Tracing the interplay between syntactic and lexical features: fMRI evidence from agreement comprehension.

Short title: **Tracing lexico-syntactic interplay.**

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Abstract

The current fMRI study was designed to investigate whether the processing of different gender-related cues embedded in nouns affects the computation of agreement dependencies and, if so, where this possible interaction is mapped in the brain. We used the Spanish gender agreement system, which makes it possible to manipulate two different factors: the agreement between different sentence constituents (i.e., by contrasting congruent versus incongruent determiner-noun pairs) and the formal (i.e., orthographical/morphological) and/or lexical information embedded in the noun –i.e., by contrasting transparent (e.g., libro$_{masc.}$ [book]; luna$_{fem.}$ [moon]) and opaque nouns (e.g., lápi<u>z</u>$_{masc.}$ [pencil]; veje<u>z</u>$_{fem.}$ [old age]). Crucially, these data illustrated, for the first time, how the network underlying agreement is sensitive to different gender-to-ending cues: different sources of gender information associated with nouns affect the neural circuits involved in the computation of local agreement dependencies. When the gender marking is informative (as in the case of transparent nouns), both formal and lexical information is used to establish grammatical relations. In contrast, when no formal cues are available (as in the case of opaque nouns), gender information is retrieved from the lexicon. We demonstrated the involvement of the posterior MTG/STG, pars triangularis within the IFG, and parietal regions during gender agreement computation. Critically, in order to integrate the different available information sources, the dynamics of this fronto-temporal loop change and additional regions, such as the hippocampus, the angular and the supramarginal gyri are recruited. These results underpin previous neuroanatomical models proposed in the context of both gender processing and sentence comprehension. But, more importantly, they provide valuable information regarding how and where the brain's language system dynamically integrates all the available form-based and lexical cues during comprehension.

Introduction

The decoding of grammatical information constitutes a fundamental piece in the comprehension of linguistic signals. Unsurprisingly, there are important ongoing efforts to understand how our brain manages this grammatical information (for different perspectives see Friederici, 2012; Friederici and Gierhan, 2013; Hagoort, 2014; Hagoort and Indefrey, 2014). Even so, several questions still remain unclear. Does the brain have a circuit specialized in the computation of the grammatical relations between words? How do the different formal (i.e., orthographical/morphological) and conceptual cues embedded in our linguistic code affect the establishment of grammatical relations? Does the interplay between these different types of information leave a trace in the brain response? In the current study, this topic will be addressed using the Spanish gender agreement system that makes it possible to control for formal factors while focusing on the effects of lexico-semantic factors and vice versa. This allows us to disentangle the different neural mechanisms underpinning the establishment of grammatical relations.

The Spanish gender agreement system can rely on conceptual cues (e.g., the biological sex of the referent, such as abuelo$_{masc.}$ [grandfather] or actriz$_{fem.}$ [actress]), or on purely formal cues, with no conceptual representation on the reference –i.e., independently of the meaning (e.g., faro$_{masc.}$ [lighthouse] or lápiz$_{masc.}$ [pencil]). In addition, nouns can be classified into two main groups, depending on gender-to-ending regularities (Bates et al., 1995; Harris, 1991). The first group, *transparent nouns*, includes those nouns whose ending has a regular correspondence with a specific gender class ("–a" for feminine and "–o" for masculine, e.g., libr$\underline{o}_{masc.}$ [book]; lun$\underline{a}_{fem.}$ [moon]). The second group, *opaque nouns*, includes those nouns whose ending is not informative of the gender class to which a given noun belongs (e.g., lápi$\underline{z}_{masc.}$ [pencil]; veje$\underline{z}_{fem.}$ [old age]). A similar situation can be seen in English: plural marking on nouns is typically transparent by suffixing "–s" (e.g., dog$_{sing.}$-dogs$_{pl.}$), while some irregular nouns are marked by other opaque means (e.g., foot$_{sing.}$-feet$_{pl.}$).

