 was focused in areas associated with visual processing and executive control, with activity peaking just after stimulus onset, and it did not contain above-chance information about syntax, event semantics, or (sub)lexical information ($p > .05$, permutation test across all time points after correction for multiple comparisons). Cluster 5 was concentrated in speech-motor cortex and superior temporal gyrus, with activity peaking just after speech onset. It contained

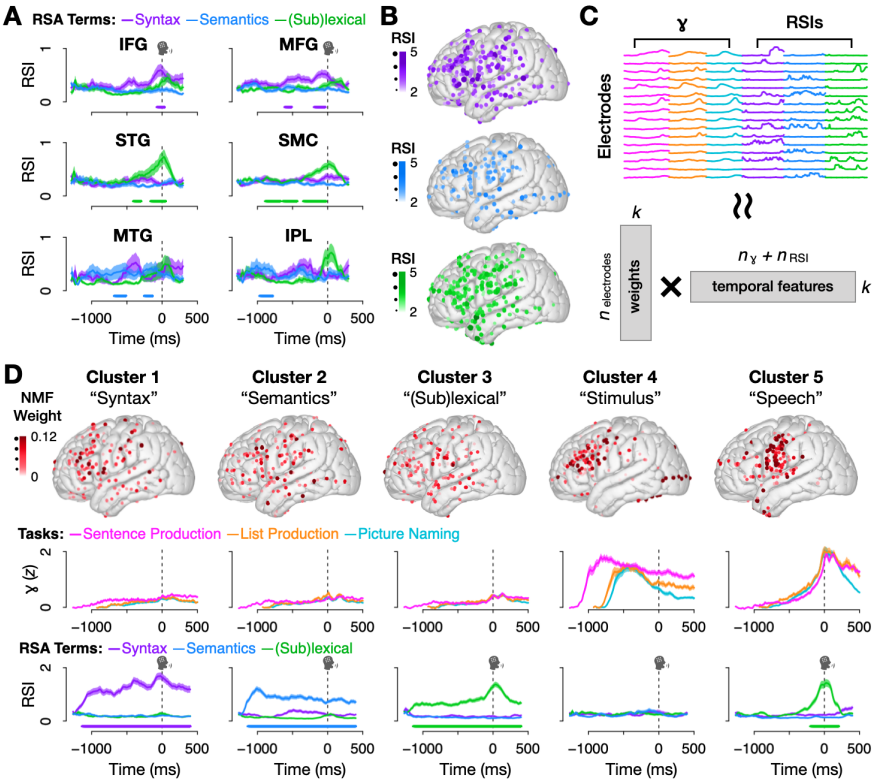

Fig. 3 (A) Mean and standard error of electrodes' RSIs by ROI. (B) Significant electrodes ($p < .05$ for 100 ms; one-tailed permutation test) for all three RSIs; color and size correspond to peak RSI value. (C) Non-negative Matrix Factorization (NMF), a matrix decomposition technique particularly suited for identifying prototypical patterns, was used to cluster electrodes based on their concatenated high gamma activity (trial means for the three tasks) and RSIs. (D) Clustering results. Top: electrode localizations; color and size correspond to NMF weight. Middle: weighted mean and standard error of high gamma for all three experimental tasks. Bottom: weighted mean and standard error of RSIs. Bars denote significance ($p < .001$ for 100 ms, permutation test).

above-chance information only for the (sub)lexical RSI ($p < .05$ for 100 ms, permutation test) at the time when activity peaked, consistent with the correlation between (sub)lexical processing and neural activity (Figs. 2F,G).

However, while syntax is often treated as a single entity, it in fact consists of multiple processing stages [63, 64, 80]. We asked whether the syntax network we identified might itself show evidence of these temporal stages. We clustered the syntax RSIs from all electrodes with a significant syntax RSI (regardless of neural activity level). This analysis revealed three subnetworks with peaks at 1062 ms, 422 ms, and 16 ms before speech onset (Fig. 4A). The early and late clusters were informationally selective – containing information about syntax ($p < .05$ for 100 ms, permutation test) but not words or event semantics. The middle cluster additionally encoded event semantic information ($p < .05$ for 100 ms, permutation test), suggesting a role in mapping from

semantics to syntax. We found two significant patterns in these clusters' spatial distributions. First, we found more MFG electrodes in the early cluster (16 electrodes, or 43% of the cluster; Fig. 4B) than expected by chance (21%) based on the distribution of the original dataset (FDR-corrected $p = .012$, binomial test). Second, we looked for differences between clusters and found a significant increase in IFG electrodes in the Late cluster relative to the Early and Middle clusters (Fig. 4C; FDR-corrected $p = .040$, binomial test). While IFG is commonly associated with syntax [8–12, 14–19, 81–83], MFG is not. Some recent evidence suggests a role for posterior MFG in higher-order language [19, 84, 85], however posterior MFG came online primarily in our Late cluster. The highest concentration of syntactic structure-dependent information in our data was in anterior MFG in the Early cluster. A closer analysis of the syntactic processing timecourse (Fig. 4D) showed a rostral-caudal gradient within MFG. This observation was statistically verified (Fig. 4E) by comparing MFG electrodes' peak syntax RSI times to their position along the principal axis of MFG. This finding suggests a cascade of syntactic information from more anterior areas starting at stimulus onset to more posterior areas just before speech onset ($p = .027$, linear regression).

3 Discussion

Here, we leveraged the high spatial and temporal resolution of intracranial recordings in order to investigate the dynamics of sentence production and its associated cognitive processes. We showed that one of the most common approaches to separating lexical information from higher-order information like syntax and semantics, comparing sentences to lists, identified only a small fraction of electrodes that were sensitive to a manipulation of syntactic frame. We then used a representational similarity approach to disentangle the contribution of structure-dependent, event semantic, and (sub)lexical processing in each electrode. A widespread assumption in the field holds that information processing corresponds to areas with elevated neural activity. However, we found that information associated with differences in syntactic frames and event semantics was uncorrelated with the degree of neural activity measured. That is, while electrodes encoding syntax and event semantics showed differences in activity, those differences did not systematically correspond to times when the overall degree of activity in the electrode was high. This "magnitude-independent coding" scheme explains why the sentence-list comparison failed to identify nearly all of the electrodes that were sensitive to the active/passive manipulation, and has potentially critical implications for how the field should go about studying higher-order linguistic processes. A clustering approach identified three broadly distributed networks that uniquely encoded either syntax, event semantics, or (sub)lexical information based on neural activity and representation processing. Lastly, temporal clustering of information sensitive to syntactic frame revealed three subnetworks, and a cascade of processing through MFG over the course of sentence planning.

