

# Semantic and syntactic information processing during auditory language comprehension: A spectral stereo-EEG approach

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## Article

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# Abstract

There is no consensus regarding clear-cut brain functional dissociations of semantic and syntactic information processing networks. Recent studies proposed a functional dissociation at the spectral level in which semantic and syntactic processes were associated with neural network activity at different frequency intervals. This study aimed at investigating this functional dissociation for semantic and syntactic information during auditory language comprehension. For this purpose, we collaborated with 11 drug-resistant epilepsy patients undergoing deep electrode implantation brain recordings. Patients were instructed to listen to four different types of auditory stimuli (in which semantic and syntactic information were manipulated): sentences, jabberwockys, word lists, and pseudoword lists. Results showed no clear dissociation between semantic and syntactic processing in the left language canonical network. In the temporo-parietal regions two distinct subnetworks, each with its own spectral signature, were observed. Semantic information processing appeared to elicit stronger high frequency activity in the temporal pole, while syntactic information processing elicited low frequency activity increases in the middle temporal as well as the supramarginal gyri. Interestingly, a specific spectral functional dissociation in the *pars triangularis* was observed suggesting that a single region could support both functional processes within distinct neural frequency intervals.

## Introduction

During speech comprehension, various linguistic processes are hierarchically and incrementally recruited. Specifically, after the initial acoustic-phonological processing (speech perception), the analysis of structural relationship between words, required for sentence comprehension, is performed. A distinction between the syntactic structure (grammatical identity and word order in the phrase) and the semantic information (meaning) can be made. To fully understand a sentence, these two pieces of information must be used and integrated. Different hypotheses have been proposed regarding how semantic and syntactic information is processed during sentence comprehension (e.g., <sup>1-3</sup>). The most important discrepancies highlighted in the literature is related to the specific weight given to each of these type of information at the cognitive and neural levels. For instances, regarding brain representations some authors proposed neuroimaging evidence of a distinction between anatomo-functional processes involved in syntactic and semantic mechanisms, as well as in terms of spectral activity.

One of the first studies to suggested a brain dissociation between these two types of information was the study of Dapretto and Bookheimer <sup>4</sup>. Using fMRI measures with a task presenting auditory sentences, they showed activity segregation in the left inferior frontal gyrus (IFG). More specifically, their results revealed that the *pars triangularis* presented a semantic processing selectivity while the *pars opercularis* was critically involved in syntactic processing (see also <sup>5</sup>). Similar results were observed by Friederici, Optiz and von Cramon <sup>6</sup> using others semantic (abstract vs concrete word presentation) and syntactic (assessed with a grammatical categorization including nouns vs function words) tasks at the level of the left IFG. They also showed a functional activity differentiation between semantic and syntactic

information processing in the temporal regions with the posterior middle and superior temporal gyrus more involved during semantic than during syntactic task. More recently, also using fMRI, Schell and collaborators<sup>7</sup> presented to participants oral two-word phrases (e.g., “bleu boat”) containing more semantic (adjective-noun phrases, “bleu boat”) or more syntactic (determiner-noun phrases, “this boat”) information. Interestingly, the authors showed an IFG activity dissociation in terms of ventral and dorsal representation with higher activity during semantic processing in the dorsal part of the anterior IFG while left ventral-posterior parts of the IFG was more involved in syntactic processing. Thus, authors observed a double dissociation between the two information types and their activated regions within the IFG

Nevertheless, some authors did not observe such dissociation in brain activation during syntactic and semantic processing<sup>1,8</sup>. For instance, using an experimental paradigm allowing the assessment of semantic and syntactic information processing in fMRI, Fedorenko et al.<sup>1</sup> showed that each of the canonical language regions was similarly sensitive to semantic and syntactic information processing (see also<sup>9</sup>). In this experiment authors proposed the manipulation of the absence / presence of semantic and syntactic information in an orthogonal experimental design allowing a more ecological way to evaluate information processing dissociation (see<sup>10</sup> for the first proposition of such experimental protocol). This was possible by presenting Jabberwockys stimuli that are sentences from which all content words are replaced by pseudo-words while closed-class words are kept (inspired from Lewis Carroll’s poem). This way, Jabberwockys stimuli allow to evaluate syntactic structure processing without semantic information. (semantic-/syntax+). In this type of experimental design 2X2 crossing conditions are proposed: presence/absence of semantic information (present in the Sentence and in a Word-list conditions, absent in the Jabberwocky and in the Pseudo-words-list conditions) with the presence/absence of syntactic information (present in the Sentence and Jabberwocky conditions, absent in the Word-list and Pseudo-word-list conditions). More recently the same research team used this orthogonal experimental design with a multi-voxel pattern analysis and showed that “pure lexico-semantic” information (Word-list condition) was represented more robustly than “pure syntactic” information (assessed by Jabberwocky condition) across different brain regions of the language network, including IFG and posterior temporal cortices. The authors suggested that given the goal of the language systems (constructing and decoding meanings) it makes sense that semantic information was more “robustly” represented in the brain. These results go against the Serial Syntax-First model (e.g.,<sup>11</sup>) in which it is postulated that syntactic information is processed first and is necessary for further semantic processing (e.g.,<sup>11-13</sup>). This implied that the syntactic information is crucial for language comprehension. Nevertheless, results proposed by Siegelman, Mineroff, Blank, & Fedorenko<sup>8</sup> give a more important place to the semantic information in sentence comprehension processing. Indeed, their results suggested that the lexico-semantic information is an important source of information that can guide sentences understanding, in line with a more Interactive model of semantic and syntactic information interaction<sup>14</sup> and a larger brain representation (see<sup>15</sup>).

Pallier et al.<sup>16</sup>, used fMRI with a similar experimental design as proposed in Fedorenko et al.<sup>1</sup> study and observed a specific syntactic effect in the IFG and in the posterior part of the superior temporal gyrus.

They also observed specific semantic processing brain activity in the anterior superior temporal gyrus, the temporal pole, and the temporo-parietal junction. To characterize semantic and syntactic processing, Fedorenko and collaborators<sup>17</sup> asked patients with intracranial recordings from the surface of the brain (ECOG) to read and listen to the same type of stimuli with a word by word presentation (i.e., sentences, jabberwockys, word-lists, and pseudo-word-lists) and recorded high frequency activity (70–170 Hz). The authors observed a monotonic increase in brain activity in language regions through the stimuli only for sentences and no specific pattern for semantic only or syntactic only conditions. They interpreted this result as an evidence that both semantic and syntactic processing involve the same brain network. By comparing written sentences to unconnected phrases in a similar experimental design, Matchin et al.<sup>18</sup> observed an effect of syntactic processing in the posterior temporal gyrus suggesting that this region is critical for syntactic processing. Authors also observed higher brain activity in the anterior and posterior temporal regions as well as in the left IFG during sentences than during jabberwockys suggesting an involvement of these regions in semantic processing. Discrepancies are observed in the brain networks at work during language comprehension and the distinction of semantic and syntactic processing does not seem to appear only in terms of brain representation.