In Spanish, nouns are typically preceded by their corresponding definite determiners (singular forms: "la" for feminine and "el" for masculine, e.g., el$_{masc.}$ libr$\underline{o}_{masc.}$ [the book]; la$_{fem.}$ lun$\underline{a}_{fem.}$ [the moon], and plural forms: "las" for feminine and "los" for masculine, e.g., los$_{masc.}$ libr$\underline{os}_{masc.}$ [the books]; las$_{fem.}$ lun$\underline{as}_{fem.}$ [the moons]). These two sentence elements –nouns and determiners– should always be morphosyntactically congruent. Thus, investigating how local relations between determiners and nouns are established can provide valuable information about how agreement operates within the noun-phrase domain. The comparison between grammatical and ungrammatical determiner-noun pairs will be the starting point of the current study, which seeks to identify the brain regions sensitive to local agreement information. Subsequently, by turning the spotlight on the gender-to-ending regularities characterizing transparent and opaque nouns, we will be able to investigate how our brain manages different gender-related cues during agreement computation.

There have been numerous studies exploring how lexical and formal gender-related information is represented and accessed during the processing of nouns (Barber and Carreiras, 2005; Bates et al., 1996; Bates et al., 1995; Cacciari et al., 2011; Cacciari and Padovani, 2007; Caffarra and Barber, 2015; Caffarra et al., 2014; Caffarra et al., 2015; De Martino et al., 2011; Gollan and Frost, 2001; Hernandez et al., 2004; Padovani et al., 2005; Schiller and Caramazza, 2003). Most of them have taken advantage of the different gender-to-ending rules characterizing transparent and opaque nouns. Despite the variability in their methodological approaches (i.e., different tasks, languages, and stimulation modality), these studies give rise to the following claim (see also Bates et al., 1995; De Martino et al., 2011 for a comparison across tasks in both comprehension and production; Gollan and Frost, 2001; Hernandez et al., 2004; Holmes and Segui, 2004, 2006; Padovani et al., 2005): gender-to-ending cues might affect the processing of a given noun, even in those tasks where participants have not been required to explicitly identify the gender (but see Bates et al., 1995; De Martino et al., 2011; Gollan and Frost, 2001; Hernandez et al., 2004; Padovani et al., 2005). However, whereas the influence of lexical information is generally agreed upon, experimental evidence exploring the use of form-based gender cues is divergent (see Caffarra et al., 2014 for a detailed description of the gender processing accounts).

Previous neuroimaging studies have also demonstrated how and where gender-to-ending cues might affect noun processing (Hammer et al., 2007; Heim, 2008; Heim et al., 2006; Hernandez et al., 2004; Indefrey and Levelt, 2004; Miceli et al., 2002; Padovani et al., 2005). These studies have consistently shown that the processing of transparent and opaque nouns produces different brain responses. For instance, Hernandez et al. (2004) compared the brain response associated with Spanish opaque and transparent nouns using a gender decision task. These authors reported significant activation increases in different frontal regions for opaque nouns, including the left pars opercularis within the inferior frontal gyrus (IFG), the left precentral gyrus, the right and left insula, and the right and left anterior cingulate cortex. Based on their own results and previous evidence, they argued that classifying opaque nouns as feminine or masculine requires increased demands (i.e., with respect to transparent nouns) on language-related regions previously associated with articulation and phonological and morphological processing, as well as on domain-general regions such as the anterior cingulate cortex, previously related to task difficulty effects (see Padovani et al., 2005 for similar results in Italian).

Interestingly, Heim (2008) revisited the available functional neuroimaging literature on syntactic gender processing and provided an extensive review of this topic. Based on the sentence processing model proposed by Friederici (Friederici, 2011, 2012; Friederici and Kotz, 2003), this author postulated a neuroanatomical model of gender processing that emphasizes the left pars opercularis and triangularis within the IFG (BA44 and 45 respectively) as critical nodes. Specifically, this model predicts that while BA44 mediates the extraction of gender features when gender is morphologically encoded, the engagement of BA45 would be dependent on the task requirements. Activity in BA45 has been found only when the task explicitly includes the retrieval of the gender morphosyntactic feature (e.g., gender decision after generation of the corresponding determiner). This model also predicts that when no morphological cue is available (i.e., as in the case of opaque nouns), gender information is retrieved from the lexicon, which, according to this author, should be mapped in the middle part of the left middle temporal gyrus (MTG). Importantly, while Heim's proposal (2008) has attempted to explain how gender information is retrieved, it does not provide clear information on whether the availability of different gender cues might affect syntax-related operations such as agreement.

