Disentangling meaning in the brain: left temporal involvement in agreement processing

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Abstract

Sentence comprehension is successfully accomplished by means of a form-to-meaning mapping procedure that relies on the extraction of morphosyntactic information from the input and its mapping to higher-level semantic-discourse representations. In this study, we sought to determine whether neuroanatomically distinct brain regions are involved in the processing of different types of information contained in the propositional meaning of a sentence, namely person and number. While person information indexes the role that an individual has in discourse (i.e. the speaker, the addressee or the entity being talked about by speaker and addressee), number indicates its cardinality (i.e. a single entity vs. a multitude of entities). An event-related fMRI experiment was run using agreement-correct and person- and number-violated sentences in Spanish, to disentangle the processing mechanisms and neural substrates associated with the building of discourse and cardinality representations. The contrast between person and number violations showed *qualitative* and *quantitative* differences. A greater response for person compared to number was found in the left middle temporal gyrus (LMTG). However, critically, a posterior-to-anterior functional gradient emerged within this region. While the posterior portion of the LMTG was sensitive to both person and number violations, the anterior portion of this region showed selective response for person violations. These results confirm that the comprehension of the propositional meaning of a sentence results from a composite, feature-sensitive mechanism of form-to-meaning mapping in which the nodes of the language network are differentially involved

Key words: Agreement, meaning, semantics, discourse, left temporal cortex, fMRI

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1. Introduction

A major goal in the study of language comprehension concerns unveiling the mechanisms and the neural substrates that lead to understanding "who does what" in the sentence. Whether lexically- or syntactically-driven, both theoretical and cognitive models agree that the on-line construction of sentence interpretation is reliably accomplished through a *form-to-meaning mapping* mechanism (Chomsky, 1995, 2000, 2005; Mancini et al. 2013; Pollard and Sag, 1994; Wechsler and Zlatić, 2003), which consists of the extraction of relevant morphosyntactic information from the input and its linking to higher-order representations, such as semantics and discourse.

The vast majority of neuro-cognitive studies have investigated sentence comprehension by attempting to dissociate form and meaning and thus testing the sensitivity of cortical areas to either type of analysis. This has usually involved contrasting linguistic phenomena thought to belong to a purely formal dimension – such as subject-verb agreement - with aspects thought to have greater relevance for the building of the overarching meaning of the sentence, such as thematic role assignment. Critically, here we demonstrate that understanding "who does what" in a sentence is not limited to case and thematic role assignment, but comprises other relations, features and roles that differentially engage the fronto-temporal network supporting language processing. To this end, we investigated subject-verb agreement in Spanish with the goal of disentangling the mechanisms and neural substrates underlying the analysis of the two features involved in this, namely person and number.

1.1. Form and meaning in the brain

From a processing perspective, at least three basic mechanisms are needed for form-to-meaning mapping to take place (Molinaro et al. 2011): Firstly, a system responsible for extracting morphosyntax and projecting the underlying syntactic structure information from the input. Secondly, a system that handles the

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integration of the incoming input with previously-encountered elements, based on the evaluation of their morphosyntactic and semantic-discourse fit, to ensure proper building of relations among sentence parts. Thirdly, integration mechanisms presuppose the presence of an amodal unit – a conflict-monitoring system – responsible for the implementation of attentive mechanisms that permit the detection of conflict between the expected and the perceived input (see van den Meerendonk et al. 2009 for a review of conflict-monitoring mechanisms in language processing).

Current neuro-cognitive models agree that sentence processing relies on a left-lateralized fronto-temporal network (Bornkessel-Schleswesky & Schleswesky, 2013; Friederici, 2011, 2013; Hagoort, 2003, 2005, 2013; Lau et al. 2008; Saur et al. 2008) that involves posterior/anterior temporal and inferior frontal regions. However, which mechanisms each node supports is still an open question, since across models substantial differences are found in the localization of linguistic functions.

Retrieval and projection of underlying syntactic structure is described by the Memory, Unification and Control model (MUC, Hagoort, 2003, 2005, 2014) as a lexicalist process in which syntactic frames associated with the input analyzed are retrieved from semantic memory based on lexical information. This mechanism would be supported by the posterior portion of the middle/superior temporal gyrus (pMTG/STG, henceforth), a proposal that directly connects to studies on the role of the same region in the linking of words to their corresponding concepts (Dronkers et al. 2004; Lau et al. 2008). This lexicalist view contrasts with the claim advanced by Pallier et al. (2011), who propose pMTG/STS involvement in hierarchical constituent structure assembly, regardless of lexical information.

There are, however, contrasting views with regard to integration mechanisms . In keeping with its lexicalist account, the MUC model proposes that the integration of syntactic frames relies on unification operations: syntactic frames incrementally retrieved from semantic memory are unified in the so-called Unification Workspace in the left inferior frontal gyrus (LIFG, henceforth). Here, syntactic and semantic

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analyses are functionally and neuro-anatomically dissociated. BA44/45 is thought to support unification at a syntactic level, involving mechanisms such as checking the compatibility of two syntactic frames in terms e.g. of morphosyntactic features.In contrast, BA45/47 would be engaged in semantic unification, i.e. the combination of semantically compatible frames.

Along similar lines, Bornkessel-Schlesewsky & Schlesewsky (2013) propose a lexicalist model that advances a distinction between syntactic and semantic processes that rely on the neuro-anatomical and functional dissociation existing between ventral and dorsal pathways. In their model, unification of syntactic frames is supported dorsally by a pathway that connects the posterior portion of the MTG/STS to frontal areas. In contrast, fiber bundles connecting these two areas ventrally, via the anterior portion of the temporal lobe (ATL), are thought to subserve the analysis of meaning. Importantly for the purpose of the current study, Bornkessel & Schlesewsky posit posterior STG/MTG involvement in the mapping between syntactic and lexico-semantic information, such as the identification of Actor and Undergoer roles. In contrast, the ATL would play a major role in the incremental unification of information concerning different semantic aspects of an event (e.g. the "who", "what", "where" and "when"), irrespective of the part of speech that conveys them. According to the authors, this fits nicely with fMRI data showing ATL involvement in semantic combinatorial mechanisms (Pallier et al. 2011), and connects to a larger literature on semantic memory and conceptual combination that assumes the ATL to be an amodal semantic hub (Baron et al. 2010; Patterson et al. 2007).

A third view, reflected in Friederici (2011, 2013), holds that integration of linguistic input in syntactic structure is subserved ventrally by a pathway that connects the anterior temporal cortex (ATC) to the frontal operculum in the LIFG (see also Grodzinsky & Friederici, 2006). It should be noticed that this model does not provide any neuro-anatomical distinction between syntactic operations dealing with phrase structure building and mechanisms dealing with feature-consistency checking, such as those primarily involved in

agreement processing. In contrast, the pars orbitalis and triangularis are indicated as regions supporting sentence-level semantics (Friederici & Gierhan, 2013). Of relevance for the current study is the localization in the pMTG of interface level processing, as required for the mapping between syntactic and lexical-semantic information in thematic role assignment.

Some of the models reviewed above include conflict-monitoring mechanisms in their architecture, as in the case of the MUC and Bornkessel-Schlesewsky & Schlesewsky (2013) models. The Control function in the MUC model implements monitoring processes, which are supported by the dorso-lateral prefrontal cortex and the anterior cingulate cortex, in line with proposals that link these regions to amodal monitoring operations, such as the detection of conflicting cues to prevent behavioral mistakes (Carter & Van Veen, 2007; Taylor et al., 2007). Similarly, Bornkessel-Schlesewsky & Schlesewsky (2013) argue that the LIFG does not perform any linguistic processing per se and its function is described as that of a point of convergence between the dorsal and the ventral stream, to exert cognitive control and conflict resolution functions in syntactic and semantic analysis (see also Novick et al. 2005; Thompson-Schill et al. 2005).

1.2. Computing different features

Recent experimental studies that have made use of violation paradigms (i.e. contrasting anomalous and correct stimuli) have suggested that the performance of the mechanisms described above can be sensitive to fine-grained properties of the input, lending support to the hypothesis that form-to-meaning mapping is not a monolithic operation, but a composite process through which the information extracted from the input - nouns and verbs for example - is interfaced with different types of higher-level representations (Mancini et al. 2011; Mancini et al. 2014) . Such is the case of the person and number features in subject-verb agreement, the violation of which has been found to yield distinct behavioral

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(Mancini et al. 2014) and electrophysiological responses (Mancini et al. 2011; see Molinaro et al. 2011 for a review of agreement studies).

In particular, the reading of person-anomalous verbs similar to those illustrated in (1) below has been found to yield significantly longer reading times compared to number–mismatching verbs, suggesting that the former type of violation impacts the processing system more severely. A possible explanation of this result is offered by theoretical analyses that describe qualitatively different types of form-to-meaning mapping for person and number interpretation, as a result of the intrinsically different information that the two features convey. While person (1st, 2nd, 3rd) encodes the discourse role played by an individual (speaker, addressee and non-participant), and thus contributes to indicating the perspective from which an event is told, number indexes his/her cardinality (a single entity vs. a multitude of individuals). This inherent difference between person and number has structural and interpretive differences, which amount to the autonomous representation of the two features in the hierarchical syntactic tree (Bianchi, 2006; Shlonsky, 1989) and to different mapping options. Specifically, because of its direct link to discourse, person is posited to occupy a higher node in syntactic structure compared to number (Bianchi, 2006; Mancini et al., 2013; Shlonsky, 1989; Sigurdsson, 2004), making it possible to associate each morphological realization of person (1st, 2nd or 3rd) with a specific participant (speaker, addressee, non-participant) and thus assign a discourse role. In contrast, no such linking to discourse is required for number: the number information extracted from verb is mapped onto the cardinality representation invoked by the subject argument, independently of the discourse role of this argument (see Mancini et al. 2013 and Mancini et al. 2014 for a detailed theoretical explanation of person and number difference in mapping points).