In terms of brain dynamic, Friederici and collaborators<sup>19</sup> observed an early left anterior negativity (ELAN) around 180ms after a syntactic violation during an auditory language comprehension task and a classic left negativity around 400ms after a semantic violation (N400) (see also<sup>20</sup>). This observation of an ELAN supports the *Syntax-First* approach according to which language comprehension mechanisms start with syntactic processing. Nevertheless, other authors propose that both syntactic and semantic information are processed in parallel<sup>21,22</sup>. A study by Hinojosa et al.<sup>23</sup> supported this hypothesis. Indeed, in their study, participants performed either a visual perception task or a semantic categorization task with single visual words while their brain activity was recorded with scalp-EEG. The authors observed similar electrophysiological patterns with an early recognition potential (around 225ms after the stimuli presentation) for both the perception and the semantic tasks suggesting that lexico-semantic mechanisms also appear early. In a similar study, Martin-Loeches et al.<sup>24</sup> also observed an early recognition potential in a semantic categorization task suggesting an early access to word meaning and supporting the view of a parallel processing of syntactic and semantic mechanisms during language comprehension. Thus, evidence for both early syntactic and semantic processing during language comprehension have been proposed in the literature.

In this context an alternative hypothesis could be proposed regarding the spectral brain activity to explain semantic and syntactic information processes during sentence comprehension. This alternative proposition suggests a dissociation between semantic and syntactic processing could be reflected in brain responses in distinct frequency bands<sup>25</sup>. Indeed, as some hemodynamic results in the literature suggest an absence of functional segregation between semantic and syntactic processing, Bastiaanse and Hagoort<sup>26</sup> tested whether these processes could be segregated in the frequency domain. To test this hypothesis, the authors asked participants to read correct sentences, sentences without meaning but with a syntactic structure (like the jabberwockys sentences previously described), word lists (containing

meaning but no syntax) or sentences with a semantic or syntactic violation while recording their brain activity through EEG. Interestingly, by comparing sentences with and without semantic information the authors observed a semantic effect in terms of high frequency activity (gamma-band, 40-60Hz); and by comparing sentences with and without syntactic violation they observed a syntactic effect in terms of low frequency activity (10-20Hz) (see also <sup>27-29</sup>). Moreover, syntactic processing has also been linked to delta frequency activity (4Hz). Indeed, Ding and collaborators <sup>30</sup> manipulated different types of phrasal structures in the native language of participants or in another language. They observed a delta-band entrainment only when participants listened to stimuli in their native language suggesting that delta-band activity supports syntactic processing (see also, <sup>31</sup>). Using the same procedure with magnetoencephalography (MEG) and MRI measures, Sheng and collaborators <sup>32</sup> observed a regional dissociation for stimuli varying in their structure (words, phrases, sentences). More specifically, the authors observed that phrase and sentence stimuli induced entrainment in the left anterior temporal lobe and in the left IFG, while all type of linguistic items induces an entrainment in the left superior temporal gyrus. This entrainment was also observed in high frequency activity (> 70Hz) in an experiment of Ding and collaborators <sup>30</sup> using electrocorticography (ECoG) measures. Indeed, in this experiment, authors observed an entrainment of high-gamma activity on phrase and sentence stimuli. Similarly, using ECoG, Nelson et al., <sup>33</sup> observed high-gamma activity modulations in relation to the syntactic structure being processed. Results in terms of frequency activity suggest that segregation in terms of stimuli hierarchy (linguistic units) and linguistic mechanisms could be observed in spectral brain activity. It is possible that different frequency bands are involved in different speech processes at the same time. Finally, functional dissociations mirrored in distinct spectral responses have also been observed for perception and attention in humans <sup>34,35</sup> and primates <sup>36</sup>, suggesting a plausible mechanism for cortical functional dissociation.

The aim of the present study was to investigate the possible dissociation of syntactic and semantic mechanisms not only in terms of brain region segregation and specialization but also in terms of brain spectral activity. We collaborated with epileptic patients recorded with intracranial electrodes for therapeutic purposes, and measured high-frequency four different frequency band in line with high-gamma (50-150Hz), low-gamma (30–50 Hz), alpha-band (16-24Hz) and beta-band (8-12Hz). We used the orthogonal experimental design proposed by several studies (e.g., <sup>6,10,16</sup>) involving processing of sentences, jabberwockys, word-lists and pseudo-word-lists during auditory stimulation and allowing to dissociate semantic and syntactic processing.

## Results

### Semantic effects

In the IFG we observed a positive amplitude in almost all of the three ROI in terms of comparison to the baseline for each condition and each of the four-frequency bands evaluated. This could suggest a significant activity in the IFG for all of the language conditions. An absence of such difference between

conditions and the baseline was observed specifically in the *IFG Tri* for the beta frequency band as well as in the *IFG Oper* for the low-gamma band. A difference between semantics and non-semantic conditions in the *pars triangularis* ROI in terms of low-gamma activity was observed as marginally significant with Bonferroni correction ( $t = 2, p = 0.046$ ). This could suggest stronger response for semantic as compared to non-semantic stimuli processing (Fig. 4).

We observed two different activity patterns at the level of the temporo-parietal ROIs and in terms of amplitude difference against the baseline. Indeed, the temporal pole, the post MTG, ant MTG, and the SMG presented a similar activity pattern in the four-frequency band. This pattern was characterized by a positive amplitude for both semantic and non-semantic conditions. The ant STG and the post STG showed a similar and specific pattern that was characterized by negative amplitude in the low frequency band including alpha and beta band while a positive amplitude was observed in high frequency band including low- and high-gamma band. This similar specific patterns in the STG could suggest a single functional unit in this anatomical region.

A semantic effect in the temporal pole for both low-gamma ( $t = 2.21, p = 0.027$ ) and high-gamma ( $t = 2.54, p = 0.011$ ) activity was observed as marginally significant after the Bonferroni correction. This effect was characterized by a higher activity during semantic than during non-semantic stimulus processing (Fig. 5). In a descriptive way, we observed that in this region the low-gamma band presented an interesting pattern showing an amplitude response increase for the stimuli that contained the most linguistic information (i.e., sentences > jabbercockys > word lists > pseudowords lists) (see Supplementary Fig. 1). The inverse pattern was observed in the post STG in which we observed a marginally significant effect in the high-gamma band after the Bonferroni correction ( $t = -2.43, p = 0.015$ ) showing a larger amplitude response for non-semantic items (i.e., jabberwockys and pseudoword lists) than for semantic ones. In a descriptive manner, we also observed that this region showed a lower amplitude for stimuli that contained the most linguistic information specifically in the high-gamma band with the following specific pattern: sentences < jabberwockys < word-lists < pseudo-word lists, see Supplementary Fig. 1).