In contrast to the large number of studies investigating how gender information is retrieved, research exploring how formal gender cues might affect the establishment of grammatical relations is markedly scarce. Some behavioral and ERP studies have investigated whether the transparency of the nouns affects agreement operations, examining the interaction between gender marking and congruency patterns (determiner-noun and possessive pronoun-noun in Spanish: Afonso et al., 2014; adjective-noun in Russian: Akhutina et al., 1999; determiner-noun in Spanish: Caffarra and Barber, 2015; Caffarra et al., 2014; noun-adjective in Hebrew: Gollan and Frost, 2001; determiner-noun in French: Holmes and Segui, 2004; noun-adjective in Spanish: Martin et al., 2017). Most of these studies have consistently reported differences between transparent and opaque nouns. However, the picture is far from conclusive: while some studies have demonstrated that gender information has no influence on the establishment of grammatical relations (Caffarra and Barber, 2015; Caffarra et al., 2014; Caffarra et al., 2015), others have suggested the opposite (Akhutina et al., 1999; Holmes and Segui, 2004; Taft and Meunier, 1998). Thus, further evidence is required about this possible interaction.

The present study seeks to investigate whether the processing of different gender-related cues embedded in nouns affects the computation of agreement dependencies. Crucially, there is no fMRI evidence concerning where the interaction between gender marking and congruency patterns (if there is an interaction between these two factors) is mapped in the brain. In this light, by combining behavioral and fMRI data here we investigated a) what brain regions are sensitive to gender agreement within a noun phrase; b) whether the brain processes transparent and opaque nouns in the same way or differently; and c) whether and how different formal gender-to-ending cues modulate the neural mechanisms underlying agreement processing. In the current experiment we investigated the effects of Gender Marking (*Transparent Nouns* vs. *Opaque Nouns*) and Gender Congruency (*Gender Match* vs. *Gender Mismatch*) using Spanish determiner-noun pairs. The construction of a noun phrase representation requires accessing and integrating morphosyntactic information in both types of pairs (i.e., determiner + transparent noun [$el_{masc.}$ $libro_{masc.}$] and determiner + opaque noun [$el_{masc.}$ $lapiz_{masc.}$]). However, different sources of gender information are available depending on the transparency of the nouns (Bates et al., 1995; Gollan and Frost, 2001; Heim, 2008). Gender information in transparent nouns can be accessed based on both form-based and lexical cues. In contrast, gender information in opaque nouns cannot be derived from form-based cues, since their ending does not inform about the gender values (i.e., whether the noun is feminine or masculine), but relies exclusively on lexical cues. Thus, in order to reveal how these sources of gender information might affect morphosyntactic integration processing in a within-constituent domain, we tested both the main effects and the interaction.

A distinction between the neural activation patterns involved in the processing of congruent and incongruent determiner-noun pairs (i.e., a main effect of Gender Congruency) is expected. According to previous evidence, the pars opercularis within the left IFG seems to be the most plausible candidate emerging from this effect (Carreiras et al., 2010; Carreiras et al., 2015; Hammer et al., 2007; Mancini et al., 2017; Nieuwland et al., 2012; Quiñones et al., 2014). The gender-marking manipulation should trigger differences in the neural correlates underlying the processing of transparent and opaque nouns (i.e., a main effect of Gender Marking), as previous studies have suggested (see Heim, 2008 for a review of this topic; Hernandez et al., 2004; see also Padovani et al., 2005). According to the neuroanatomical model proposed by Heim (2008), these differences would cover regions such as the left IFG (pars opercularis and triangularis) and MTG (see also Indefrey and Levelt, 2004). In addition, if the formal information available for transparent nouns does not modulate the establishment of grammatical relations, we should expect no interaction between Gender Congruency and Gender Marking. In contrast, if the coding of form-based gender-marking cues affects agreement processing, we should expect an interaction between Gender Congruency and Gender Marking. The left IFG is an ideal candidate for this interaction, since this region is a critical node for both agreement processing and the retrieval of gender-related information. However, crucially, this issue has not yet been addressed using fMRI and the emergence of such interaction is still disputable.