(1) a. *Number Violation*

*El español$_{3.sg}$ celebraron$_{3.pl}$ la victoria de la selección de futbol en las calles.

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The Spaniard$_{3.sg}$ celebrated$_{3.pl}$ the win of the national soccer team in the streets

b. *Person Violation*

*El español$_{3.sg}$ celebraste$_{2.sg}$ la victoria de la selección de futbol en las calles.

The Spaniard$_{3.sg}$ celebrated$_{2.sg}$ the win of the national soccer team in the streets

c. *Correct Agreement*

Los españoles$_{3.pl}$ celebraron$_{3.pl}$ la victoria de la selección de futbol en las calles.

The Spaniards celebrated the win of the national soccer team in the streets

Evidence from an ERP study in Spanish (Mancini et al. 2011) suggests an even more articulated scenario. In their study, Mancini and colleagues reported both similar and qualitatively different electrophysiological patterns for person and number anomalous sentences like the ones illustrated in (1). In both cases, a positive deflection was found about 600 ms post-stimulus onset (P600) with qualitative differences between the two types of anomalies emerging in early components. While person violations gave rise to N400 effects, number agreement anomalies elicited a LAN effect. Importantly, the authors pointed out that the negative effect elicited by person anomalies could be the result of a superimposition of LAN and N400 effects, as suggested by the failure to find a difference between the two violations in frontal scalp areas in the 300-500 ms window, and by the similar latency and onset of the two topographically different negativities. As suggested by the authors, this pattern of data can be taken to indicate that person and number agreement do differ, but also have something in common. Particularly, the two types of agreement could share similar feature-checking mechanisms, of which the similar left-anterior negative effect could be evidence. What differentiates person from number would be the distinct mapping options (cardinality and discourse) that the interpretation of the two features requires, which would be behind the different posterior negative effect elicited by the two violations.

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The findings and theoretical analyses described above invoke a more precise characterization of the basic mechanisms underlying form-to-meaning mapping, and point to a language processing system that i) functionally dissociates checking and mapping during integration processes; and ii) employs feature-based mapping procedures to assign an interpretation to an agreement dependency (see Bianchi, 2006; Sigurdsson, 2008). In this respect, Mancini and colleagues (Mancini et al. 2013) have proposed that feature-checking and feature-mapping mechanisms are dealt with by two different mechanisms that separately target person and number. A mechanism operating at a morphosyntactic level (*φ-value checking)* controls person and number consistency between subject and verb. More specifically, φ-value checking ensures that the morphosyntactic values of person and number are consistent across subject and verb, e.g. that both elements carry a 3rd person or a singular number value. Evaluation of morphosyntactic fit is accompanied by evaluation of semantic-discourse fit: this relies on a mapping mechanism that links person and number φ-values to higher levels of analysis where the discourse roles and cardinality representations (σ-values) underlying subject and verb are encoded. Successful checking and mapping mechanisms lead to integration of incoming input with previously encountered elements, and therefore to the interpretation of the overall agreement dependency.

A testing ground for the hypothesis outlined above is to investigate whether person and number agreement recruit different and/or overlapping neural regions as a result of the similar checking and different mapping mechanisms they undergo during processing. To test this goal, in the current experiment person and number processing are contrasted in an event-related fMRI study.

2. The current study

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Feature-specific mechanisms are not considered in current sentence processing models, despite the relevance of such mechanisms for an in-depth functional characterization of the language network. In this study, we seek to fill this gap by uncovering the neuro-anatomical substrates involved in the construction of agreement dependencies and their interpretation, capitalizing on the distinction between person and number interpretation. To this end, we will examine agreement between subject and verb by creating person and number anomalies as in (1) above, a paradigm that has proved to be effective in highlighting behavioral and electrophysiological differences in the elaboration of different aspects of sentence interpretation (Mancini et al. 2014; Mancini et al. 2011).

By contrasting Correct Agreement with both Person and Number violations (Correct Agreement > Agreement Violations), we aim to isolate the neural network involved in the building and interpretation of correct agreement dependencies. We assume that the system attempts to assign an interpretation both to a congruent and to an incongruent sentence, and that it will extract morphosyntactic information for checking and mapping purposes in both cases, although only in one case (Correct Agreement) will these operations be smoothly carried out. If this is on the right track, we expect agreement violations to show partially common patterns with Correct Agreement in areas engaged in the building and interpretation of agreement dependencies. Previous work (Kuperberg et al. 2003, 2008; Quiñones et al. 2014) points to cortical areas that are part of the language network, such as the LIFG and the MTG, as primarily involved in the comprehension of congruent sentences. Within this network, the finding of differential responses for Person and Number Violations (Person Violation > Number Violation) would provide evidence for feature-specific mechanisms in the building and interpretation of a sentential relation, in line with theoretical analyses (Bianchi, 2006; Mancini et al. 2013; Sigurdsson, 2004, 2008). Based on this, one could expect to find a dissociation i) in areas that are thought to support the extraction of morphosyntactic information to build syntactic structure (Hagoort, 2005; Pallier et al. 2011); ii) in areas supporting the mapping between

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morphosyntactic and semantic-discourse information, to derive the overall interpretation of a sentence. In the former case, we expect a difference between person and number to emerge in *quantitative* terms, because of the higher position in syntactic structure that person occupies compared to number. Specifically, access to information encoded in a higher syntactic node could generate greater cognitive cost and so greater activation in the posterior portion of the MTG/STS (Hagoort, 2005; Lau et al. 2008; Pallier et. al. 2011). As for mapping mechanisms, a *qualitative* difference could arise between person and number. While determining the perspective from which the event is told strongly contributes to building the propositional meaning of the sentence, establishing whether there are one or more entities taking part in an event does this to a significantly lesser extent. Hence, a larger response for person compared to number anomalies could be expected in areas involved in the elaboration of the propositional meaning of the sentence, such as the aMTG/STG (Bornkessel-Schlesewsky and Schlesewsky, 2013; Lau et al. 2008, 2013) and the pars triangularis/orbitalis of the IFG (Friederici, 2011).

The contrast between the two violations and the correct sentences (Agreement Violations > Correct Agreement) will permit the identification of the neural substrates involved in the checking of feature consistency between subject and verb. Based on the ERP results reported by Mancini et al. (2011), the reading of anomalous subject-verb relations (regardless of the feature manipulated) could engage areas associated with the detection of morphosyntactic mismatches. Quiñones et al. (2014) suggested the left frontal gyrus as a potential candidate for the so-called φ-checking operations (Mancini et al. 2013). If person and number agreement share similar feature-checking mechanisms, the superimposition of the Person Violations > Correct Agreement and the Number Violation > Correct Agreement contrasts should evidence common response patterns in middle frontal areas.

We assume that domain-general processes that involve conflict-monitoring, attention and working memory systems are constantly engaged in the processing of both correct and incorrect agreement

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dependencies, but that their degree of involvement should be more sizeable in incorrect compared to correct stimuli. We therefore expect recruitment of conflict-monitoring areas, including the dorso-lateral pre-frontal cortex and the anterior cingulate cortex bilaterally, to emerge from the comparison between the two violations and correct agreement (Agreement Violation > Correct Agreement contrast). Previous work on the processing of agreement and other morphosyntactic dependencies has consistently demonstrated the involvement of this network as a result of a (task-driven) mismatch detection process (see Van de Meerendonk et al. 2009 for a review; Kuperberg et al. 2008; Nieuwland et al. 2012; Quiñones et al. 2014).

3. Materials and Methods

3.1. Participants

A total of 21 healthy volunteers (9 females), with ages ranging from 17 to 35 years (mean = 22.62, standard deviation = 4.43), gave written informed consent to participate in this study. Selection criteria required all participants to have normal or corrected to normal vision, no psychiatric or neurological records and to be native speaker of Spanish. According to an abbreviated Spanish version of the Edinburgh Handedness Inventory (Oldfield, 1971) all were right-handed. This study was approved by the Ethics and Research Committees of Basque Center on Cognition, Brain and Language.