## Syntactic effect

The IFG showed a positive amplitude response in almost all of the three ROIs in terms of comparison to the baseline for each of the four-frequency bands assessed. This could suggest a significant activity in the IFG for all of the language conditions. An absence of such difference between condition and the baseline was only observed for the non-syntactic condition (i.e., word and pseudoword lists) in the *IFG Tri* for the beta band and in the *IFG Oper* in the low-gamma band. In line with this absence of difference in these two regions, a pattern of syntactic-like effect was observed. Indeed, in these two cases only the syntactic condition (i.e., sentences and jabberwockys) presented a significant difference compared to the baseline (Fig. 5). Nevertheless, this patterns is not observed when we compared both syntactic and non-syntactic conditions. A marginal uncorrected effect of syntax was observed in the *IFG Oper* in the beta frequency band ( $t = 1.9, p = 0.058$ ) with a higher beta activity for syntactic than for non-syntactic items (Fig. 6).

At the level of the temporo-parietal ROIs and in terms of amplitude difference against the baseline, as for semantic effect, we observed two different amplitude patterns. The first pattern included: the temporal pole, the post MTG, ant MTG and the SMG for which we observed a positive activity in the four-frequency bands. This pattern was characterized by a positive amplitude response for both syntactic and non-syntactic conditions. The second pattern includes: the ant STG and the post STG for which we observed a negative amplitude response in the low frequency band (i.e., in alpha and beta bands) while a positive amplitude response was observed in high frequency bands including (low- and high-gamma bands). In the post STG, in terms of high-gamma activity, we observed a significant effect of syntactic information ( $t = -3.05, p < .0056$ ) highlighting a higher activity for the non-syntactic condition compared to the syntactic one (Fig. 6). Results also revealed a significant syntactic effect in the post MTG for both beta ( $t = 2.95, p < .0056$ ) and low-gamma band ( $t = 2.81, p < .0056$ ) activity with a larger amplitude response during syntactic item processing (i.e., sentences and jabberwockys) than during non-syntactic ones (i.e., word and pseudoword lists) (Fig. 6). In the ant MTG, analyses revealed a marginally significant syntactic effect in the beta frequency band ( $t = 2.15, p = 0.032$ ). This effect suggested a higher beta activity during syntactic stimuli processing than during non-syntactic ones. In the SMG, analyses revealed a significant syntactic effect in both beta ( $t = 2.97, p < .0056$ ) and low-gamma bands ( $t = 2.93, p < .0056$ ) showing a higher activity during syntactic than during non-syntactic item processing. Interestingly, beta and low-gamma activity was not different from the baseline during non-syntactic stimuli ( $t = -0.71, p = 0.48$ , and  $t = -0.15, p = 0.88$ , respectively) but was during syntactic ones ( $t = 3.53, p < .0056$ , and  $t = 3.89, p < .0056$ , respectively) (Fig. 7).

## Discussion

This study aimed at evaluating the brain segregation of semantic and syntactic mechanisms during language comprehension on a spatial and frequency level. To do so, we used a well-known experimental paradigm that involves processing normal sentences, jabberwockys, word lists, and pseudoword lists, using continue auditory stimuli.

First, it is important to highlight that the majority of the regions explored in the canonical language network in the present study (including here frontal and temporo-parietal regions) presented a similar pattern of activation. Indeed, the more representative pattern in all of the regions and in terms of frequency band assessed showed a similar implication for semantic and syntactic information as recently suggested by Siegelman et al.,<sup>8</sup> using fMRI measures.

Furthermore, when we look specifically at the frontal and temporo-parietal regions we observe a similar pattern of implication of these regions in terms of spectral activity regardless of the linguistic effect. Indeed, frontal regions presented in all frequency bands an amplitude increase for both semantic and syntactic processing. We only showed a tendencial pattern of specific functional dissociation in the inferior frontal gyrus (IFG) for the *pars triangularis* that seemed to depend on the frequency band. In fact, we showed a preferential semantic information processing in the low-gamma band while a preferential syntactic information processing in the beta band. Importantly and even if this result need to be

replicated (because only marginal effects were observed here), this observation suggests that one region can support dissociated processes at the spectral level. Several studies have linked the *pars triangularis* to semantic processing (e.g., <sup>37,38</sup>). Our results suggest that both semantic and syntactic processes can occur in the same region and at the same time but in different frequency bands. Such dissociation of linguistic processing at the spectral level has already been observed in EEG and MEG studies (e.g., <sup>26-28</sup>). Similar functional spectral dissociations have been observed for perception and attention in humans <sup>35</sup> and primates <sup>34,36</sup>.

In line with the temporo-parietal regions assessed we showed that these regions presented in both semantic and syntactic information two different patterns in terms of spectral activity. Specifically, we showed that the superior temporal gyrus -STG- (in both the anterior and the posterior subregions) presented a specific pattern highlighted by an amplitude decrease in the lower frequencies and an amplitude increase in the higher frequency bands. Conversely, the other temporo-parietal regions (temporal pole, anterior and posterior middle temporal gyrus -MTG- and the supramarginal gyrus -SMG) presented a similar amplitude increase in all frequency bands. This could suggest two different functional networks with specific spectral signature. This is relatively supported by the effect observed in high frequency activity in the STG and specifically in the posterior STG. Interestingly, the effect observed in the posterior STG in terms of high-gamma activity highlights that this region is more involved when less linguistic information was provided regardless of the assessed effect (semantic or syntactic, see the Supplementary Fig. 1). This could be related with results proposed by Brown et al. <sup>39</sup> that showed a similar effect comparing forward and reverse speech in an ECoG study with a larger high-gamma amplitude in the posterior STG for reverse speech than for forward speech. These effects might be explained by the increase in attentional demands when less linguistic information is available. In fact, it has been suggested that high-gamma activity in the STG increased with selective attention for auditory stimuli <sup>40,41</sup>. Hence, it is possible in our task that patients' auditory attention increased for meaningless linguistic information in order to force meaning extraction by increasing focus, similar to increased attentional gain during noisy sensory stimulus presentation <sup>42</sup>.

The temporal pole seems to present a more important activity for semantic information in high frequency bands (including low- and high-gamma bands). Indeed, a marginal semantic effect was observed with a more important activity on the high frequency bands for the semantic than for non-semantic conditions. This in line with the role of the anterior temporal lobe described in the literature. Indeed, the temporal pole has been shown to play a role in semantic processing and language comprehension in neuroimaging <sup>16,43,44</sup>, MEG <sup>45</sup> and neuropsychological <sup>46,47</sup> studies (see also <sup>48</sup>).

Conversely, a syntactic effect was observed specifically in the SMG and in the posterior MTG only in beta and low-gamma bands. The SMG syntactic effect is observed in previous fMRI studies <sup>4,49</sup> in which an increased activation was observed in this region for syntactically complex sentences compared to syntactically simpler ones. It is important to note that the effect observed in our study is induced not only by the increased activity during the syntactic information processing but also by the absence of the

activity during the non-syntactic condition (absence of difference of non-syntactic condition against the baseline) in these frequency bands. It suggests that this region is not engaged for non-syntactic information.