The striking dissociation between higher-order linguistic information and degree of neural activity has potentially profound implications. It suggests a need to reassess common assumptions about the relationship between information processing and the overall degree of neural activity. It also highlights the danger in relying on elevated

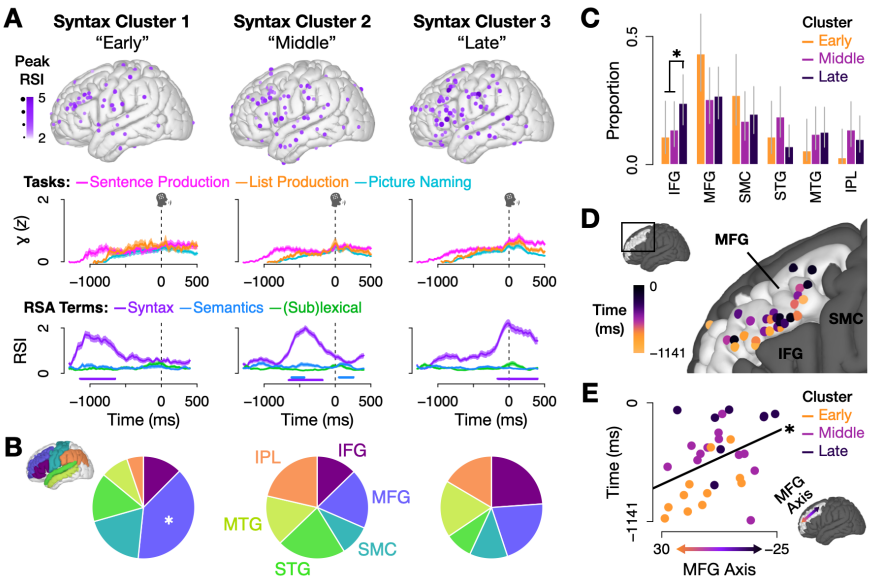

Fig. 4 (A) Temporal clusters of electrodes with significant syntax RSIs ($p < .05$ for 100 ms, permutation test). Columns contain data from only electrodes in each cluster. Top row: Electrode localizations in each of the three clusters; color and size correspond to each electrode's peak syntax RSI value. Middle row: Weighted mean and standard error of high gamma activity by experimental task (weighted by NMF weights). Bottom row: Weighted mean and standard error of the three RSIs; bars denote significance per term ($p < .05$ for 100 ms, permutation test). (B) ROI representation by cluster, scaled by each ROI's representation in the original dataset (i.e., the chance distribution is 6 equal slices). MFG was significantly overrepresented in the Early cluster compared to the original distribution ($p = .012$, binomial test); no other regions survived multiple comparisons corrections. (C) Proportion of electrodes in each region of interest by cluster (error bars: 95% confidence intervals, Wilson score). Comparing across clusters, there was a significant increase in IFG electrodes in the Late cluster relative to the the Early and Middle clusters ($p_{adj.} = .040$, binomial test) and a marginally significant increase in STG electrodes in the Middle cluster relative to the Early and Late clusters ($p_{adj.} = .053$, binomial test). (D) Significant syntax electrodes in MFG, colored by the time when the syntax RSI peaked (median latency from stimulus to speech was 1141 ms). (E) Electrodes' peak syntax RSI time was significantly predicted by position along the main axis of MFG ($p = .027$, linear regression) (only including MFG electrodes with significant syntax RSIs). Electrode position was calculated by projecting electrodes onto the main axis of MFG, which was the first principal component of the y and z MNI coordinates for MFG electrodes (see arrow on brain).

activity as a test for the presence of information, underscoring the importance of fine-grained analytical tools (e.g., RSA and multivariate pattern analysis), and cautions against the common practice of a priori excluding electrodes with low-activity responses [e.g., 79, 86, 87, 87–91]. In terms of experimental design, an important consequence is that sentence-list comparisons may be misleading when it comes to identifying syntax. That is, sentence-list comparisons, which rely on the assumption that syntactic processing elevates neural activity, will only identify a small fraction of electrodes sensitive to syntactic structure – just 5% in our data (Fig. 2B). While it is likely that not all of these encode syntax (with a number of other factors differing between actives and passives), the near absence of electrodes with higher activity

for lists than sentences among these electrodes indicates that in general, structure-dependent processes like prosody and structural complexity do not elevate activity more than lists, at least in production. As for why this might be the case, there are a number of possibilities. It may be related to the nature of production, in which case our findings would not necessarily contradict those of previous studies. Alternatively, lists may not control for syntax as intended. Previous research shows that single words engage syntactic processing [58–60] and that comprehending apparently ungrammatical sequences of words triggers syntactic analysis [92–94]. Both of these findings suggest that lists might also engage syntax. Moreover, the ability to recognize a list as a list and not a sentence implies syntactic processing. Given this, it may even be reasonable to hypothesize that lists engage syntax *more* than sentences, as the comprehension system struggles to identify a syntactic structure that fits the input. This would be consistent with our finding that sentence activity was only greater than list activity in 5% of syntactic electrodes: if lists and sentences both involve syntax, we should not expect to be able to identify syntactic information by comparing them. Regardless, our findings indicate that finer-grained manipulations are necessary to understand syntax more thoroughly (see [95] for further discussion).

The question of selectivity has been argued to hold implications for the cognitive architecture of language, where the degree of separation between syntax, semantics, and the lexicon is a matter of heated debate [13, 15, 25, 45, 96–106]. While various regions have been reported to be selective for syntax [11, 22, 27–34], recent studies taking individual subject anatomy into account have consistently failed to identify syntax selectivity in any region. This lack of evidence has been interpreted as support for so-called "lexicalist" models, where syntax is inextricably linked to particular words [23–25, 35–37] (although see [107] for discussion of the link between brain and theory). But we argue that the question of whether any regions are selective for syntax is ill-posed. That is, the critical issue is whether syntax is dissociable from lexical and semantic information in the brain. Given that syntax is encoded in broadly distributed networks rather than regions, the relevant question is whether these networks are selective for syntax. By leveraging production and a direct comparison of syntactic structures, we show that selectivity is in fact the predominant pattern for syntax, both within syntactic clusters (Fig. 4A) and at the level of individual electrodes (Fig. 2E). To the extent that neural separability bears on cognitive separability [107], this finding suggests that syntax is at some level represented independent of words and meaning.