3.2. Experimental Materials

The experimental material consisted of 120 sentences divided into three experimental conditions (in the proportion of 1:1:1), as illustrated in 3 above. All sentences contained a 3rd person subject followed by a past tense verb (the critical word), which was always followed by at least two words. The *Correct Agreement* condition presented a plural subject (*los españoles*) followed by a 3rd person plural verb (*celebraron,*), while the *Number Violation* and the *Person Violation* conditions both contained a singular

subject (*el español*) followed by a 3rd person plural (*celebraron*) and 2nd person singular verb (*celebraste*), respectively. The use of subjects specified for different number features in correct and incorrect stimuli was due to two factors. Firstly, the grammar of Spanish allows 3rd person plural subjects to be followed by both 1st and 2nd person plural verbs (the so-called "unagreement" pattern, see Mancini et al. 2011 and Quiñones et al. 2014), which makes it impossible to create person agreement violations with plural subjects. Secondly, the use of singular subjects for person and number violations allowed us to keep the length of the critical word equivalent across conditions [*Correct Agreement and Number Violation*: mean length = 9.66, SD = 2.5; *Person Violation*: mean = 9.38, SD = 2.34; planned statistical comparisons showed no differences across conditions]. Critical words were also balanced for (logarithmic) frequency (EsPAL, Duchon et al. 2013) [3rd person plural (Correct Agreement, Number Violation): mean frequency = 0.44, SD= 0.39; 2nd person plural (Person Violation): mean frequency=0.42, SD=0,46; planned statistical comparison showed no differences between the two types of verbs). In order to maintain the same number of correct and incorrect sentences and to avoid expectations concerning the morphological form of the verb, experimental sentences were intermixed with 120 filler sentences containing 3rd person plural subjects followed by 1st person plural (e.g. *españoles celebramos*", we Spaniards celebrated), as well as with stimuli containing 3rd person plural subjects followed by singular verbs (e.g. "**los españoles celebró*", the Spaniards$_{3.pl}$ celebrated$_{3.sg}$,) and 3rd person singular subjects followed by 3rd person singular verbs verbs (e.g. "*el español$_{3.sg}$ *celebró*", the Spaniard celebrated$_{3.sg}$). The experimental material was randomly assigned to three different lists according to a Latin Square design, so that each subject saw only one version of the same sentence.

3.3. Procedure

Sentences were visually presented word by word. Words were displayed in white letters on a dark background. Each word was presented for 300 ms, followed by a 500 ms blank screen. A fixation point ("+") was presented between successive sentences with jittered durations (1.87, 3.56, 4.96 seconds, with a 57:28:15 proportion, see Dale, 1999). Sentence order was randomized and, after each sentence, participants were asked to evaluate its acceptability by pressing the relative YES/NO button on a response pad.

3.4. Image acquisition

Experiment was performed on a 3-T Siemens TrioTrim scanner, using a standard thirty two-channel phased-array surface coil (Siemens, Erlangen, Germany), which provided high spatial resolution and signal-to-noise ratio. Two functional event-related scans consisting of 625 echoplanar images were acquired using a T2*-weighted gradient-echo pulse sequence with the following parameters: field of view (FOV) = 192 x 192 mm; matrix = 64 x 64; echo time (TE) = 30 ms; repetition time (TR) = 2.0 s with no time gap; flip angle = 78°. The volume was comprised of 32 axial slices with 3 mm thick and 3 x 3.75 mm of in-plane resolution. The first six volumes of each run were discarded to ensure the steady state tissue magnetization.

In the structural session, a MPRAGE T1-weighted structural image (1 x 1 x 1 mm resolution) was acquired with the following parameters: TE = 2.97 ms, TR = 2530 ms, flip angle = 7° and FOV = 256 x 256 x 160 mm^3. This yielded 176 contiguous 1 mm thick slices.

3.5. Functional data analysis

Data processing and statistical analysis were performed using the Statistical Parametric Mapping SPM8 software package and related toolboxes (http://www.fil.ion.ucl.ac.uk/spm). Outlier functional scans

and slices were repaired with the Artifact Repair Toolbox, (Gabrieli Cognitive NeuroScience Lab; http://cibsr.stanford.edu/tools/ArtRepair/ArtRepair.htm), after which the images were slice-time corrected taking the middle slice as reference, spatially realigned, unwarped, coregistered with the anatomical T1 (Collignon et al., 1995), normalized to the MNI space using the unified normalization segmentation procedure and smoothed using an isotropic 8mm Gaussian kernel. Resulting time series from each voxel were high-pass filtered (128 s cut-off period).

The pre-processed functional volumes per participant were then submitted to a within-subject mixed-effect model, which included for each stimulus type a regressor obtained by convolving the canonical hemodynamic response function with delta functions at stimulus onsets. These models also comprised the six motion-correction parameters as regressors. Parameters of the univariate general linear model were estimated with a robust regression using weighted-least-squares that also corrected for temporal autocorrelation in the data (Diedrichsen and Shadmehr, 2005).

A pair-wise contrast comparing activity for each condition (Person Violations, Number Agreement Violations and Correct Agreement) relative to the fixation baseline was performed. Resulting contrast images were then entered into a second level Repeated Measures One Way ANOVA design to enable population inferences. Population-level inferences were tested using a threshold of $p < 0.001$ uncorrected with a voxel extent higher than 100 such that only those peaks or clusters with a p-value corrected for multiple comparisons with family-wise error (FWE; Nichols and Hayasaka, 2003) and/or false discovery rate (FDR; Genovese et al. 2002) were consider as significant. All local maxima were reported in the results tables as MNI coordinates (Evans et al., 1993).

4. Results

4.1. Behavioural results

Percentage of correct response (Hits) for *Correct Agreement*, *Number Violation* and *Person Violation* are presented in Table I, with the corresponding standard error between parentheses. One way ANOVA with the accuracy of the three conditions (*Correct Agreement*, *Number Violation* and *Person Violation*) as factor was performed. For all experimental conditions percentage of correct responses was above 90% and the ANOVA showed no significant difference among the three conditions ($F_{(1, 20)} = 0.14$, $p = 0.98$, $\varepsilon = 0.83$), indicating that the participants correctly judged the sentences as acceptable or not.

[Insert Table I about here]

4.2. fMRI data

To characterize the functional neuro-anatomical network that was recruited by the processing of sentences independently of the experimental manipulation, we compared all sentences with the fixation point condition. The statistical parametric map resulting from this contrast was displayed on the surface of the MNI single-subject T1 image. All sentences minus fixation revealed significant activation of a widespread fronto-parieto-temporal network, bilaterally distributed but with a strong left lateralization (see Table II and Figure 1). This network includes brain regions such as the left pars opercularis and triangularis within the inferior frontal gyrus, the anterior and posterior part of the left middle temporal cortex and the left superior temporal pole, as well as the left and right fusiform gyrus, the left and right inferior and middle occipital cortex, parietal regions, the supplementary motor area and the precentral and postcentral cortex in both hemispheres (for a detailed list of the regions activated in this contrast, see Table II).

[Insert here Table II and Figure 1]

4.3. Correct Agreement versus Agreement Violations

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To highlight the neural regions involved in the analysis of subject-verb agreement dependencies, the Correct Agreement > Agreement Violations (Person Violation + Number Violation) contrast was carried out. The resulting statistic parametric map included regions with higher responses for grammatically correct sentences than for ungrammatical constructions, revealing a significant increase of activation in left temporal and frontal regions. The frontal activation patch comprised two inferior frontal regions (pars triangularis and pars orbitalis) and the precentral cortex, while temporal areas included the anterior and posterior part of the left middle temporal gyrus (see Table III and Figure 2).[1]

[Insert Table III and Figure 2 about here]

4.4. Agreement Violations vs. Correct Agreement

A significant increase of activation for the Incorrect Agreement relative to the *Correct Agreement* condition was observed in the middle frontal gyrus, the middle cingulate cortex and the precuneus. All these neural regions showed a similar activation pattern in both cerebral hemispheres. In addition, we found a significant increase of activation in the supramarginal, the inferior parietal and the middle temporal gyrus exclusively in the right hemisphere (see Table IV and Figure 2).

When contrasting each type of anomalous sentence (*Person Violation* and *Number Agreement Violation*) with the *Correct Agreement* sentences a similar fronto-parieto-temporal network was found for both contrasts (see Table IV and Figure 3). In particular, the superimposition of the significant neural

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[1] It could possibly be argued that any difference in activation patterns observed for the three conditions may be the result of semantic differences between singular and plural verbs (see Wagers et al. 2009, Journal of Memory and Language). As pointed out in the Methods section, the rationale behind the use of singular verbs for person anomalies and plural verbs for correct and number violation sentence was mainly methodological. To test for possible differences, responses elicited by singular and plural verbs were compared within each condition (i.e. singular vs. plural verbs for correct agreement, person mismatch and number mismatch). No significant differences emerged.

activations of these contrasts (*Person Violation > Correct Agreement* and *Number Violation >Correct Agreement*) demonstrated that the activation of the right and left middle frontal gyrus, the right and left inferior parietal region, the right and left middle cingulate cortex, the right and left precuneus, the right supramarginal and the right middle temporal gyrus are common to both types of violations. Figure 3 shows this comparison, where the common response for both contrasts is represented in yellow, the specific *Person Violation* response is represented in red and the *Number Violation* response is represented in green. Note that the response patterns of these regions with respect to the fixation are different: While the left anterior cingulate cortex, the right middle temporal and the right middle frontal gyrus exhibited negative response (de-activation) compared to the fixation baseline condition, with greater de-activation for matching than mismatching constructions, the rest of the regions exhibited positive response with respect to the fixation, with higher amplitude for anomalous sentences (see the bar graph in the left side of the Figure 3B).

[Insert Table IV and Figure 3 about here]

4.5. Person versus Number Agreement

Person Violation relative to Number Violation sentences evoked significant ($p<0.001$ corrected for multiple comparisons) increases of activation in the anterior and posterior part of the left middle temporal gyrus (see Table V and Figure 4). However, as can be observed in Figure 4, the response pattern of these two regions with respect to the baseline differs: While the anterior part of the middle temporal gyrus is sensitive only to Person Violation, the posterior portion is sensitive to both Person Violation and Number Violation, although with higher amplitude for Person Violation. In addition, this contrast also revealed significant ($p<0.001$ uncorrected) responses in the pars triangularis and orbitalis within the left IFG, with

neural responses being more conspicuous for Person than for Number Violations (see Table V and Figure 4).