The syntactic effects observed in the posterior MTG for the beta and low-gamma frequencies are in line with findings in the literature showing an involvement of this region during syntactic processing (see <sup>39,45,50-53</sup> for a review). More specifically, several authors suggested that the posterior MTG plays a hub role for hierarchical lexical-syntactic processing <sup>54</sup>. In line with the syntactic effect observed in the beta frequency band, Bastiaansen et al. <sup>27</sup> also observed an increase in beta oscillations during correct sentence processing as compared to sentences containing a syntactic violation (see also <sup>26</sup>). Hence, the posterior MTG seems to play an important part in syntactic processing as reflected by beta and low-gamma frequency activity.

## Conclusion

We showed that the majority of canonical language regions included in the present study exhibited a pattern of spectral activity suggesting an absence of semantic and syntactic segregation. Indeed, these regions showed in a general view similar activity for both semantic and syntactic auditory information. Nevertheless, interestingly, in the frontal regions a functional specificity was found in *pars triangularis* with a syntactic-like effect in terms of beta activity and a semantic-like effect in terms of low-gamma activity. This dissociation effect, which needs to be replicated, opens new perspectives in language processing. Finally, results showed a temporo-parietal dissociation in two different functional frequency networks. The first involved the superior temporal gyrus (in both anterior and posterior regions) that showed a specific pattern highlighted by an amplitude decrease in the lower frequencies and an amplitude increase in the higher frequency bands. The second one involved temporo-parietal regions that exhibited an increase in amplitude response in all of the frequency bands explored regardless of the semantic or syntactic information. The syntactic effect observed in the posterior middle temporal gyrus and in the supramarginal gyrus in terms of beta and low-gamma amplitude suggests an involvement of these regions during syntactic processing. Conversely the temporal pole seems to be a more important for semantic information processing in terms of low-gamma activity. Even if we need to replicated these results with larger sample, they show that the spectral activity is an essential component of language processing (and cognition in general) and allowed to define functional specificity in the canonical language network.

## Method

### *Participants*

Eleven patients with drug-resistant epilepsy participated in this study (1 woman and 10 men, mean age = 36.9; SD = 11.5) during their pre-surgical evaluation with stereotactic electroencephalography (sEEG) recording at the Grenoble-Alpes University Hospital (see Table 1 for patients' information). All patients

gave written informed consent to participate in the present study. The study was approved by the National Ethics Advisory Committee (CPP MAPCOG: N° Id RCB: 2017-A03248-45, local CHUGA number: 38RC17.357). All research was performed in accordance with relevant guidelines/regulations and in accordance with the Declaration of Helsinki.

**Table 1: Demographic and clinical information of patients included in the study**

P	A iEEG	G	H	EZ LAT	EZ LOC	NCS
1	54	M	R	L	PARIETAL	17
2	28	M	R	L	TEMP	22
3	26	M	R	L	TEMP	49
4	44	F	R	L	TEMP	31
5	37	M	R	L	FRONTAL	9
6	25	M	R	L	TEMP	31
7	21	M	R	R	OCCIPITAL	3
8	31	M	R	L	MULT	24
9	46	M	L	L	TEMP	20
10	53	M	R	R	TEMOP	21
11	41	M	R	L	INSULA	18

Abbreviation P: patient; AiEEG: age at the iEEG acquisition; G: Gender; H: handedness; EZ LAT: epileptic zone lateralization; EZ LOC: epileptic zone location; TEMP: temporal lobe; MULT: multilobe; NCS: number of cortical sites included.

### *Electrode implantation and positioning*

Eleven to 15 semi-rigid, multilead electrodes were stereotactically implanted in each patient. Each electrode had a diameter of 0.8 mm and, depending on the target structure, consisted of 8–18 contact leads 2 mm wide and 1.5 mm apart (DIXI Medical, Besançon, France). Electrode implantation were strictly related to individual clinical hypotheses. A preoperative MRI and post-operative MRI or CT scan were co-registered to assess the locations of the electrode contacts for each patient using a coordinate system in relation to the anterior commissure / posterior commissure plane. Electrode contact positions were finally expressed in the Montreal Neurological Institute (MNI) coordinate system to allow group analyses after brain spatial normalization using Statistical Parametric Mapping 12 software (SPM12, Wellcome Department of Imaging Neuroscience, University College London, [www.fil.ion.ucl.ac.uk/spm](http://www.fil.ion.ucl.ac.uk/spm)). Visual inspection of the contact locations was also used to check whether each electrode contact was located in

grey or white matter. Seven patients were implanted only in the left hemisphere and 4 had a bilateral implantation. For this study we only included cortical sites recorded in the left hemisphere (see Figure 1).

### *SEEG recordings*

SEEG recordings were performed using a video-EEG monitoring system (Micromed, Treviso, Italy) that allowed to simultaneously record up to 256 monopolar contacts, so that a large range of mesial and cortical areas, as well as fissural cortices, was sampled for each patient. Sampling rate was 1024 Hz, with an acquisition band-pass filter between 0.1 and 200 Hz. Data were acquired using a referential montage with reference electrode chosen in the white matter. All other recording sites were chosen in the grey matter. For data analysis, we used a bipolar montage between adjacent contacts of the same electrode to improve sensitivity to local current generators. Coordinates of virtual bipolar contacts that were used to construct images were chosen to be at an equal distance of two successive contacts.

### *Language comprehension task and stimuli*

The task used in the present study was adapted from Pallier et al. <sup>16</sup> see Figure 2. Stimuli were 240 auditory streams including 80 sentences (i.e., with semantic and syntactic information), 80 jabberwockys (i.e., with syntactic information and without semantic information), 40 words lists (i.e., with semantic information and without syntactic information) and 40 list of pseudowords (i.e., without semantic and without syntactic information). All stimuli were controlled in terms of amplitude. The 80 sentences were taken from the study by Pallier, Devauchelle, and Dehaene <sup>16</sup>. From these 80 sentences, we generated the 80 jabberwockys by modifying the content words of the sentences with pseudowords while keeping a similar phonology for each last syllable. We then generated 40 sequences of words and 40 sequences of pseudowords by randomly selecting words and pseudowords from the sentences and jabberwockys. In addition, for each sentence, a comprehension question was created that induced a "yes/no" response.

During the language comprehension task patients were instructed to carefully listen to the auditory stimuli and to answer the question presented at the end of some trials. Typical trial started with a fixation cross during 500ms, followed by an auditory stimulus (a sentence, a jabberwocky, a list of words or a list of pseudowords), and then a grey background (interstimulus interval) for 1500ms. On 25% of sentence trials, following the auditory stimulus, a written verification question was presented on the screen, in order to evaluate if the patients were performing the task correctly. Participants were instructed to give yes or no responses to the comprehension questions using two buttons. The question remained on the screen until the patient responded and was followed by a 500ms inter-stimulus interval. A total of 240 trials were randomly presented and a pause was proposed every 50 trials.