Regarding the spatial organization of linguistic information, event semantics was broadly distributed across cortex, similar to previous work showing similarly broad distribution for lexical semantics [86]. We are more limited in our ability to draw conclusions about the spatial organization of syntax given the difficulty of isolating syntactic information from, e.g., prosody and complexity effects in this dataset. If the syntax RSI is taken at face value, it suggests a hybrid organization, with syntactic electrodes distributed across traditional language regions (Fig. 3B), but also concentrated in IFG and MFG (Figs. 4B,C). Such a hybrid pattern might explain the ongoing debate in the syntax literature, which often considers only two possibilities: broad distribution or localized hubs. Our analyses also revealed a cascade of syntactic information from anterior to posterior MFG. Posterior MFG (pMFG), including

area 55b [108], has previously been implicated in both low-level speech-motor planning [108–114] and high-level syntactic processing [19, 84], although the latter is also consistent with prosodic planning [85]. Interestingly, the highest concentration of syntactic information in our data was in fact in anterior MFG (aMFG), a region not typically associated with language. In contrast to the low-level functions of pMFG, aMFG is primarily associated with executive functions like attention [115–118] and working memory [119, 120], and to some degree lexical semantics [121–125]. One possibility is that the unexpected sensitivity of aMFG to the active/passive distinction reflects task demands. That is, passive sentences may have been harder to produce than actives, and signatures of this may have remained in the data despite our efforts to control for such effects (e.g., by informing patients that there were no right or wrong responses, temporally warping trials, and including response time covariates). However even if this interpretation accounts for some of the electrodes we identified as syntactic, it would only deepen the mystery of why so few electrodes had higher activity for sentences than lists. Perhaps more so than for syntactic processing, one would expect that regions recruited to process difficult tasks should show elevated activity. Regardless, it remains the case that our analyses would have also identified truly syntactic electrodes as well. Given the robustness of the lack of overlap between electrodes sensitive to syntax and those with higher activity for sentences than lists, an executive function interpretation does not undermine our conclusions in general. Another intriguing possibility, consistent with the functional and connectivity attributes of aMFG, is that MFG plays a role in syntactic planning. Specifically, aMFG is connected via white matter tracts to several key language regions including IFG, IPL, and posterior temporal lobe [115], supporting a role in language. Taken together with the known role of pMFG in language, this suggests a processing pipeline where disparate linguistic representations are integrated in anterior portions of MFG and propagated posteriorly to generate a speech-motor plan. The production-specific nature of this function may explain why previous research, predominantly focused on comprehension, has overlooked MFG's role in syntax.

Finally, our data reveal a distinction in how the brain processes different kinds of information. While (sub)lexical processing was strongly correlated with degree of neural activity, differences associated with sentence structure and event semantics did not show such a relationship. This distinction may belie a deeper taxonomic generalization. That is, (sub)lexical processing is not alone: low-level sensorimotor processes in general show a similar relationship with neural activity, including vision [47, 48], audition [126, 127], and motor movement [128, 129]. The divergence between lexical information on one hand and syntactic and event semantic information on the other may therefore be part of a broader dichotomy, whereby lower-level systems encode information in a way that elevates activity, while higher-order cognition does not. Such an account may go some distance to explaining why cognitive neuroscience has progressed more slowly than sensory neuroscience. We hypothesize that just as low-level information shares encoding properties, higher-order processing may in general be encoded in neural populations with varying degrees of overall neural activity. Such a divergence in coding schemes could derive from any number of differences between low- and high-level cognitive systems, including their spatial distribution, evolutionary

age, or informational complexity. One possibility is that because higher-level representations are generally sustained over longer periods of time, they require a metabolically efficient neural code. In contrast, lower-level representations like phonemes are relatively short-lived [130, 131], and higher firing rates may therefore be achieved without depleting resources. Taken together, our findings constitute a significant advance in understanding the neural underpinnings of sentence production, providing evidence for widespread representational selectivity and a magnitude-independent coding scheme that may underlie higher-order cognition in general.

4 Methods

4.1 Participants

Ten neurosurgical patients undergoing evaluation for refractory epilepsy participated in the experiment (3 female, mean age: 30 years, range: 20 to 45). All ten were implanted with electrocorticographic grids and strips and provided informed consent to participate. All consent was obtained in writing and then requested again orally prior to the beginning of the experiment. Electrode implantation and location were guided solely by clinical requirements. Eight of the participants were implanted with standard clinical electrode grid with 10 mm spaced electrodes (Ad-Tech Medical Instrument, Racine, WI). Two participants consented to a research hybrid grid implant (PMT corporation, Chanassen, MN) that included 64 additional electrodes between the standard clinical contacts (with overall 10 mm spacing and interspersed 5 mm spaced electrodes over select regions), providing denser sampling but with positioning based solely on clinical needs. The study protocol was approved by the NYU Langone Medical Center Committee on Human Research.

4.2 Data collection and preprocessing

Participants were tested while resting in their hospital bed in the epilepsy monitoring unit. Stimuli were presented on a laptop screen positioned at a comfortable distance from the participant. Participants' voice was recorded using a cardioid microphone (Shure MX424). Inaudible TTL pulses marking the onset of a stimulus were generated by the experiment computer, split, and recorded in auxiliary channels of both the clinical Neuroworks Quantum Amplifier (Natus Biomedical, Appleton, WI), which records ECoG, and the audio recorder (Zoom H1 Handy Recorder). The microphone signal was also fed to both the audio recorder and the ECoG amplifier. These redundant recordings were used to sync the speech, experiment, and neural signals.

The standard implanted ECoG arrays contained 64 macro-contacts (2 mm exposed, 10 mm spacing) in an 8×8 grid. Hybrid grids contained 128 electrode channels, including the standard 64 macro-contacts and 64 additional interspersed smaller electrodes (1 mm exposed) between the macro-contacts (providing 10 mm center-to-center spacing between macro-contacts and 5 mm center-to-center spacing between micro/macro contacts, PMT corporation, Chanassen, MN). The FDA-approved hybrid grids were manufactured for research purposes, and a member of the research team explained this

to patients during consent. The ECoG arrays were implanted on the left hemisphere for all ten participants. Placement location was solely dictated by clinical care.

ECoG was recorded at 2,048 Hz, which was decimated to 512 Hz prior to processing and analysis. After rejecting electrodes with artifacts (i.e., line noise, poor contact with the cortex, and high amplitude shifts), we subtracted a common average reference (across all valid electrodes and time) from each individual electrode. Electrodes with interictal and epileptiform activity were removed from the analysis. We then extracted the envelope of the high gamma component (the average of three log-spaced frequency bands from 70 to 150 Hz) from the raw signal with the Hilbert transform. Beta activity was quantified as the envelope of the 12 to 30 Hz band.