[Insert Table V and Figure 4 about here]

5. Discussion

The goal of the current study was to test whether person and number agreement engage different and/or overlapping neural regions, as a result of the similar checking but different mapping operations that we hypothesized. As comprehension mechanisms can be best highlighted when the system is forced to deal with mistakes (Mancini et al. 2011; Wagers et al. 2009), we manipulated subject-verb agreement relations so that the establishment of discourse roles and cardinality representations could be disrupted, by creating person and number agreement violations.

The comparison between correct and incorrect agreement dependencies provided the possibility of disentangling the neural substrates associated with the building and interpretation of congruent relations from those associated with the analysis of ungrammatical agreement. Specifically, the comprehension of Correct Agreement sentences (Correct Agreement > Agreement Violations contrast) recruited a network that included the aMTG, the pMTG and the LIFG, while sensitivity to Incorrect Agreement (Agreement Violations > Correct Agreement) emerged in a widespread bilateral fronto-parietal network.

The direct contrast between Person and Number Violations permitted the uncovering of both quantitative and qualitative differences which can be associated with finer-grained mechanisms of agreement interpretation. In particular, a clear quantitative dissociation between Person and Number Violations emerged in the pMTG, while activation patterns in the aMTG, as well as in the pars orbitalis and

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triangularis of the LIFG (although with a less strict threshold, see Figure 4), point to a qualitative difference between the two features.

Closer inspection reveals that the regions where the Person-Number dissociation is found belong to the fronto-temporal network recruited by the comprehension of Correct Agreement, suggesting that these areas, arguably involved in the building and interpretation of sentential relations, operate in a feature-specific fashion. In contrast, the failure to find a dissociation between Person and Number Violations in areas sensitive to the processing of Incorrect Agreement, such as middle frontal and parietal regions, together with the common responses evidenced by the contrast between the two violations and Correct Agreement (Person/Number Violation > Correct Agreement), seem to imply that consistency checking and conflict monitoring mechanisms operate in a feature-insensitive manner.

Critically, this pattern of results enables us to associate the main components of sentence processing – structure building, checking and mapping - to specific neuro-anatomical regions, and to outline a more precise map of linguistic functions in the brain, as discussed below in detail.

5.1. Structure building: the role of the pMTG

A significant involvement of the pMTG was found for the Correct Agreement > Agreement Violation contrast, suggesting the sensitivity of this area to well-formed agreement configurations. However, pMTG involvement was not limited to correct-agreement sentences: when contrasting the two incorrect conditions (Person > Number Violation contrast), Person Violations were found to generate a greater response in this area than Number violations, suggesting differential sensitivity to the type of information manipulated in verbal morphology. As reviewed above, functional interpretations about the involvement of the pMTG in language processing range from proposals advancing its role in the extraction of morpholological information for building syntactic structure (Pallier et al. 2011) or in the retrieval of syntactic frames from

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semantic memory (Hagoort, 2005), to views emphasizing the centrality of this region in mechanisms at the syntax-semantics interface, such as the analysis of verb-argument relations (Bornkessel-Schleswesky and Schleswesky, 2013; Bornkessel et al. 2005; Friederici, 2011). The current set of data allows us to distinguish between the two proposals.

While the activation for correct verbs found in the pMTG could be equally accounted for by proposals that claim a role for this region in lexical retrieval processes, (Hagoort, 2005, 2013), as well as positions that argue for pMTG involvement in the analysis of verb-argument relations (Bornkessel-Schleswsky and Schlesewsky, 2013; Friederici, 2011, 2012), the same cannot be said for the differential activation profile evidenced by the Person > Number contrast. The verb-argument relation hypothesis would predict activation for person, but not for number agreement anomalies in the pMTG: while the interpretation of person agreement implies the mapping of morphosyntactic information onto specific roles (i.e. discourse roles), no role assignment is involved for the interpretation of number agreement. In other words, the activation patterns that emerge from the comparison between the two violations disconfirm the verb-argument hypothesis.

A better framework for the discussion of these data is therefore provided by studies and models that assume pMTG involvement in the extraction of information from the input to build syntactic structure (Hagoort, 2005; Hickock and Poeppel, 2007; Lau et al. 2008; Molinaro et al. 2015; Pallier et al. 2011). In this respect, the quantitative dissociation found between person and number would result from their different underlying structural representations (Bianchi, 2006; S. Mancini, Molinaro, Rizzi, & Carreiras, 2011; Sigurdsson, 2008). While the extraction of person information from verbal morphology implies accessing information contained in high nodes of syntactic structure that are linked to the syntax-discourse interface, the extraction of number information does not, leading to differential processing costs.

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The information extracted from the input in the pMTG could be made available to further regions in the network, through ventral and dorsal connections to anterior portions of the temporal cortex and left frontal areas (Bornkessel-Schlesewsky and Schlesewsky, 2013; Dronkers et al. 2004; Hagoort, 2013; Molinaro et al. 2015; Papoutsi et al. 2011; Saur et al. 2008; Wilson et al. 2012), where subsequent analysis steps could be carried out, as described below.

5.2. Assignment of interpretively relevant roles: the role of the aMTG

In line with our predictions, the comparison between Correct and Incorrect Agreement revealed the activation of a large portion of the aMTG for agreeing verbs. Moreover, the comparison between Person and Number violations revealed a remarkable asymmetry between the two features, with the former producing a significant increase of activation in this area, but not the latter. As reviewed above, activity in this region has been associated with the building of local syntactic structure, thanks to the ventral pathway connecting the anterior portion of the temporal cortex and the frontal operculum (Friederici, 2011; Friederici & Gierhan, 2013). Another interpretation attributes a critical role to the aMTG in the integration of different types of information to derive the propositional meaning of a sentence (Bornkessel-Schlesewsky and Schlesewsky, 2013), a claim that connects with a larger literature on the role of this region in semantic memory and conceptual combination (cf. Baron et al. 2010; Molinaro et al. 2015; Patterson et al., 2007). Crucially, the current set of data allows us to distinguish between these two proposals. Clearly, the finding of different patterns of activation for Correct Agreement and Agreement Violation sentences in this region does not argue in favor of the local syntactic structure-building hypothesis: in this case one would have expected the three contrasts to give rise to equivalent responses in this area, since the three types of sentence are characterized by the same local syntactic structure (regardless of morphosyntactic consistency). On the contrary, the increased aMTG activation that we report for the Correct vs. Incorrect

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contrast is in line with data on agreement processing by Quiñones et al. (2014), who have reported aMTG involvement in the processing of both standard agreement and unagreement sentences, and more in general with claims advancing the role of this region in the elaboration of higher-level information (Bornkessel-Schlesewsky and Schlesewsky, 2013; Lau et al. 2008; Molinaro et al. 2015; Pallier et al. 2011). Under this assumption, the finding of a significant response in this area for person, but not for number anomalies, gives us an important insight into the type of mechanism supported by this area. Specifically, our data point to a critical role of aMTG in the assignment of interpretively relevant roles, which, in our case, correspond to discourse roles. While identifying and assigning a discourse role to the subject argument is crucial for the derivation of the overarching meaning of the sentence, the identification of whether this argument refers to a single entity or a multitude of entities is not, hence the qualitatively different response for the two violations. Critically, such an interpretation meshes well with results obtained in the ERP study by Mancini et al. (2011), who reported an N400 effect for Person Violations relative to Correct Agreement sentences. Indeed, it is possible that the anterior portion of the left temporal lobe is involved in the generation of this negative component (cf. Lau et al. 2008; 2013), although further investigation is certainly needed to validate this hypothesis.

5.3. A note on bilateral temporal activations: sentence- and message-level analysis

Worthy of note is the bilateral activation of middle temporal areas that we found for both types of anomalies (see Figure 2). It is known that right-hemisphere involvement in linguistic tasks mostly consists of co-activations with left-hemisphere homotopic areas (see Vigneau et al. 2006; Vigneau et al. 2011 for meta-analyses of left- and right-hemisphere involvement in linguistic tasks). However, in their meta-analysis, Vigneau and colleagues (2011) highlight that sentence processing is the only component in which unilateral clusters were identified in the right temporal lobe. In particular, involvement of right middle

temporal areas has been linked with inferential mechanisms necessary to achieve global coherence in discourse processing and to elaborate a message-level representation concerning the overall topic of the text being analyzed (Ferstl et al. 2007; St. George et al. 1999, among others). In the context of the current study, the bilateral activation of middle temporal areas in the analysis of person and number anomalies could be explained by assuming a distinction between sentence- and message-level interpretation mechanisms, as well as a division of labor between left and right middle temporal areas. On the one hand, sentence-level analysis, aimed at anchoring morphosyntactic and semantic-discourse information, could be supported by left middle temporal areas, with a posterior-to-anterior gradient that may reflect the graded interpretive relevance of the features being analyzed. On the other hand, analysis of global message coherence could be supported by right middle temporal areas, with person and number equally contributing to this. Further research is, however, necessary to corroborate this hypothesis.

5.4. Evaluation of subject-verb morphosyntactic fit: interplay between domain-general and domain-specific processes in frontal areas.

In frontal areas, the analysis of Correct Agreement (vs. Agreement Violations) and Agreement Violations (relative to their correct counterpart) revealed an interesting clear-cut dissociation between regions selectively involved in the analysis of congruent sentences, as opposed to regions sensitive to the presence of agreement inconsistencies. Current neuro-cognitive models advance contrasting hypotheses on the role played by frontal areas in sentence comprehension, ranging from domain-specific to domain-general functions (Bornkessel-Schlesewsky and Schlesewsky, 2013; Friederici, 2011; Friederici & Gierhan, 2013; Grodzinsky and Friederici, 2006; Hagoort, 2005, 2013; Lau et al. 2008; Novick et al. 2005; Thompson-Schill et al. 2005).