### *Preprocessing sEEG signal*

All preprocesses and data analyses were performed using FieldTrip toolbox <sup>55</sup> and custom scripts on Matlab ® (version 9.7.0, Matlab R2019b). Raw data were transformed into four time-series corresponding

to alpha, beta, low-Gamma and high-Gamma frequency band amplitudes with the following procedure<sup>40,56</sup>: Step 1: continuous sEEG signals were first bandpass-filtered in successive 2, 4 or 10 Hz wide frequency bands from 8Hz to 12Hz, 16Hz to 24Hz, 30Hz to 50Hz or 50Hz to 150Hz (for alpha, beta, low-gamma and high-gamma frequency bands respectively) using a zero-phase forward and reverse filter. Step 2: for each bandpass-filtered signal we computed the envelope using standard Hilbert transform<sup>57</sup>. Step 3: for each band this envelope signal was divided by its means across the entire recording session and multiplied by 100. This procedure yields instantaneous envelope values expressed in percentage (%) of the mean. Step 4: the envelope signals for each consecutive frequency bands were averaged together to provide one single time series (alpha activity, beta activity, low-gamma activity or high-gamma activity) across the entire session. Step 5: The obtained envelopes were epoched into data segments centered around each stimulus and baseline corrected (the baseline corresponded to the 450ms preceding the beginning of audio presentation).

### *Regions of interest (ROI)*

We computed 14 regions of interest (ROI) allowing to reduce between patient implantation variability. ROIs were defined using Harvard-Oxford atlas<sup>58</sup>. The included ROI were: the anterior superior temporal gyrus (Ant STG), the superior posterior temporal gyrus (Post STG), the anterior middle temporal gyrus (Ant MTG), the posterior middle temporal gyrus (Post MTG), the supramarginal gyrus (SMG), the temporal pole, the *pars opercularis* (IFG Oper), the *pars triangularis* (IFG Tri), and *the pars orbitalis* (IFG Orbi). The spatial distribution and the number of cortical sites included in each ROI in relation with the number of patients are shown in Figure 3. See below for the specific computation performed in order to avoid over representation of the activity of one patient who would have more contacts in an ROI

### *Amplitude Analysis*

First, we checked whether all patients performed correctly the task. Average percentage of correct answer to verification questions were well above chance level (M = 83.2%, SD = 15.1%) meaning that patients performed the task correctly. For each trial and in each frequency band, we computed the mean amplitude during the auditory stimuli from 1000ms to 2000ms after the beginning of the presentation. We selected this time windows in order to avoid perception effects after the onset of the audio stream targeting deep stimulus analysis responses. Mean amplitude was then Z-Scored for each channel using the pre-stimulus baseline as reference ([-450ms-0ms]). Z-scores allowed us to average single trials of each channels that were in the same ROI for each patient. This normalization procedure was performed in order to avoid over representation of the activity of one patient who would have more contacts in an ROI. This step was necessary to perform group analysis because patients presented an important variability in implantation anatomical coverage and in number of contact sites per ROI. Consequently, for each ROI, we were able to obtain trial Z-score means for each patient. If one patient presented more than one channel in a specific ROI an average of patient's channels was also computed.

We compared each language (sentences, jabberwockys, word-lists and pseudoword- lists) condition against the baseline condition using a *t*-test. Finally, we evaluated Semantic effects by comparing semantic (i.e., sentences and word-lists) to non-semantic conditions to (i.e., jabberwockys and pseudoword-lists) and Syntactic effects by comparing syntactic conditions (i.e., sentences and jabberwockys) to non-syntactic ones (i.e., word and pseudoword lists) using *t*-tests. The *p* value was corrected for multiple comparisons using Bonferroni procedure: as we had nine ROIs we divided the critical *p* value by nine obtaining  $p = 0.0056$ .

## Abbreviations

P

patient

AiEEG

age at the iEEG acquisition

G

Gender

H

handedness

EZ LAT

epileptic zone lateralization

EZ LOC

epileptic zone location

TEMP

temporal lobe

MULT

multilobe

NCS

number of cortical sites included.

## Declarations

### Contributions

**Conceptualization:** SEBT JRV MPB.

**Design:** SEBT JRV MPB.

**Data acquisition:** SEBT JRV.

**Analysis:** SEBT JRV EC JPL MPB.

**Funding Acquisition:** MPB.

**Project Administration:** MPB.

**Resources:** MPB PK LM.

**Supervision:** MPB.

**Interpretation:** SEBT JRV PK LM MPB

**Validation:** SEBT JRV EC JPL PK LM MPB.

**Writing – Original Draft Preparation:** SEBT JRV EC JPL PK LM MPB.

**Writing – Review & Editing:**

### **Data availability**

The datasets analyzed during the current study are available from the Grenoble Alpes University Hospital Center (CHUGA). Restrictions apply to the availability of these data, which were used under license for this study. Data are available on request with the permission of the CHUGA. To request the data please contact Philippe Kahane by email : [philippe.kahane@univ-grenoble-alpes.fr](mailto:philippe.kahane@univ-grenoble-alpes.fr)

### **Conflict of interest**

MPB. has been funded by the Institut Universitaire de France. Authors declare no potential conflict of interest.