The signal was separately epoched locked to stimulus (i.e., cartoon images) and production onsets for each trial. The 200 ms silent period preceding stimulus onset (during which patients were not speaking and fixating on a cross in the center of the screen) was used as a baseline, and each epoch for each electrode was normalized to this baseline's mean and standard deviation (i.e., z-scored).

4.3 Experimental Design

4.3.1 Procedure

The experiment was performed in one session that lasted approximately 40 minutes. Stimuli were presented in pseudo-random order using PsychoPy [132]. All stimuli were constructed using the same 6 cartoon characters (chicken, dog, Dracula, Frankenstein, ninja, nurse), chosen to vary along many dimensions (e.g., frequency, phonology, number of syllables, animacy, proper vs. common) to facilitate identification of lexical information at analysis.

The experiment began with two familiarization blocks. In the first block (6 trials), participants saw images of each of the six cartoon characters once with labels (*chicken, dog, Dracula, Frankenstein, ninja, nurse*) written beneath the image. Participants were instructed to read the labels aloud, after which the experimenter pressed a button to go to the next trial. In the second block, participants saw the same six characters one at a time, twice each in pseudo-random order (12 trials), but without labels. They were instructed to name the characters out loud. After naming the character, the experimenter pressed a button revealing the target name to ensure learning of the correct labels. Participants then completed the picture naming block (96 trials). As before, characters were presented in the center of the screen, one at a time, but no labels were provided.

Next, participants performed a sentence production block (60 trials), starting with two practice trials. Participants were instructed that there were no right or wrong answers, we want to know what their brain does when they speak naturally. On each trial, participants saw a 1 s fixation cross followed by a written question, which they were instructed to read aloud to ensure attention. After another 1 s fixation cross, a static cartoon vignette appeared in the center of the screen depicting two of the six characters engaged in a transitive event. Participants were instructed to respond to the question by describing the vignette. The image remained on the screen until the participant completed the sentence, at which point the experimenter pressed a button

to proceed. After the first 12 trials, the target sentence (i.e., an active sentence after an active question or passive sentence after a passive question) appeared in text on the screen and participants were instructed to read aloud "the sentence we expected [them] to say" to implicitly reinforce the link between the syntax of the question and the target response. If participants appeared to interpret these as corrections, the experimenter reminded them that there were no right or wrong answers.

We interleaved two picture naming trials between each sentence production trial in order to reduce task difficulty and facilitate fluent sentence production. The picture naming trials involved the two characters that would be engaged in the subsequent vignette, presented in a counterbalanced order such that on half of trials they would appear in the same order as in the expected sentence response, and in the opposite order on the other half.

Next, participants performed the listing block. List production trials were designed to parallel sentence production trials. Each trial began with a 1 s fixation cross and then an arrow pointing either left or right appeared for 1 s in the center of the screen. After another 1 s fixation cross, a cartoon vignette (the exact same stimuli) appeared on the screen. Participants named the two characters in the vignette from left to right or from right to left, according to the direction of the preceding arrow. As in sentence production trials, each list production trial was preceded by two picture naming trials with the two characters that would appear in the subsequent vignette, again in counterbalanced order.

Between each block, participants were offered the opportunity to stop the experiment if they did not wish to continue. One participant stopped before the list production block, providing only picture naming and sentence production data. The other nine participants completed all three blocks. These nine were offered the opportunity to complete another picture naming block and another sentence production block. Six consented to another picture naming block and two consented to another sentence production block.

4.3.2 Stimulus Design, Randomization, and Counterbalancing

Picture naming stimuli consisted of images of the 6 characters in pseudo-random order so that each consecutive set of 6 trials contained all 6 characters in random order. This ensured a relatively even distribution of characters across the block, and that no character appeared more than twice in a row. Characters were pseudorandomly depicted facing 8 orientations: facing forward, backward, left, right, and at the 45° angle between each of these.

Sentence production stimuli consisted of a written question and a static cartoon vignette. Questions were manipulated so half were constructed with passive syntax and half with active. All questions followed the scheme: "Who is [verb]-ing whom?" or "Who is being [verb]-ed by whom?". There were 10 verbs: *burn, hit, hypnotize, measure, poke, scare, scrub, spray, tickle, trip*. Each verb was used to create 3 vignettes involving 3 characters, counterbalanced so each character was the agent (i.e., active subject) in one vignette and the non-agent (i.e., active object) in one vignette. Each of these three vignettes was shown twice in the sentence production block, once preceded by an active question and once by a passive question to prime active and passive

responses, respectively [67]. Vignettes were flipped around the vertical axis the second time they appeared so that the character that was on the left in the first appearance was on the right in the second appearance and vice versa. This was counterbalanced so that on half of the trials in each syntax condition (active/passive) the subject was on the left. List production stimuli similarly consisted of the same 60 vignettes, also presented in pseudorandom order and counterbalanced across conditions (i.e., arrow direction).

4.4 Data Coding and Inclusion

Speech was manually transcribed and word onset times were manually recorded using Audacity [133] to visualize the audio waveform and spectrogram. Picture naming trials were excluded if the first word uttered was not the target word (e.g., "Frankenstein – I mean Dracula"). Sentence trials were excluded if the first word was incorrect (i.e., "Frankenstein" instead of "Dracula," regardless of active/passive structure) or if the meaning of the sentence did not match the meaning of the depicted scene; no sentences were excluded because the syntax did not match that of the prime (i.e., question). Sentences were coded as active/passive depending on the structure the patient used, not the prime structure. Listing trials were excluded if the first word was incorrect or if the order did not match that indicated by the arrow.

All patients were included in Figure 1 analyses, however three patients who produced 6 or fewer passive sentences during the sentence production block were excluded prior to any subsequent analyses that involved an active/passive comparison (including the RSA and NMF analyses).

4.5 Electrode Localization

Electrode localization in subject space, as well as MNI space, was based on coregistering a preoperative (no electrodes) and postoperative (with electrodes) structural MRI (in some cases, a postoperative CT was employed depending on clinical requirements) using a rigid-body transformation. Electrodes were then projected to the surface of the cortex (preoperative segmented surface) to correct for edema-induced shifts following previous procedures [134] (registration to MNI space was based on a nonlinear DARTEL algorithm). Based on the subject's preoperative MRI, the automated FreeSurfer segmentation (Destrieux) was used for labeling within-subject anatomical locations of electrodes.