A significant response for Correct Agreement sentences (relative to Incorrect ones) was present in LIFG, including the pars triangularis and orbitalis (see Figure. 2), in line with results from previous agreement processing studies in Spanish (Quiñones et al. 2014) that report a significant response of this area to grammatical agreement.

Importantly, a clearer understanding of the sentence-level processes supported by these two regions can be gained from the comparison between Person and Number violations. Although with a less strict threshold, the two anomalies differ in the pars orbitalis and triangularis of the LIFG, where Person Violations gave rise to a greater response compared to Number Violations, thus mirroring the activation profile found in the aMTG. It is possible that activity in the pars triangularis-orbitalis of the LIFG thus reflects a constant and incremental evaluation of the semantic-discourse fit of the elements being processed, that is, the matching between subject and verb in terms of σ-values, to evaluate whether the two elements can be integrated in a meaningful conceptual representation. Such a response profile is compatible with views proposing that more anterior regions of the LIFG are involved in the analysis of meaning at the sentence level (Friederici, 2011, 2013; Hagoort, 2005 and Vigneau et al., 2006 for an extensive review). In this respect, the greater response that we find for Person could be attributed to the greater relevance for propositional meaning that this feature has, because of the interpretively relevant roles that it assigns. Crucially, this interpretation suggests the existence of a tight functional connection between the aMTG and the inferior frontal gyrus, which appears to be corroborated neuro-anatomically by the presence of a ventral pathway connecting anterior temporal to inferior frontal regions (see Friederici, 2011). Critically, a recent study (Molinaro et al. 2015) has demonstrated the presence of a significant coupling between anterior temporal regions and the IFG during semantic processing.

A different scenario is found in the middle frontal gyrus, which was found to respond more to incorrect agreement stimuli (regardless of the feature manipulated). These data appear in line with those

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reported by Quiñones et al. (2014) - who showed middle frontal gyrus engagement in the processing of (grammatical and ungrammatical) person mismatches - and more in general with studies manipulating the morphosyntactic fit between sentence parts [e.g. gender mismatch between pronouns and antecedents in Dutch (Folia et al. 2009); finiteness violations in English (Kuperberg et al. 2003, 2008) and verb-object violations in Basque (Nieuwland et al. 2012)]. A number of studies point to a critical role of the middle frontal gyrus in domain-general verbal working memory mechanisms (see Katsuki and Constantinidis, 2012 and Rogalsky and Hickock, 2011 for reviews). In the context of the current experiment, the middle frontal gyrus could support working memory mechanisms aimed at comparing incoming verbal information with previously analyzed information, such as the one contained in the subject argument (see Quiñones et al. 2014 for a similar argument). Importantly, these memory mechanisms could be tightly involved in the morphosyntactic consistency-checking operations that are assumed to take place during agreement processing. This interpretation appears to be in line with the ERP data reported by Mancini et al. (2011), in which a common left-anterior negative effect was found for the two violations, suggesting the presence of a common *φ-checking* operation for the two types of agreement. Critically, studies investigating the processing of mismatches in domains other than language syntax, such as music syntax, have localized the source of early negative effects in the middle frontal gyrus (Maess et al., 2001) and have thus proposed that these regions support general mechanisms involved in checking consistency across the stimuli (see Koelsh et al., 2005 for a discussion on the interaction between music and linguistic processing).

A further remark concerns the dissociation that emerges in the frontal lobe between the inferior frontal gyrus - selectively activated by the processing of correct dependencies - and the middle frontal gyrus, which shows sensitivity to the presence of a mismatch between subject and verb. This division has already been discussed in the extant neuro-cognitive literature, especially in relation to the debate concerning the domain-general vs. language-specific function of frontal areas. One relevant position

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maintains that the role of LIFG is neither strictly domain-general nor strictly language-specific (Fedorenko et al. 2012). Indeed, handling of both types of processing is ensured by the presence of functionally complementary subregions: while BA45 is specifically engaged in linguistic processing, its surrounding areas appear to be broadly engaged in a variety of tasks across different domains. The current set of data is compatible with this proposal and contributes to characterization of the nature of the mechanisms that each sub-region supports. In particular, this dissociation could reflect the interplay between language-specific mechanisms that incrementally integrate linguistic information coming from temporal areas, and domain-general processes that ensure the detection of possible mismatches between the perceived and the expected input.

5.5. The role of the bilateral fronto-parietal network in agreement processing

There is yet another aspect of the set of data shown here that deserves to be discussed, namely the activation profile emerging in bilateral fronto-parietal areas, including the anterior and middle cingulate cortices[2], the inferior parietal cortex and the precuneus. Activity in these areas has been consistently associated with task-related conflict-monitoring operations aimed at monitoring the match between the expected and the perceived stimulus (Botvinick et al. 2004; Ye and Zhou, 2009). These could be precisely the mechanisms that led to the involvement of this fronto-parietal regions in our experiment, during which participants were required to evaluate sentence grammaticality. Importantly, this finding is consistent with other sentence processing studies that required the evaluation of the morphosyntactic fit in a variety of dependencies (Folia et al. 2009; Kuperberg et al. 2003, 2008; Nieuwland et al. 2012). Further corroboration

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[2] The negative neural responses involving these fronto-parietal areas could be reflecting a functional relationship between these regions and the default mode network (Raichle, 2015; Raichle et al., 2001; Raichle & Snyder, 2007; Utevsky et al., 2014). In parallel, our design elicited negative response patterns in right temporal regions. While we do not have a clear explanation for this result, it cannot be neglected and should be further investigated in future research.

for this interpretation comes from the fact that both person and number agreement violations elicit a P600 (cf. Mancini et al. 2011), an effect that has been linked to task-related conflict-monitoring mechanisms (see van de Meerendonk et al. 2009 for a discussion) and the sources of which sources have been localized in the anterior cingulate cortex (Du et al. 2013; Olichney et al. 2010).

6. Conclusion

There are three main findings from this study. Firstly, we had hypothesized that the on-line building of agreement comprehension relies on the application of mechanisms that specifically map morphosyntactic information onto discourse and cardinality representations, and that this dissociation could be reflected at a neural level. The current results confirm our hypothesis and show that the comprehension of an agreement dependency hinges on composite, feature-sensitive mechanisms of structure projection and mapping of information in which the nodes of the language network are differentially involved.

Secondly, the observation of the neural response to person and number agreement violations allows us to associate the main components of sentence processing to their neuro-anatomical bases, thus complementing current views on the neuro-cognition of language. On the one hand, we have been able to locate processes related to the extraction of the representation of underlying agreement features to the posterior portion of middle temporal gyrus, where differential sensitivity to the type of information manipulated in verbal morphology is found. This is of great relevance, as it provides the opportunity of disentangling the processing of person and number from a perspective that could not be approached with either electrophysiological or behavioral techniques. On the other hand, we have pinpointed the neural substrates supporting the assignment of interpretively relevant roles in the anterior portion of the left middle temporal gyrus. This is of great relevance both for neuro-cognitive and theoretical study of language, suggesting the need i) to widen the range of interpretively relevant features and dependencies and add

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person agreement to case and thematic roles, and ii) to design models that accommodate feature-based mapping procedures. Moreover, we have clarified the role of the LIFG and the middle frontal gyrus in sentence processing by positing a tight interplay between language-specific and domain-general functions, which permit integration of subject and verb at the morphosyntactic and semantic-discourse level.

Thirdly, we have identified a bilateral fronto-parietal circuit that controls attentive mechanisms and monitors conflicts between expected and perceived input. Future work will have to test the possibility of extending the assumptions made above to further features, syntactic contexts and types of sentential relations, as well as to different populations.

Acknowledgements

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Figure captions

Figure 1

Significant activation clusters resulting from the contrast All Sentences vs. Fixations were projected on the surface of the MNI single-subject T1 image. The lower part of the figure shows a more detailed anatomical localization of the maximum peaks of activation using the sagittal and axial sections of the T1 image. All clusters depicted at p<0.05 corrected for multiple comparisons. L= left; R=right; A= anterior; P=posterior; I=inferior; S=superior.

Figure 2

Significant activation clusters resulting from the contrast Person Violation+Number Violation vs. Correct Agreement (in yellow) and Correct Agreement vs. Person Violation+Number Violation (in purple). Statistical parametric maps were overlaid on the surface of the MNI single-subject T1 image. The lower part of the figure shows a more detailed anatomical localization of the maximum peaks of activation using the sagittal and axial sections of the T1 image. L= left; R=right; A= anterior; P=posterior; I=inferior; S=superior.

Figure 3

A) Superimposition of the significant activation clusters resulting from the contrasts Person Violation vs. Correct Agreement (in red), Number Violation vs. Correct Agreement (in green). Yellow voxels represent significant activated voxels in both contrasts. Statistical maps were projected on the surface of the MNI single-subject T1 image. B) Bar graphs display the contrast estimates and 90% confidence intervals for the three experimental conditions compared to the fixation baseline (CA= Correct Agreement, in blue; NV=Number Violation, in green; PV= Person Violation, in blue) at different maximum peaks, representative of the significant activated clusters. The right-hand side of (B) shows a detailed anatomical localization of the maximum peaks of activation using the sagittal and axial sections of the T1 image.