Materials and Methods

Participants. Fifty-three healthy participants took part in the current study as paid volunteers. All were highly proficient speakers of Spanish and all gave informed consent as stipulated in the ethics approval procedure of the *BCBL Research Ethics Committee.* They all have right-hand dominance, normal or corrected to normal vision and no history of psychiatric or neurological diseases or learning disabilities. Participants were assessed for handedness through an abridged Spanish version of the Edinburgh Handedness Inventory (Oldfield, 1971). They were also asked about claustrophobia, or any other criteria that could exclude them from participating in an fMRI experiment. After the experimental session, the quality of the fMRI data of each individual was explored using the Artifact Repair toolbox (Gabrieli Cognitive NeuroScience Lab; http://cibsr.stanford.edu/tools/ArtRepair/ArtRepair.htm). Those subjects whose fMRI data exhibited more than 40 % of the scan-to-scan motion estimation higher than 1 mm were excluded from subsequent statistical analysis. After these exploratory analyses, a total of forty-seven participants (twenty-nine females), age ranging from 18 to 42 years (mean = 23.1, standard deviation = 6.0), were used to make population inference.

Stimuli and experimental procedure. In the current experiment, participants took part in a single scanner session comprising an event-related 2 x 2 factorial within-subject design, which consisted of a serial presentation of 120 Spanish determiner-noun pairs. The gender agreement between determiners and nouns was manipulated, resulting in grammatical and ungrammatical associations (with a proportion of 1:1). The nouns selected could be either transparent or opaque (with a proportion of 1:1). Transparent nouns refer to nouns that are morphologically marked for gender using the Spanish canonical suffixes "–o" for masculine and "–a" for feminine. Opaque nouns refer to nouns that end with non-canonical suffixes (e.g. "–e", "–n", "–l", "–d", "–z"). The resulting 2 x 2 factorial design used Gender Marking [*Transparent Nouns* and *Opaque Nouns*] and Gender Congruency [*Gender Match* and *Gender Mismatch*] as factors. Two different stimulation lists were created with the same nouns. Half of the nouns appeared in association with the feminine/singular determiner "la" in one list and in association with the masculine/singular determiner "el" in the other list. Thus, the same noun was presented in both conditions, *Gender Match* and *Gender Mismatch*, in different lists. These two lists were counterbalanced between participants in such a way that participants saw all nouns once.

All the nouns included in the current design (Table IS) referred to inanimate and concrete entities (e.g., *luna* [moon], *balón* [ball]) [mean of concreteness = 5.51 (±0.75)], so that only formal gender information and not conceptual information concerning the biological sex of the referent was present. In each condition, half of the nouns referred to masculine entities and the other half to feminine entities. In Spanish, opaque nouns constitute a highly restricted subset of the total nouns in the lexicon (Anderson, 1961; Eddington, 2004). Thus, all the opaque and transparent nouns included in the current experiment were selected from the lower side of the lexical frequency distribution [mean = 36.85 per million, SD = 34.53]. The length of the opaque and transparent nouns was also controlled, with a minimum of 4 and a maximum of 8 letters [opaque: mean = 5.20, SD = 0.91; transparent: mean = 5.60, SD = 1.65]. All the lexical measures considered were extracted from the Spanish ESPaL database (Duchon et al., 2013). In addition, in order to avoid possible interaction effects between gender and number agreement features, only the singular form of the determiners and nouns were included. All determiner-noun word pairs agreed in number.