4.6 Significance testing and corrections for multiple comparisons in time series data

Statistical tests on time series data were performed independently at each time sample, resulting in the same number of p-values as there are samples in the time series. To correct for multiple comparisons we follow [135, 136] and establish a conservative criterion for significance for all time series comparisons: an uncorrected p-value that remains below .05 for at least 100 consecutive milliseconds.

4.7 Permutation tests for ROIs

To determine whether activity was significantly above chance for a given ROI (Figs. 1D and 3A), we randomized electrodes' ROI labels and re-calculated ROI means 1000 times. We derived p-values by determining what proportion of these chance means were above the real mean value at each time sample. If the p-value was less than .05 for at least 100 consecutive milliseconds (see Sec. 4.6), it was considered significant, denoted by a bar at the bottom of the plot.

4.8 Temporal warping

Our analyses focused on the planning period – the time between stimulus and speech onsets, when hierarchical syntactic structure is planned [11, 54, 63, 64]. The duration of the planning period varied considerably both across and within patients, meaning that cognitive processes become less temporally aligned across trials the farther one moves from stimulus onset in stimulus-locked epochs or speech onset in speech-locked epochs. This was potentially problematic for comparing syntactic structures, as passive trials took longer to plan (median RT: 1,424 ms) than active trials (median RT: 1,165 ms; $p < .001$, Wilcoxon rank sum test). The farther from the time lock, the more misaligned active and passive trials would be, and the more likely significant differences would be to reflect temporal misalignment rather than syntax.

Temporal warping reduces such misalignments [72–74, 137, 138]. Following [72], we linearly interpolated the data in the middle of the planning period (from 150 ms post-stimulus to 150 ms pre-speech) for each trial to set all trials' planning periods to the same duration (Supplementary Fig. S1): the global median per task (1141 ms for sentences; 801 ms for lists; 758 ms for words). Specifically, for each task we started by excluding trials with outlier response times, which we defined as those in the bottom 2.5% or top 5% per participant. We then calculated the median response time per task across participants (1,142 ms for sentences, 800 ms for lists, and 758 ms for words), and for each electrode and each trial, concatenated (a) the stimulus-locked data from 150 ms post-stimulus to $\frac{1}{2}$ the median reaction time with (b) the production-locked data from $-\frac{1}{2}$ median reaction time to 150 ms pre-speech. We then linearly interpolated this time series to the number of time samples corresponding to the median reaction time minus 300 ms (i.e., the two 150 ms periods following stimulus onset and preceding speech onset). Finally, we concatenated (a) the unwarped data leading up to 150 ms post-stimulus, (b) the warped data from the previous step, and (c) the unwarped data starting 150 ms before speech onset to form the final epochs used in the analyses in Figs. 2, 3, and 4.

Improved temporal alignment leads to better signal-to-noise ratio, which can be seen in higher trial means [74]. We leveraged this fact as a diagnostic for whether temporal warping in fact improved alignment in our data. For electrodes whose mean high gamma peaked in the warped period (between 150 ms post-stimulus and 150 ms pre-speech), we compared the peak mean values in the unwarped and the warped data. Peak values were significantly higher for the warped data than the unwarped data (Supplementary Fig. S3) for both the sentence and list production tasks ($p = .003$ and $p.008$ respectively, Wilcoxon signed rank tests), indicating that warping significantly

improved temporal alignment in the data. (There was no significant difference between peak values in the picture naming data ($p = .592$). This likely reflects the fact that these trials were relatively short, with a median reaction time of just 758 ms, meaning that warping made relatively minor changes to a smaller number of time samples.)

For comparison, we reproduced Fig. 1 in Supplementary Fig. S2 using the warped data. The results of the statistical tests in these figures were qualitatively identical: The spatial distributions of significant electrodes were nearly identical over time (Fig. 1C and Supplementary Fig. S2C) and the same ROIs (IFG, MFG, MTG, and IPL) showed significantly higher activity for sentences than lists during the planning period (Fig. 1D and Supplementary Fig. S2D).

4.9 Representational Similarity Analysis (RSA) and Representational Similarity Indices (RSIs)

To uniquely identify variance associated with syntactic, event-semantic, and (sub)lexical processing, we used multiple linear regression to model the neural activity from each electrode and at each time sample as a linear combination of syntactic, event-semantic, and (sub)lexical properties of the sentence the patient was planning/producing. Multiple regression is ideal in this context because it fits coefficients (slopes/betas) that can be used to derive t-values and corresponding p-values which reflect the *unique* contribution of each independent variable, effectively partitioning variance that can be unambiguously ascribed to just one term [139].

However, event semantic and (sub)lexical representations are highly complex and multidimensional, requiring a choice of which dimensions/features to use in a multiple regression model. To avoid this scenario, we leveraged a Representational Similarity Analysis-style approach and modeled pairwise differences between trials [75–78]. This resulted in just one vector per construct representing pairwise trial differences syntax, event semantics, and word content.

4.9.1 Linguistic and Neural Dissimilarity Models

The syntax term was binary: 1 if one trial was active and the other was passive and 0 otherwise. We modeled event-semantic representations using outputs from GPT-2's 8th hidden layer, where embeddings correlate most highly with neural activity [140]. Specifically, for each unique stimulus vignette, we fed the corresponding sentence with active syntax into GPT-2 and averaged the embeddings in layer 8 for all of the words in the sentence. By inputting only active sentences (rather than a combination of actives and passives depending on the structure of the specific trials), we ensured that the resulting vector contains just the semantic information from the trial, not the relevant syntactic information (i.e., whether it was active or passive).

To quantify event-semantic dissimilarity between trials, we correlated the vectors corresponding to each pair of trials' stimuli. Prior to modeling, correlation coefficients (r) were centered, scaled, and multiplied by -1 so that a value of 1 corresponded to more dissimilar meanings, and -1 meant that the two trials had the same exact stimulus. (Each stimulus appeared twice in each sentence production block, once with an active prime and once with a passive prime.)

The (sub)lexical term was also binary: 1 if the first word of the two trials' sentences were different, 0 if they were the same. This encoding scheme was meant to absorb variance associated with a host of extraneous linguistic features at the lexical and sub-lexical levels including phonetics, phonology, articulatory/motor information, auditory feedback, lemma-level representations, and lexical semantics (the meaning of individual words rather than the global event meaning).

We also included differences in response time (RT) as a covariate in the model, as this is known to index other extraneous non-linguistic features like difficulty that might be correlated with our syntactic manipulation. This term was quantified as the absolute value of the difference in the log of each trial's reaction times, so that higher values corresponded to bigger differences in reaction times.