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## Figures

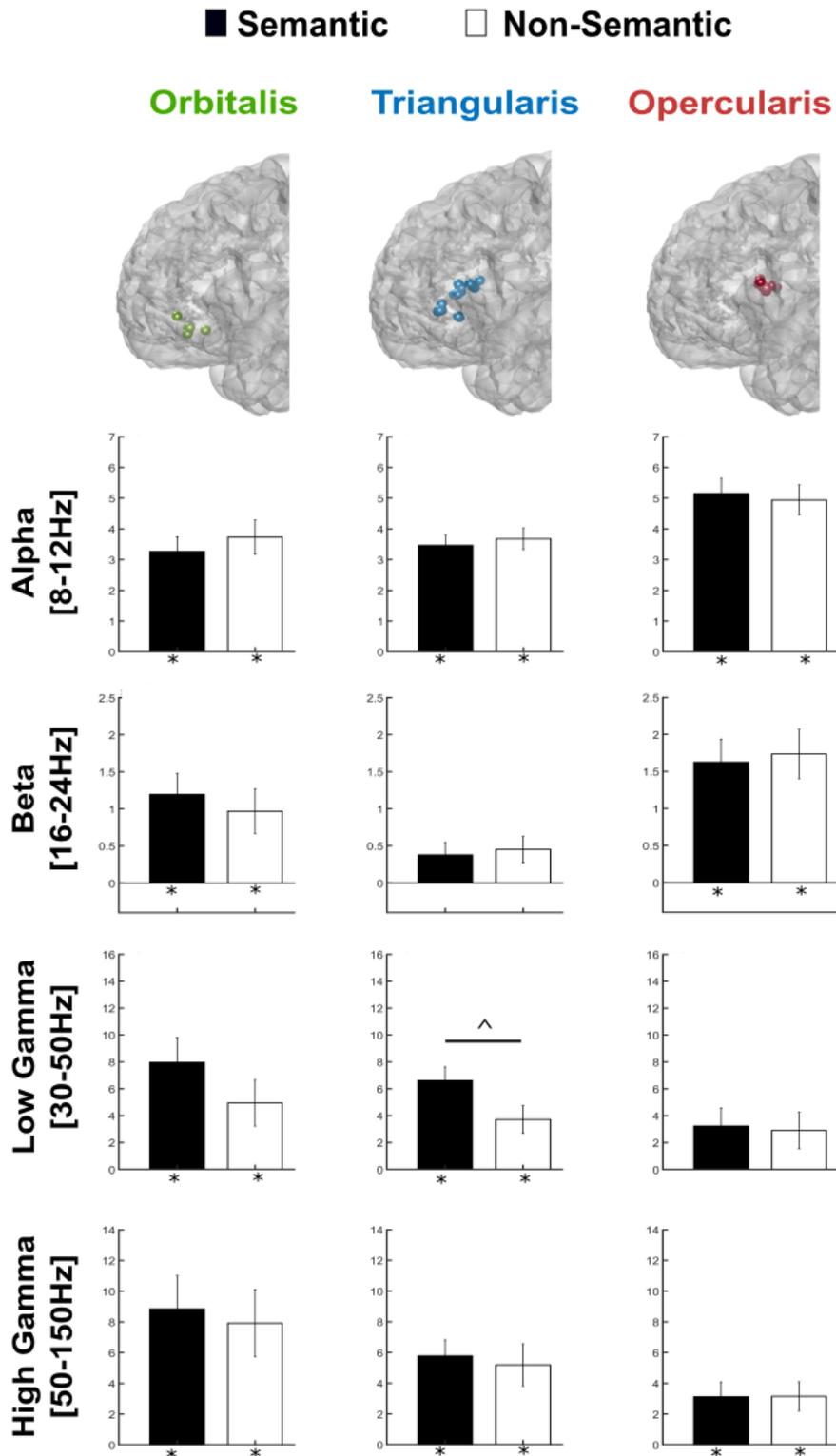


Figure 1

Anatomical coverage for the P1-P11 in the left hemisphere. A total of 1182 cortical sites were included

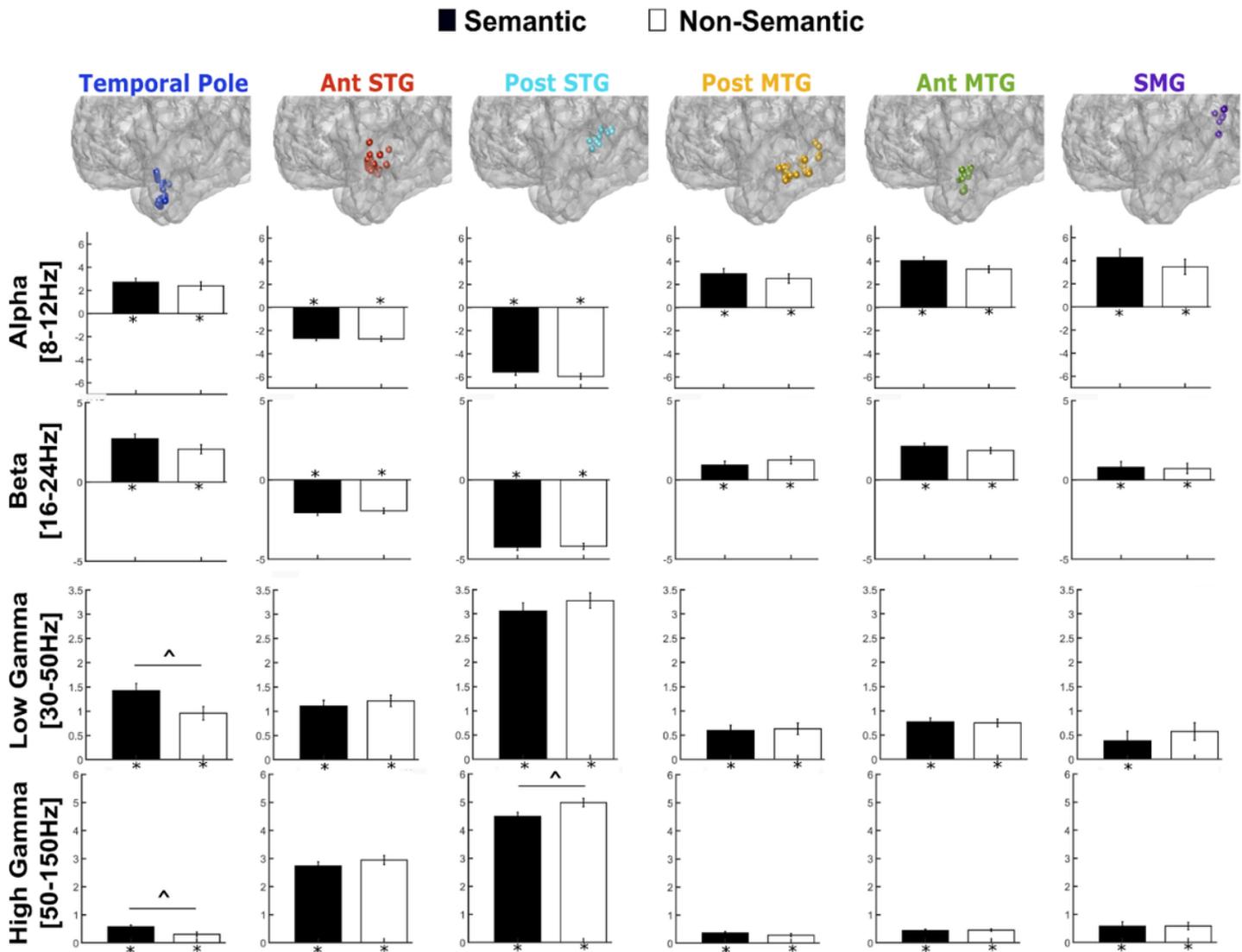
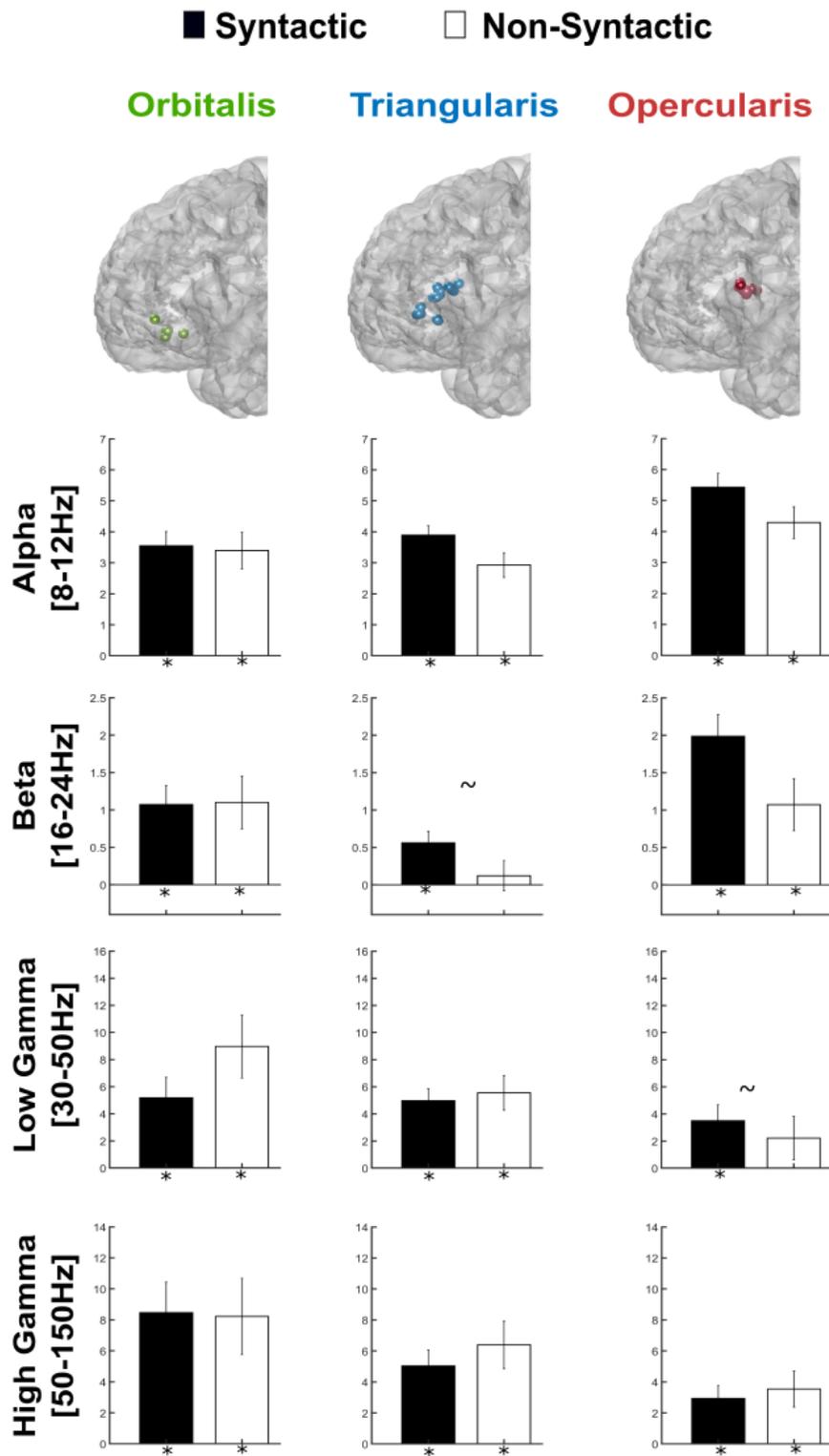