Figure 4

A) Significant activation clusters resulting from the contrast Person Violation vs. Number Violation. Statistical parametric map was overlaid on the surface of the MNI single-subject T1 image. B) Bar graphs display the contrast estimates and 90% confidence intervals for the two experimental conditions relative to fixation baseline (NV= Number Violation, in green; PV=Person Violation, in red; n.s= not significant). The right-hand side of (B) shows a detailed anatomical localization of the maximum peaks of activation using the sagittal and axial sections of the T1 image. The asterisks in the upper part of the bars indicate that the comparison between each condition and the fixation baseline was statistically significant. L: left; R: right; n.s.: non-significant t-test.

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Figure 1
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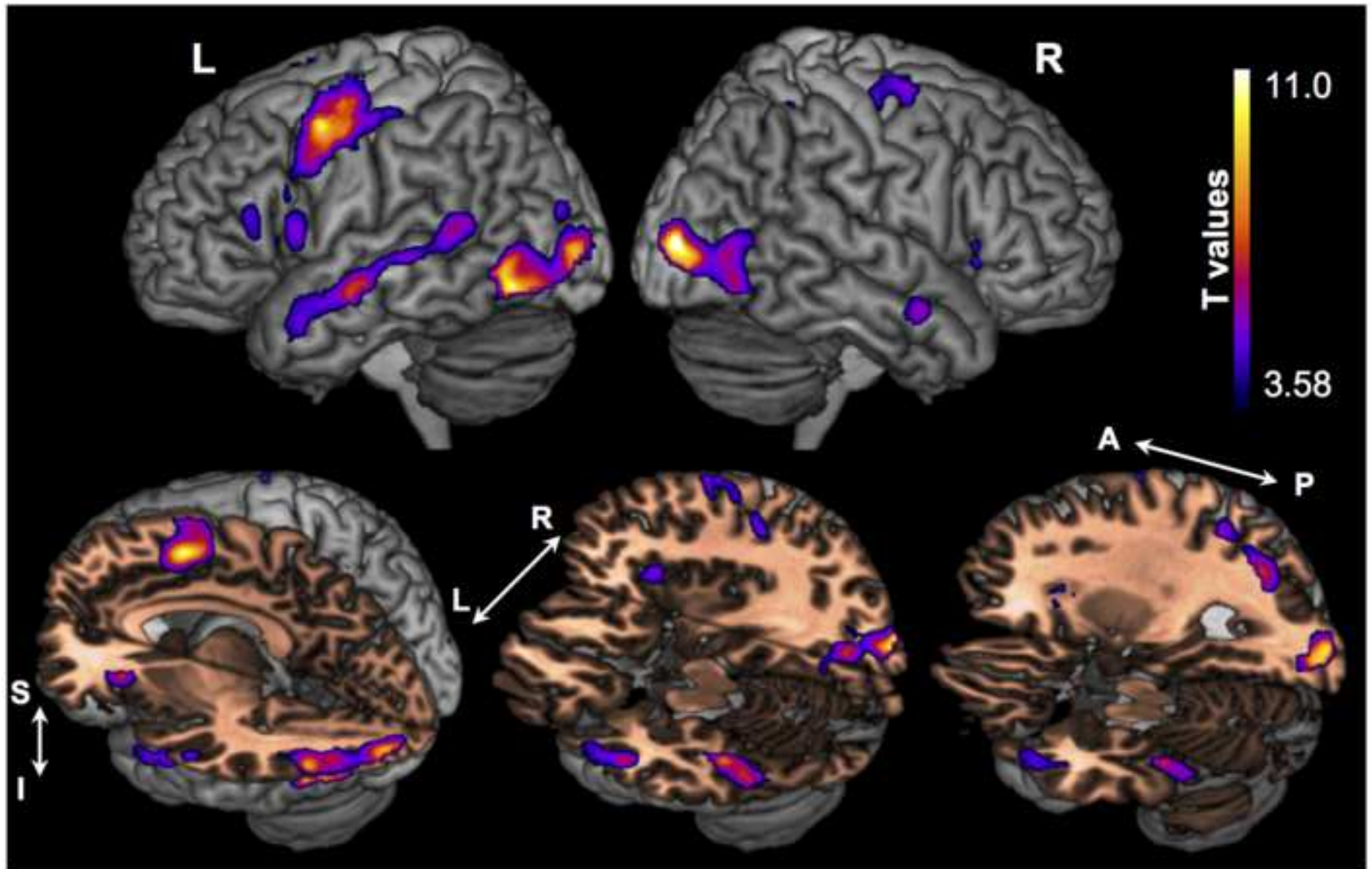
Figure 2
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PV + NV > CA
CA > PV + NV

x = 5, z = 1   x = 39, z = -29   x = 39, z = 5   x = 53, z = -7
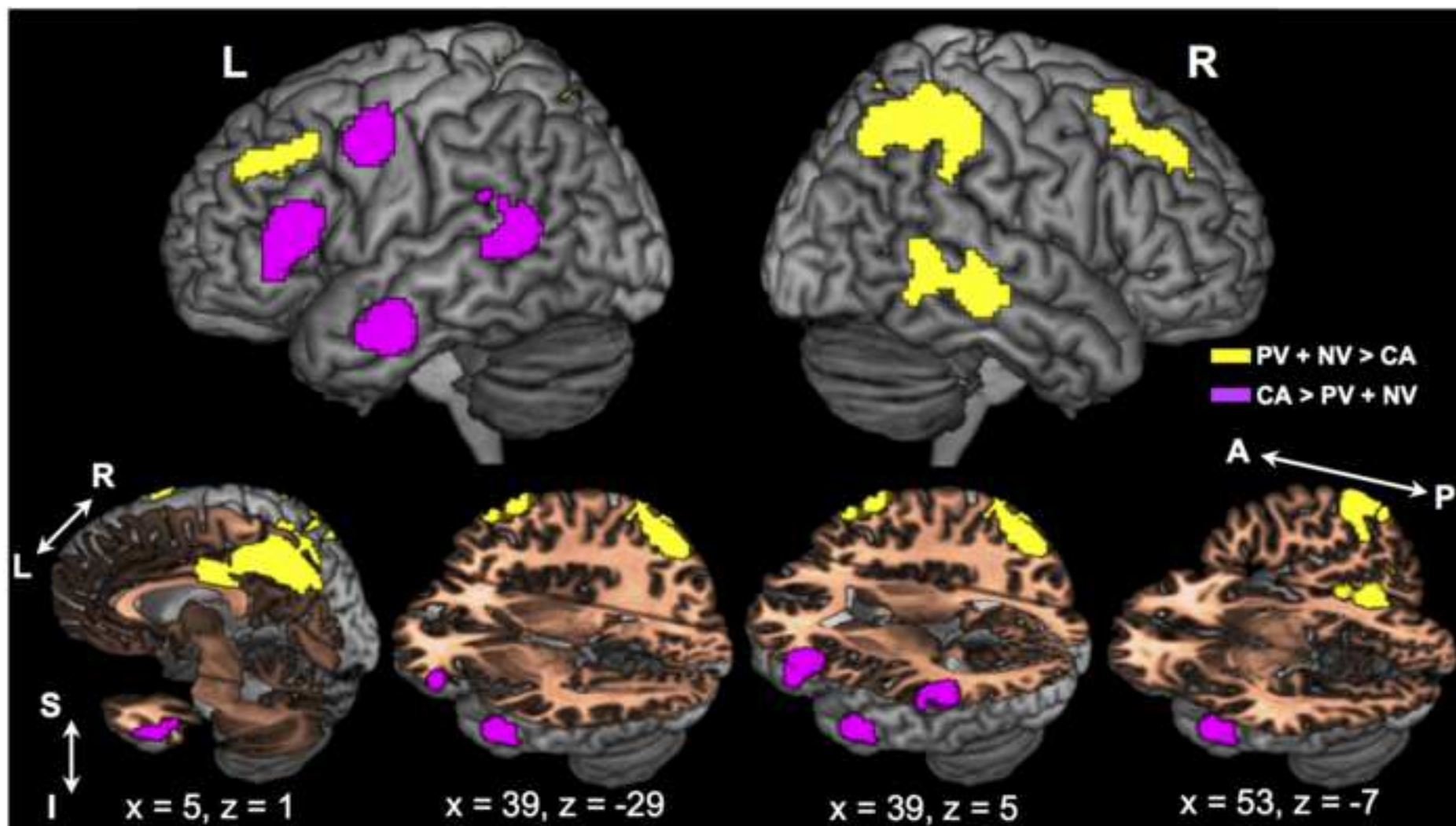
Figure 3
[Click here to download high resolution image](#)

A)

Person Violation > Number Violation

L   R

PV
PV and NV

B)

Left Posterior Middle Temporal

Left Anterior Middle Temporal

Left Inferior Frontal (Pars Orb.)

Left Inferior Frontal (Pars Tri.)