We then modeled pairwise trial differences in neural activity (the magnitude of the difference between z-scored high gamma activity at a given sample for a given electrode) as a linear combination of these four dissimilarity (D) terms:

$$|\Delta\gamma| = \beta_0 + \beta_1 D_{syntax} + \beta_2 D_{semantics} + \beta_3 D_{(sub)lexical} + \beta_4 D_{RT} + \epsilon \tag{1}$$

4.9.2 Electrode Significance

The data used in the RSA regression did not clearly meet the assumptions of standard linear regressions: it was not clear that the residuals should be normally distributed (high gamma activity is gamma-distributed), and imbalances in the datasets due to trial exclusions and the varying effectiveness of priming across patients were exacerbated by the implementation of pairwise trial differences. To err on the side of caution, rather than directly interpreting model statistics, we ran a permutation analysis, shuffling the neural activity with respect to linguistic features in the original datasets, reconstructing the neural dissimilarity models, and re-running the linear regression at each time sample 1000 times.

To assess whether a given electrode was significant for the syntax, semantics, and (sub)lexical terms, we started by calculating the t-values corresponding to the each term's coefficient, which corresponds to the amount of evidence against the null hypothesis. Then we smoothed the real and shuffled t-values over time with a 100 ms boxcar function. Finally, we z-scored the real t-values by time sample and electrode with respect to the 1000 t-values from shuffled models in the same time sample and electrode. The resulting z-values reflect an estimate of evidence against the null that is standardized across patients and electrodes and independent of the number of trials. Significant electrodes for each representation were defined as those which maintained a z-value of at least 1.645 (corresponding to a 1-tailed p-value of less than .05) for at least 100 consecutive milliseconds.

4.9.3 Representational Similarity Indices (RSIs)

To derive RSIs, we performed additional transformations on these z-values to make them more interpretable and conservative. First, We scaled z-scores, dividing by 2.326, which corresponds to a p-value of .01. Consequently, values greater than 1 could be interpreted as very likely to reflect positive results, and values less than 1 were likely to reflect negative results. Next, to reduce the possibility of extremely high values

having an undue influence on aggregate statistics and NMF, we applied a logarithmic penalty to values grater than 1, replacing them with $log(x) + 1$. Similarly, to reduce values more likely to correspond to negative results, we shrunk low values toward 0 by replacing values less than 1 with (e^x), and then cubing the resulting values (i.e., $(e^x)^3$) to impose an even more severe penalty on low values. Notably, this renders all values non-negative, naturally resolving issues related to the uninterpretability of negative relationships in RSA [75, 141] and facilitating the use of NMF for subsequent clustering. Finally, we re-scaled values by multiplying them by 2.326 (undoing Step 1) so that the final RSI scale more closely matched the z scale in interpretation. Like z-scores, RSI values over 2.326 can be safely interpreted as significant at the $\alpha = .01$ threshold.

4.10 Non-negative Matrix Factorization (NMF)

We used NMF to cluster electrodes according to prototypical patterns in the data [142, 143]. In the first clustering analysis (Fig. 3), we analyzed RSIs and mean neural activity from all three tasks for all electrodes that were either "active" (non-zero neural activity; $p < .05$ for 100 ms, Wilcoxon signed rank test) or inactive, but with at least one significant RSI ($p < .05$ for 100 ms, permutation test).

High gamma activity was in units of standard deviations (i.e., z-scores), while RSIs were z-scores that had been smoothed and transformed to be non-negative, with extreme values in both directions shrunk (see Section 4.9.3). To ensure that NMF weighted the two types of information the same way, we applied the same transformation used to create the RSIs (Sec. 4.9.3) to the neural data prior to performing NMF.

We then concatenated these three time series (i.e., mean high gamma per task) and the three RSI time series (i.e., syntax, event semantics, and (sub)lexical), excluding pre-stimulus time samples and those after 500 ms post-speech onset. This resulted in a matrix of dimensionality 741 (electrodes) $\times$ 4364 (time samples from 3 high gamma and 3 RSI time series).

We fed this matrix to the `nmf()` function in R (*NMF* library v0.25 [144]) using the Brunet algorithm [145] and 50 runs to mitigate the risk of converging on local minima. We tried a range of model ranks: 3 to 9 for the full analysis (Fig. 4) and 2 to 7 for the syntax analysis (Fig. 4). The optimal rank (5 for the full analysis; 3 for the syntax analysis) was determined by finding the elbow in the scree plots.

Acknowledgments

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Data and Code availability

The data set generated during the current study will be made available from the authors upon request and documentation is provided that the data will be strictly

used for research purposes and will comply with the terms of our study IRB. The code is available upon publication at https://github.com/flinkerlab/low_activity_syntax.

Declarations

The authors declare that they have no competing interests.

Appendix A Supplementary Information

A.1 Data Warping

Supplementary Figs. S1, S2, and S3 show the methods and efficacy checks for our temporal warping procedure (see Sec. 4.8). Supplementary Fig. S3 analyses were performed on the maximum values of electrodes' trial means. Prior to finding the maximum, we took the absolute value of the trial mean to capture electrodes with negative peaks (reflecting suppression) that might have been enhanced by warping. We included only those electrodes that peaked during the warped period (between 150 ms post-stimulus and 150 ms pre-speech), as other electrode's maxima remained unchanged.

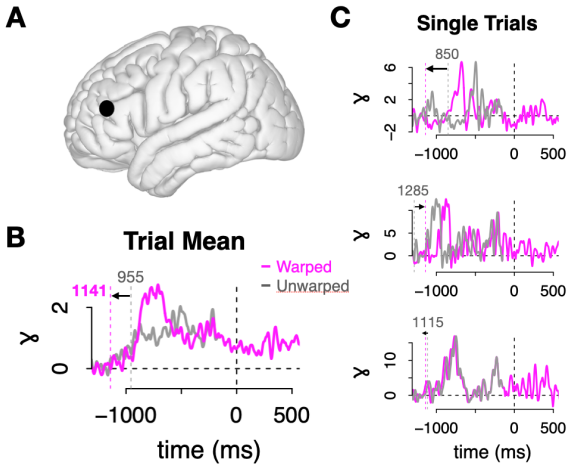

Fig. S1 Warped and unwarped sentence production data from a sample electrode. The data in each trial between 150 ms post stimulus and 150 ms pre-speech were linearly interpolated to set the duration of the planning period to the global median per task (1142 ms for sentence production) [72]. (A) Sample electrode localization in MFG. (B) The mean of this electrode's warped (pink) and unwarped (grey) trials. Prior to warping, this patient's median sentence response time was 995 ms; after warping it was 1,141 ms: the median sentence production response time across patients. The peak of the warped data was higher than the unwarped peak, a sign that warping resulted in better temporal alignment and consequently higher signal-to-noise ratio. (C) Three sample trials: warped (pink) and unwarped (grey) data.