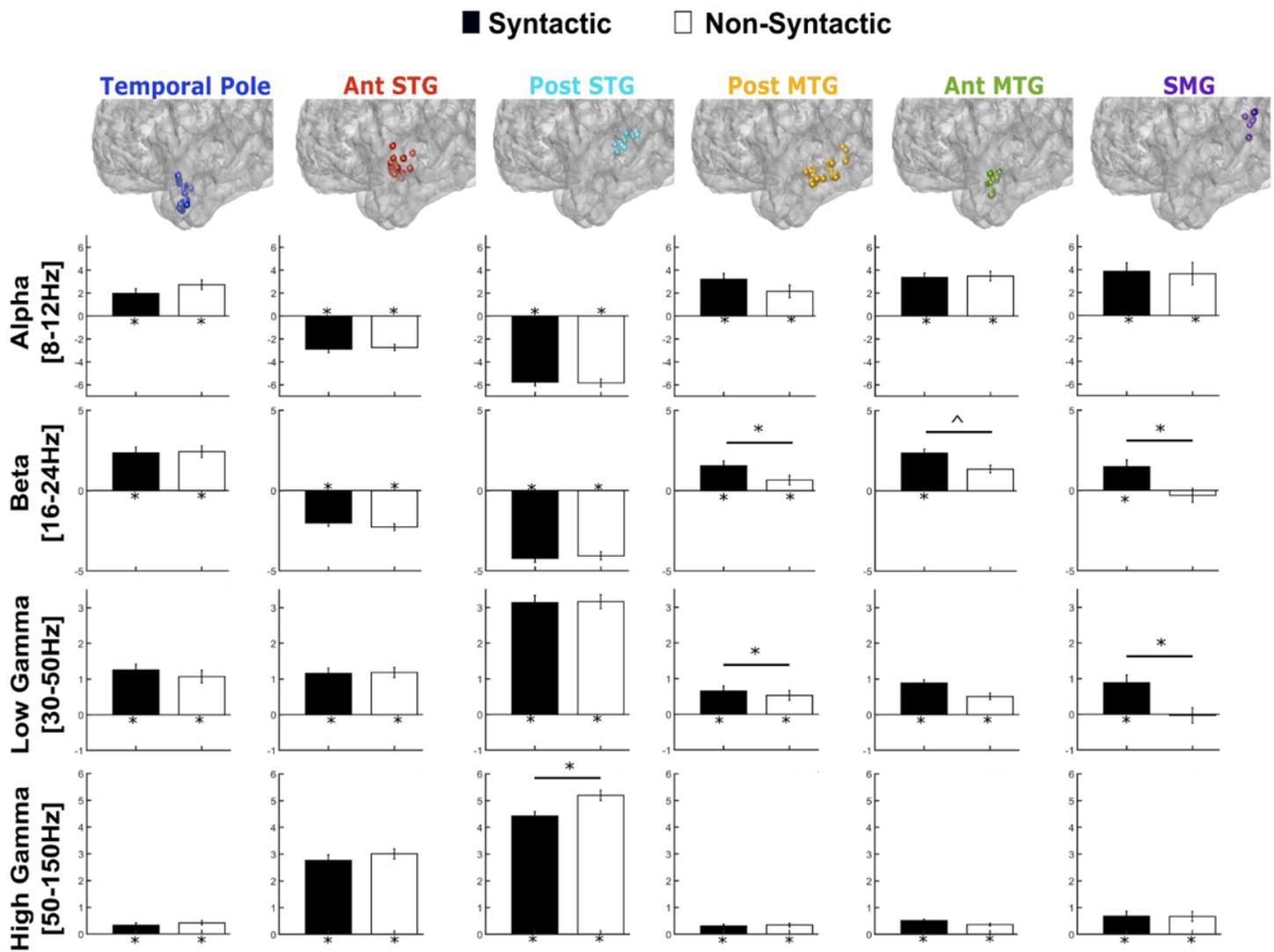
Figure 2

Trial examples for each of the four experimental conditions according to the semantic and syntactic information manipulation (Sentences, Word lists, jabberwocky and pseudoword lists). Items in the present study was adapted from Pallier et al. <sup>16</sup>