Contrast estimates and 90% of confidence intervals

NV   PV
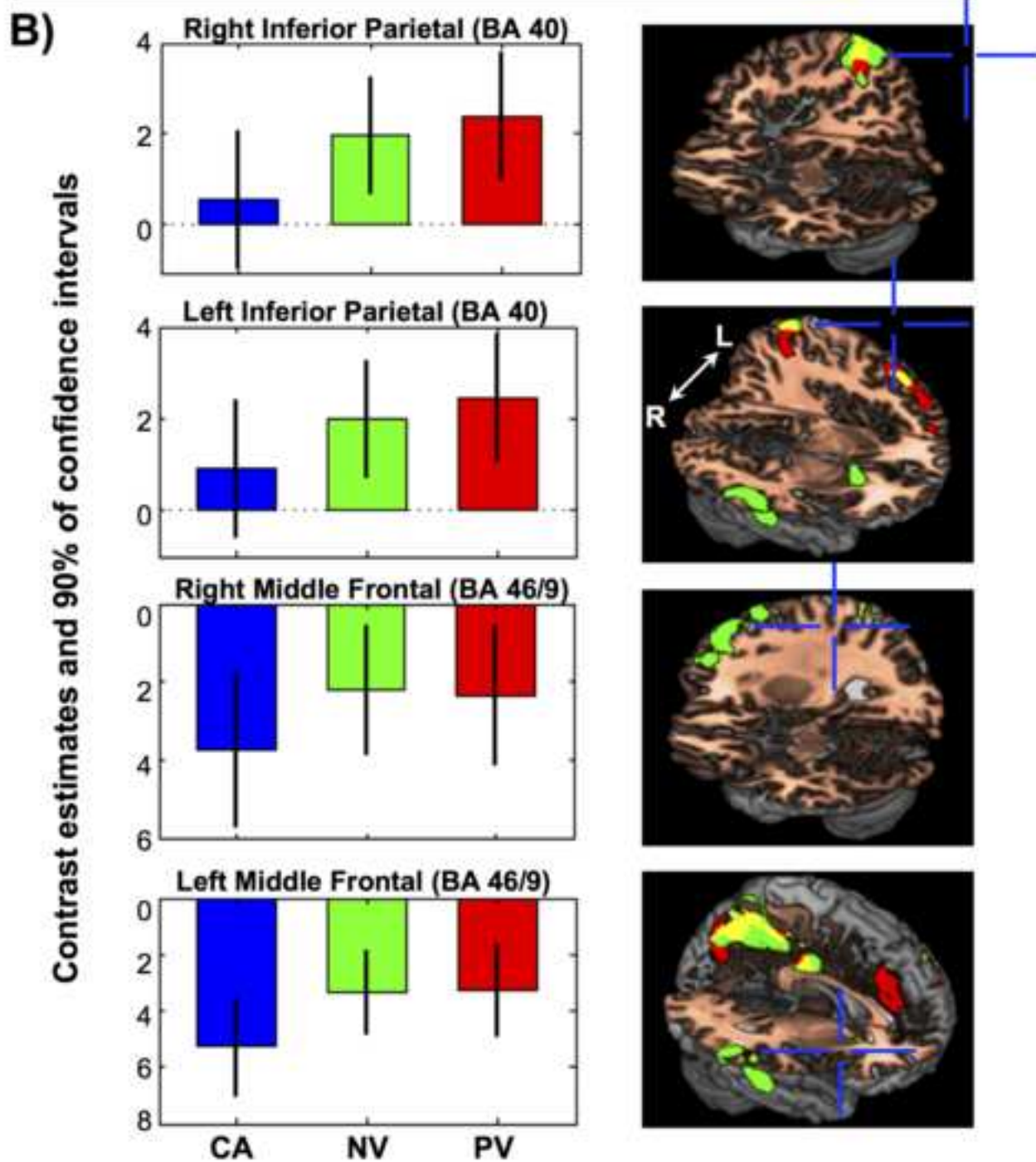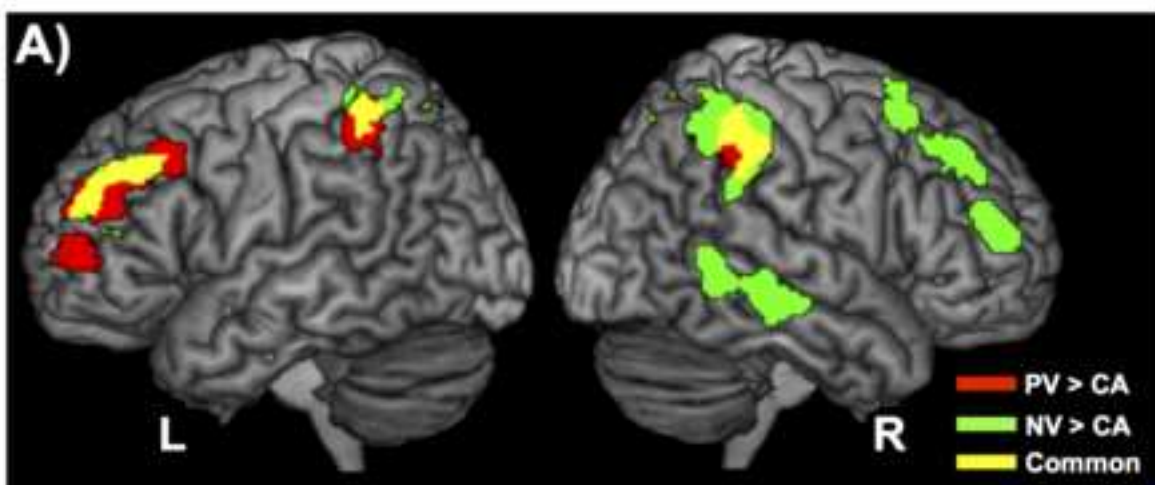
Table

Table 1. Percentage of correct responses (hits) for the three conditions (standard error between parentheses).

	Hits
Correct Agreement	90.37 (1.80)
Number Violation	91.13 (2.31)
Person Violation	90.00 (2.68)

Table 2. Significant activation clusters resulting from the contrast *All Sentences* versus *fixation baseline*.

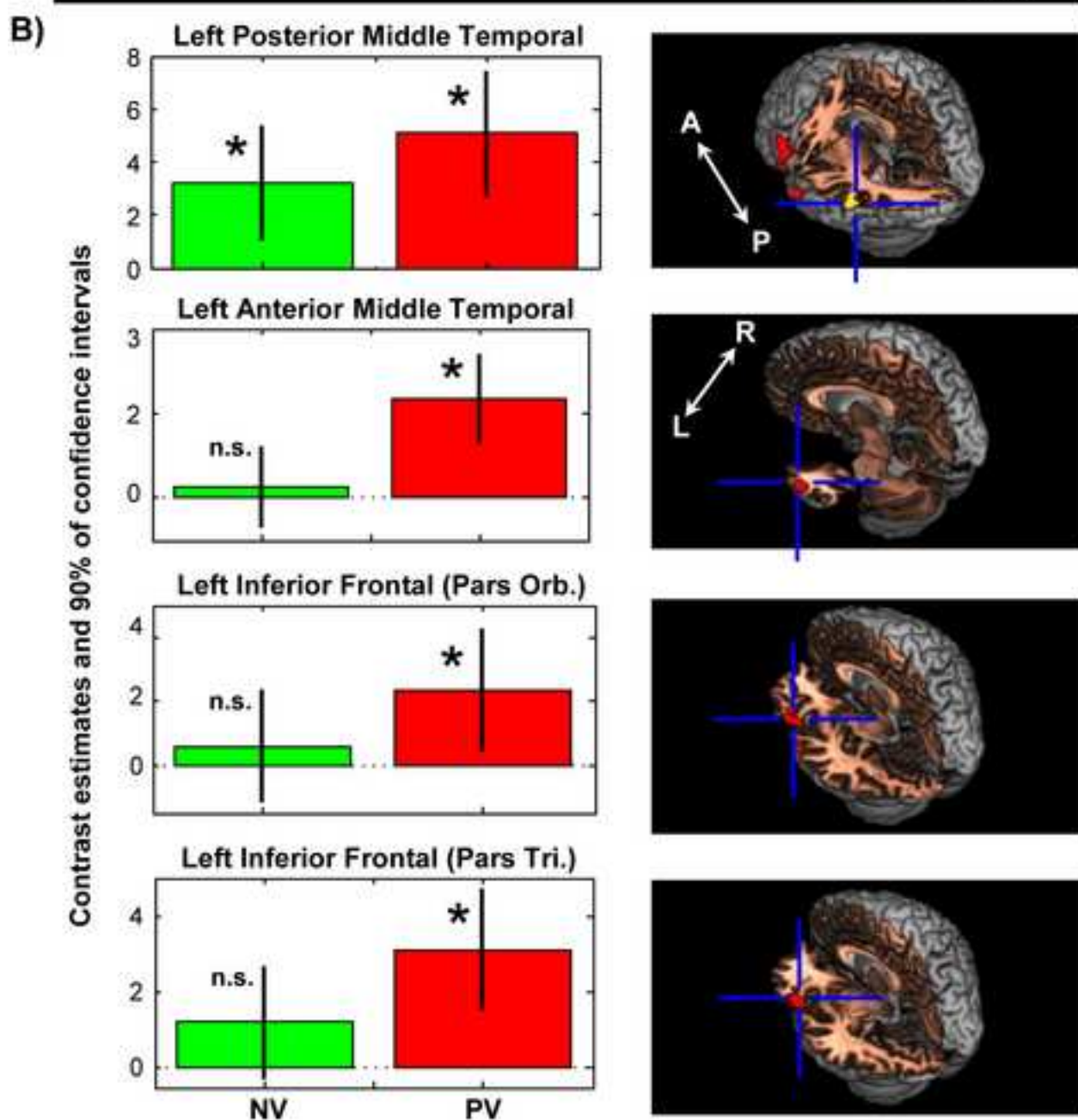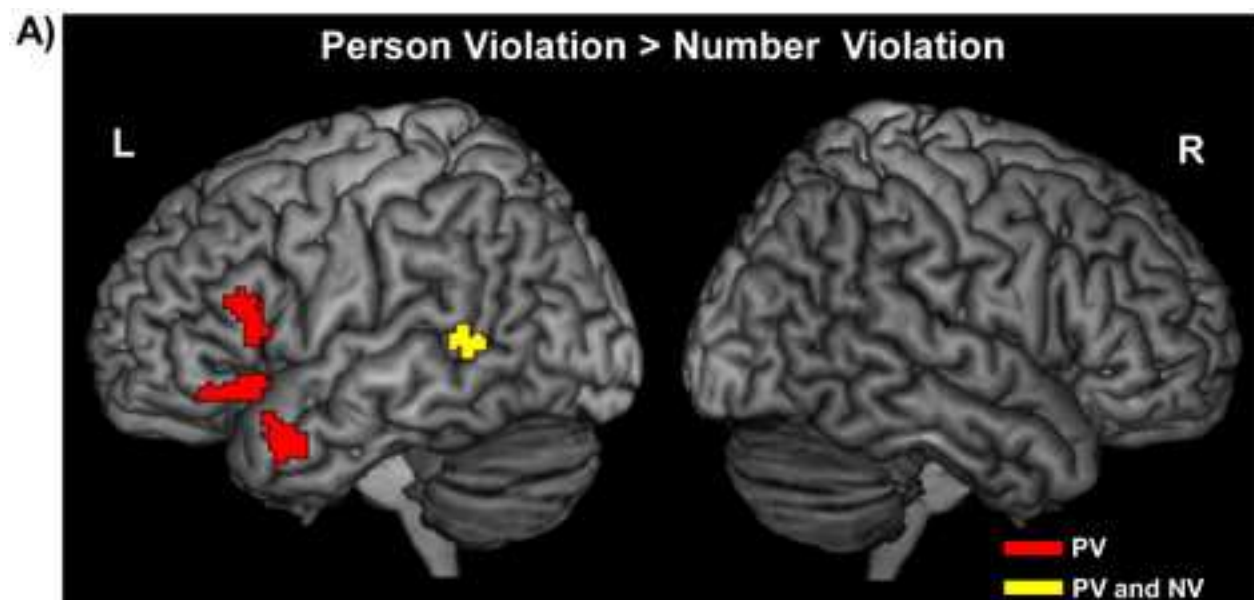| Hemisphere	Region	All Sentences > Fixation		
		x,y,z {mm}	Z	Vx
Left	Inferior Frontal Gyrus (BA45 - Tri)	-46 28 16	4,06	196
	Insula (BA47)	-30 26 0	**5,25**	227
	Precentral (BA6)	-50 2 48	**6,04**	2272
	Postcentral (BA40)	-54 -6 46	**5,41**	2272
	Supplementary Motor Area (BA32/6)	-4 12 50	**6,2**	1339
	Anterior Middle Temporal (BA21)	-56 -10 -12	**5,37**	3156
	Inferior Occipital (BA37)	-44 -66 -10	**6,01**	3156
	Middle Occipital (BA37)	-28 -90 2	**5,82**	3156
Right	Insula (BA47)	34 24 2	**4,64**	223
	Precentral (BA6)	38 -6 64	**4,5**	483
	Postcentral (BA3)	42 -26 46	**4,67**	483
	Inf Parietal (BA40)	30 -46 52	4,4	363
	Middle Temporal (BA21)	42 -70 2	**4,98**	1284
	Inferior Occipital (BA18)	28 -86 -2	**5,83**	1284
	Middle Occipital (BA18)	36 -90 6	**6,73**	1284
	Superior Occipital (BA19)	28 -62 36	**5,06**	363