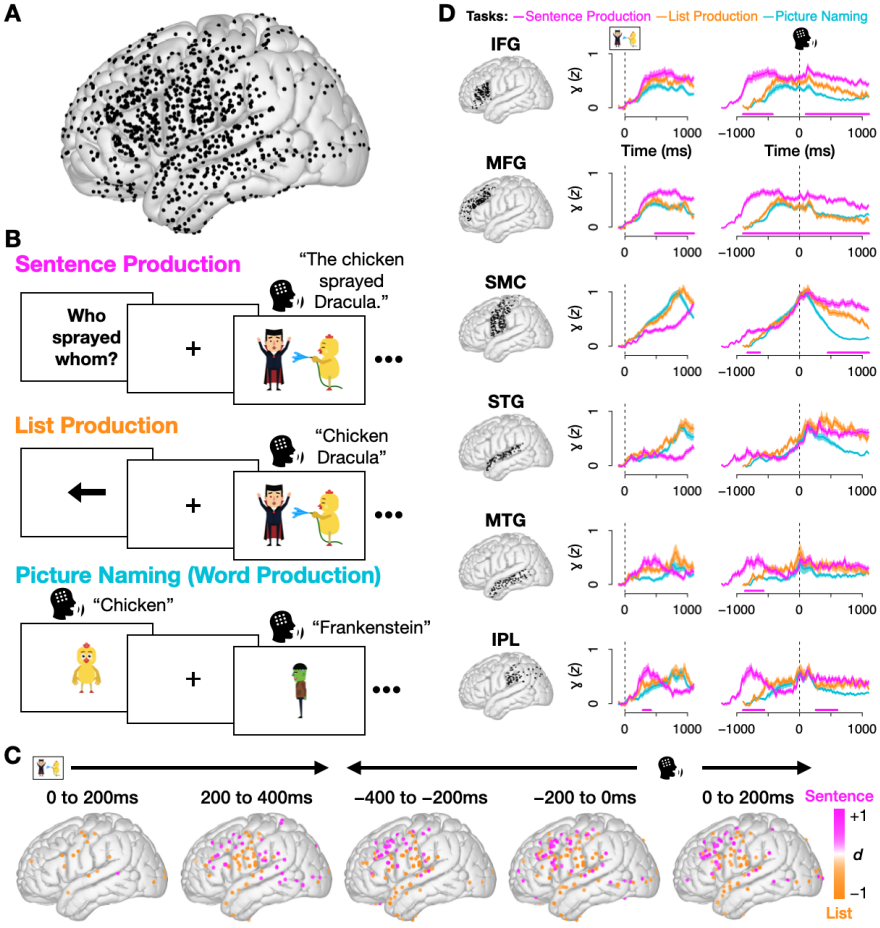

Fig. S2 Replication of Figure 1 using warped data. Results are qualitatively identical: (C) the spatial distribution of electrodes with significant differences between sentences and lists over time was nearly identical and (D) both identify IFG, MFG, MTG, and IPL as having significantly higher sentence than list activity during the planning period.

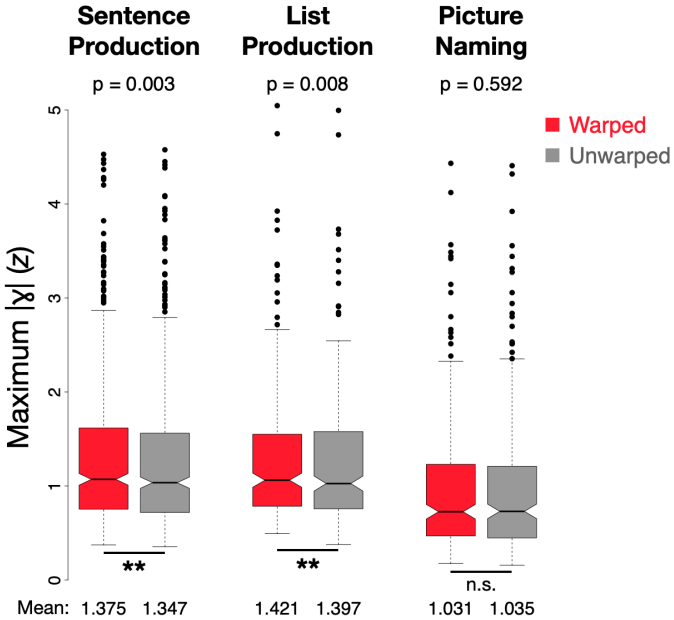

Fig. S3 Peak high gamma activity for each electrode (dot) in the warped (red) and unwarped (grey) data, by task. Warping resulted in significantly higher peaks for sentence production ($p = .003$, Wilcoxon signed rank test) and list production ($p = .008$, Wilcoxon signed rank test), evidence that it successfully improved the temporal alignment of trials [74]. No effect was found for picture naming ($p = .592$).

A.2 Analyses of Beta Activity

Supplementary Fig. S4 replicates the Figure 1 analyses but using beta activity (12-30 Hz). Beta is another important frequency band in cognition [70, 71]. In Supplementary Fig. S5, we test the hypothesis that beta activity tracks syntactic processing better than high gamma. We present three replications of the analysis in Fig. 2F (copied in Supplementary Fig. S5A). Analyses appear in a 2×2 factorial design: regressing either beta or high gamma activity over RSIs, where RSIs were derived from RSA performed on either high gamma (left) or beta (right) activity. Across all four sets of results, the only significant finding is that reported in the main text: a positive relationship between mean sentence high gamma and (sub)lexical signal in the high gamma trial activity ($p < .001$, linear regression).

To determine whether representational encoding in beta activity might be anatomically localized more than in high gamma, we replicated the analyses in Fig. 2A,b using beta. We analyzed the resulting "beta RSIs" by region of interest (Supplementary Fig. S6A). There was significant evidence for syntax in SMC and, as in the high gamma data, IFG ($p < .05$ for 100 ms, permutation test), but unlike high gamma there was no evidence that beta activity encoded syntactic information in MFG. (Notably, as MEG research frequently imposes a band-pass filter capped at 30 Hz during data pre-processing, this could be another reason that previous work has failed to identify the role of MFG in syntax.) We also plotted electrodes with significant beta RSIs on cortex (Supplementary Fig. S6B), revealing distributed networks similar to those observed in high gamma.