**Figure 3**

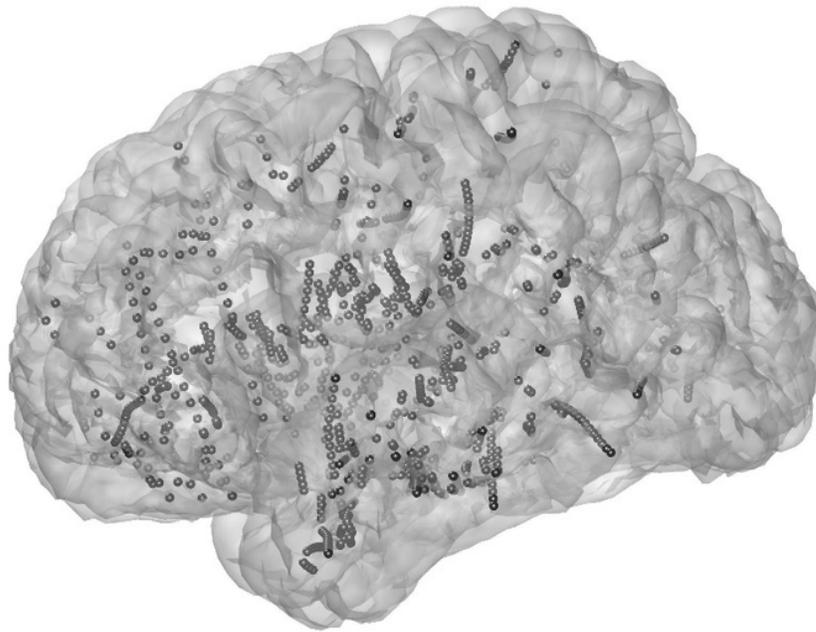
Spatial distribution of each of the region of interest including the specific number of cortical sites (numerator) and the number of patients (denominator).



**Figure 4**

Semantic effect in each of the IFG ROI for each of the frequency band evaluated. Error bars represent the Standard Error from the Mean (SEM)

^ depicts marginally significant differences; \* depicts significant differences between the condition and the baseline



**Figure 5**

Semantic effect in each of the temporo-parietal ROI for each of the frequency band explored. Error bars represent the Standard Error from the Mean (SEM)

^ depicts marginally significant differences; \* depicts significant differences between the condition and the baseline

# Syntactic information

+ → -

Semantic information

+  
↓  
-

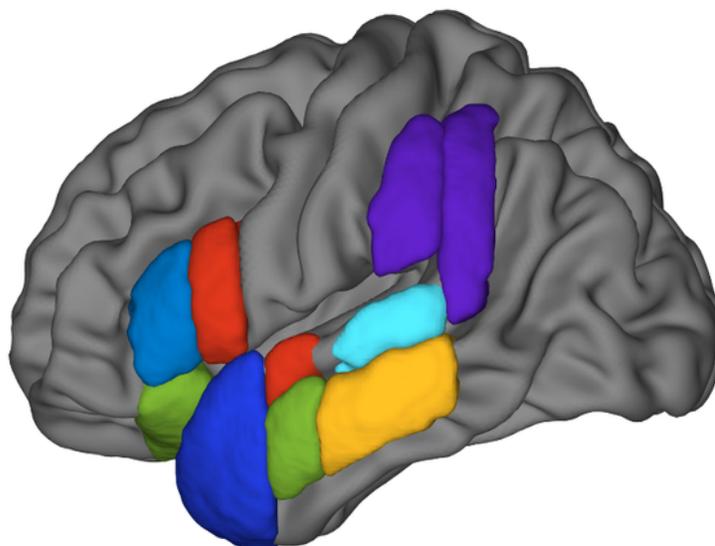
<b>Sentences</b> <i>Le discours que le politicien a préparé était trop long pour la réunion</i>	<b>Word lists</b> <i>Politicien par nouveau long millions tout peur directions matin la trop goût</i>
<b>Jabberwocky</b> <i>Le pescours que le ticilocien a trifaré lajait trop clond pour la batunion</i>	<b>Pseudoword lists</b> <i>tilipiant querluest lonille epilouter pront rupilait manisilet robudi croba da foti lor</i>

Figure 6

Syntactic effect in each of the IFG ROI for each of the frequency band explored. Error bars represent the Standard Error from the Mean (SEM)

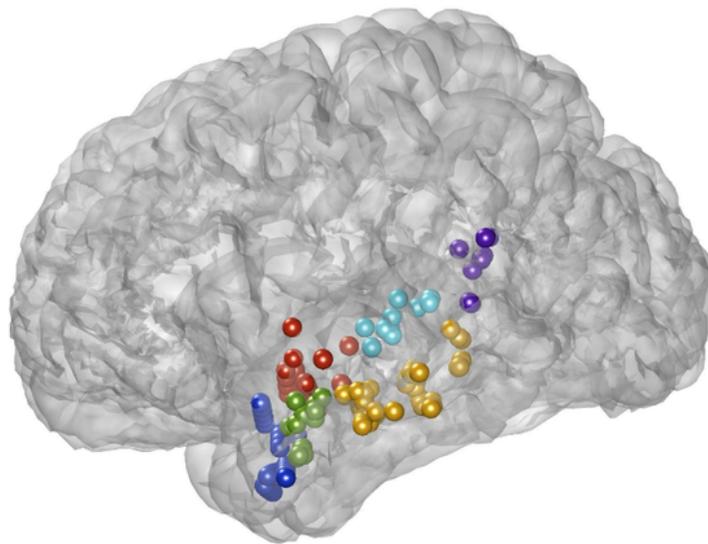
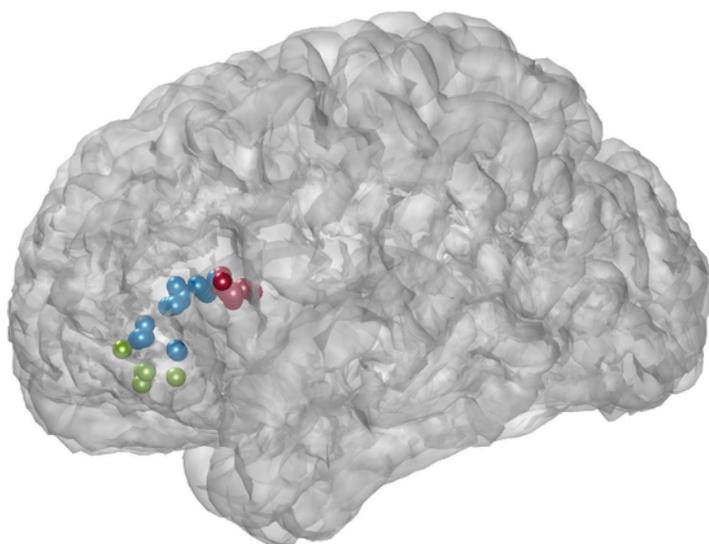
~ depicts patterns in line with the effect of interest; \* depicts significant differences between the condition and the baseline

## REGIONS OF INTEREST (ROIs)



**FRONTAL**

**TEMPORAL**



**IFG Orb** (26/8)  
**IFG Tri** (15/5)  
**IFG Oper** (25/7)

**Temporal Pole** (28/6)  
**Ant STG** (26/8)  
**Ant MTG** (25/7)  
**Post STG** (15/5)  
**Post MTG** (63/9)  
**SMG** (9/3)

**Figure 7**

Syntactic effect in each of the temporo-parietal ROI for each of the frequency band explored

Error bars represent the Standard Error from the Mean (SEM)

^ depicts marginally significant differences; \* depicts significant differences between the condition and the baseline

## Supplementary Files

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- [SupplementaryMaterial.docx](#)