x,y,z {mm} = Coordinates of the local maxima. Z = Z scores. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. Z scores and Vx are reported in bold if they are significant at the peak level after FWE or FDR correction (p<.05), if underlined, they are significant at p<.001 uncorrected. All others are significant at the cluster level after FWE or FDR correction (p<.05). Tri: Pars Triangularis. BA: Brodmann Area.

Table3. Brain activation resulting from the comparisons between grammatical and ungrammatical conditions.

Hemisphere	Region	Correct Agreement > Violations		
		x,y,z {mm}	Z	Vx
Left	Inferior Frontal Gyrus (BA45 - Tri)	-56 24 14	**5,63**	2785
	Inferior Frontal Gyrus (BA47/38 - Orb)	-48 34 -6	**4,61**	2785
	Superior Frontal Gyrus (BA9)	-8 50 44	**4,66**	456
	Middle Temporal Pole (BA38)	-46 16 -28	**5.12**	971
	Superior Temporal Pole (BA38)	-46 16 -21	3,37	971
	Anterior Middle Temporal Gyrus (BA20)	-56 -10 -16	**4,67**	971
	Posterior Middle Temporal Gyrus (BA22)	-58 -38 4	**5,1**	1155
	Posterior Middle Temporal Gyrus (BA21)	-52 -54 12	**4,78**	1155

x,y,z {mm} = Coordinates of local maxima. Z = Z scores. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. All the regions reported are significant at the cluster level after FWE or FDR correction (p<.05). Z scores and Vx are reported in bold if they are significant at the peak level after FWE or FDR correction (p<.05). Tri: Pars Triangularis; Orb: Pars Orbitalis; BA: Brodmann Area.

Table 4. Brain activation resulting from the comparisons between ungrammatical and grammatical conditions.

Hemisp.	Region	Violations > Correct Agreement			Person Violation > Correct Agreement			Number Violation > Correct Agreement		
		x,y,z {mm}	Z	Vx	x,y,z {mm}	Z	Vx	x,y,z {mm}	Z	Vx
Left	Middle Frontal Gyrus (BA45)				-40 46 22	4,26	459	-40 32 36	3,21	626
	Middle Frontal Gyrus (BA46)	-32 44 34	4,24	190	-32 46 34	4,68	459	-32 44 34	3,97	626
	Middle Frontal Gyrus (BA44)	-40 22 40	3,56	190	-44 22 36	4,33	459			
	Middle Frontal Gyrus (BA10)				-34 54 6	4,02	109			
	Middle Cingulate (BA23)							-2 -16 32	3,49	164
	Inferior Parietal (BA40)				-42 -46 58	4,31	238	-48 -48 56	2,8	118
	Superior Parietal (BA40)							-36 -54 58	3,19	118
	Paracentral				10 -32 52	4,43	1195			
	Postcentral (BA40)							-42 -44 62	3,23	118
	Precuneus (BA7)	-4 -62 58	**5,38**	2261	-6 -66 50	**5,14**	1195	-10 -62 44	4,62	2770
Right	Middle Frontal Gyrus (BA46)							40 52 8	3,2	232
	Middle Frontal Gyrus (BA45)							36 46 18	4,2	232
	Middle Frontal Gyrus (BA48)							32 18 56	3,37	325
	Middle Frontal Gyrus (BA8)	28 18 58	3,71	290				24 16 52	3,07	325
	Middle Frontal Gyrus (BA9)	32 38 40	4,42	290				30 38 40	3,98	243
	Medial Superior Frontal Gyrus (BA32)				2 34 34	**4,89**	408			
	Anterior Cingulate (BA11)				6 40 26	4,36	408			
	Middle Cingulate	6 -36 52	**5,07**	2261	8 -22 38	4,06	396			
	Supplementary Motor Area (BA8)							14 14 60	4,18	325
	Inferior Parietal (BA40)	42 -56 52	**5,3**	873	56 -42 50	4,25	438	48 -44 52	3,95	689
	Supramarginal Gyrus (BA40)	56 -34 46	4,42	873	58 -36 44	4,19	438	52 -32 42	4,33	689
	Middle Cingulate (BA23)							2 -12 40	3,41	164
	Precuneus (BA5)	8 -58 58	**5,4**	2261				8 -60 56	4,69	2770
	Middle Temporal (BA21)	54 -44 -6	4,58	458				68 -24 -12	3,82	468
	Caudate (BA11)							14 18 -8	3,75	112

x,y,z {mm} = Coordinates of local maxima. Z = Z scores. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. All the regions reported are significant at the cluster level after FWE or FDR correction (p<.05). Z scores and Vx are reported in bold if they are significant at the peak level after FWE or FDR correction (p<.05). Hemisp. = Hemisphere. BA: Brodmann Area.

Table 5. Brain activation resulting from the comparisons between Person Violation and Number Violation.

Hemisphere	Region	Person Agreement Violation > Number Agreement Violation		
		x,y,z {mm}	Z	Vx
	Inferior Frontal Gyrus (BA45 - Tri)	-58 20 16	<u>3.31</u>	192
	Inferior Frontal Gyrus (BA47/38 - Orb)	-48 22 -10	<u>3.65</u>	161
Left	Superior Temporal Pole (BA38)	-46 16 -20	3,41	89
	Middle Temporal Pole (BA38)	-50 12 -24	3.85	89
	Anterior Middle Temporal (BA21)	-52 6 -26	4,09	89
	Posterior Middle Temporal (BA20/21/22)	-56 -46 6	3,72	62

x,y,z {mm} = Coordinates in MNI space of local maxima. Z = Z scores. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. Z scores and Vx are reported in bold if they are significant at the peak level after FWE or FDR correction (p<.05), if underlined, they are significant at p<.001 uncorrected. All others are significant at the cluster level after FWE or FDR correction (p<.05). Tri: Pars Triangularis; Orb: Pars Orbitalis; BA: Brodmann Area.