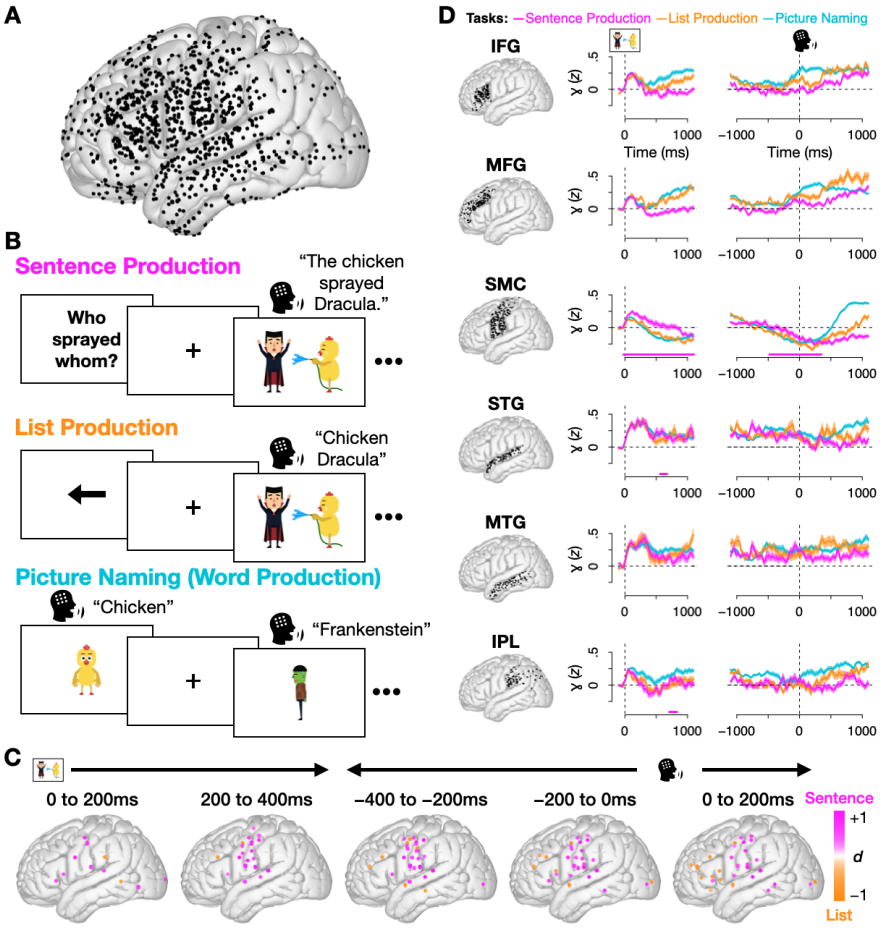

Fig. S4 Replication of Figure 1 using beta activity (12-30 Hz; unwarped data). (C) The distribution of electrodes that are significantly greater for sentences than lists was largely reversed from the high gamma activity. This likely reflects a well-documented phenomenon where activity in high gamma is often coupled with beta suppression, leading to effects in the reverse direction in beta [146, 147]. (D) SMC, STG, and IPL show significantly higher beta activity for sentences than lists, possibly also reflecting beta suppression corresponding to increases in high gamma during speech and auditory feedback.

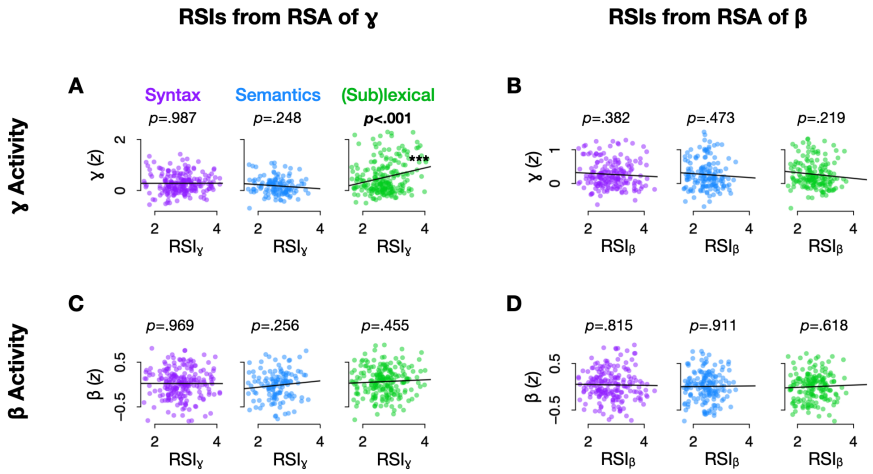

Fig. S5 Four attempts at uncovering a relationship between mean neural activity during sentence production and linguistic processes. Only one significant relationship was found across all analyses: mean high gamma activity was positively related to high gamma (sub)lexical processing ($p < .001$). (A) Mean high gamma activity vs. linguistic RSIs encoded in high gamma trial activity (panel is identical to Fig. 2F). (B) Mean high gamma activity vs. linguistic RSIs encoded in beta trial activity. (C) Mean beta activity vs. linguistic RSIs encoded in high gamma trial activity. (D) Mean beta activity vs. linguistic RSIs encoded in beta trial activity.

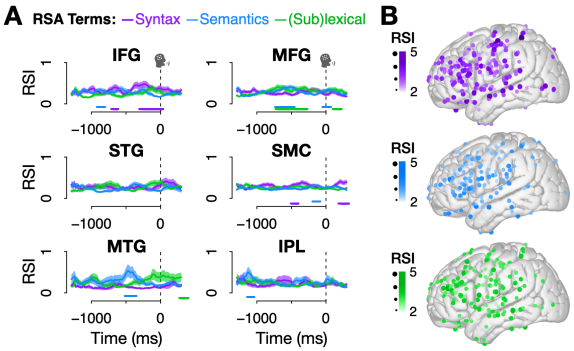

Fig. S6 Distribution of RSIs calculated from RSA on beta activity (see parallels for high gamma in Fig. 2A,B). (A) Mean and standard error by region shows significant syntax in IFG and SMC ($p < .05$ for 100 ms, permutation test), but there was no evidence for syntax in MFG as there was in the high gamma activity. (B) Significant electrodes ($p < .05$ for 100 ms; one-tailed permutation test) per RSI again show a broadly distributed pattern for all three RSIs, as in high gamma.

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