Each trial consisted of a visual presentation of determiner-noun pairs. Word pairs were displayed during 300 ms in white capital letters on a black background. Participants were instructed to answer as quickly and accurately as possible whether the word pair was grammatically acceptable or not, by pressing one of two different buttons. They could respond since the onset of the stimulus and had two more seconds after the offset of the stimulus. During this time a visual cue was displayed indicating when participants had to respond. In order to optimize the sampling of the BOLD response, an inter-stimulus interval was included. During this period a fixation point ("+") was presented with different durations across trials, varying between 2 and 8 seconds. This baseline period allows us to counteract possible expectation effects which might influence the brain response. In addition, it is also useful to improve the estimation of the time course of the BOLD response associated with each experimental condition.

MRI acquisition. The experiment was performed on a 3-T Siemens TrioTrim scanner, using a standard thirty two-channel phased-array surface coil (Siemens, Erlangen, Germany). Functional event-related scans consisted of 454 echoplanar images that were acquired using a T2*-weighted gradient-echo pulse sequence with the following parameters: Field of view (read) = 192 mm; Field of view (phase) = 100 %; Base resolution = 64 pixels; Phase resolution = 100 %; Echo time = 30 ms; Repetition time = 2 s; Time gap= No; Flip angle = 90°; Slice number = 32; Slice thickness = 3 mm; In plane resolution = 3 x 3 mm; Orientation = Axial; Distance factor = 25 %. In addition, 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. Structural and functional data can be shared under requirements[1].

fMRI data analysis. Functional data were analyzed using SPM8 and related toolboxes (http://www.fil.ion.ucl.ac.uk/spm). Raw functional scans were slice-time corrected taking the middle slice as reference, spatially realigned, unwarped, co-registered with the anatomical T1 and normalized to the MNI space using the unified normalization segmentation procedure. Normalized images were then smoothed using an isotropic 8mm Gaussian kernel. Resulting time series from each voxel were high-pass filtered (128s cut-off period).

Statistical parametric maps were generated by modeling a univariate general linear model, using for each stimulus type a regressor obtained by convolving the canonical

[1] For any further information about the fMRI data and the MATLAB codes used contact the corresponding author, Ileana Quiñones (i.quinones@bcbl.eu). We are willing to provide fMRI data and scripts upon request.

hemodynamic response function with delta functions at stimulus onsets, and also including the six motion-correction parameters as regressors. The stimuli onsets included five different components. The first four corresponded to each experimental condition (*Transparent Gender Mismatch*, *Transparent Gender Match*, *Opaque Gender Mismatch*, *Opaque Gender Match*). The last component corresponded to the fixation cross and was modeled as a single regressor, independently of the experimental conditions. Parameters of the GLM 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 was performed comparing activity to each experimental condition relative to the fixation baseline. The resulting statistical parametric maps were then submitted into a second-level 2 x 2 factorial design, using Gender Marking and Gender Congruency as within-subject factors. This analysis allows us to determine possible main effects and interactions. These effects were also included in the 2-level design statistical matrix (i.e., in SPM, Flexible Factorial Design). The statistical model implemented also considers the variability between different subjects as a source of variance. Population-level inferences were tested adjusting the statistical threshold –i.e., combining the probability values and the required number of activated voxels within each cluster– so 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 considered as significant. All local maxima were reported in the results tables as MNI coordinates (Evans, et al., 1993).

Results

Behavioral results. Statistical analyses of the behavioral responses were performed following the 2 x 2 factorial design. Because of technical problems with the response recording devices, the behavioral data of eight participants were lost. Furthermore, participants whose mean RTs and/or error rates exceeded two standard deviations above or below the mean of the group were excluded from the subsequent analyses. Following these criteria four participants were also excluded, thus a total of forty-one participants were considered in the analyses of the behavioral results. Mean RTs and error rates for each experimental condition are presented in Table I, with the corresponding standard error between parentheses.

Insert here Table I

For RTs, a significant main effect of Gender Congruency was found [F(1, 40) = 84.27, $p < 0.005$]. Additionally, a significant interaction between Gender Marking and Gender Congruency emerged from this analysis [F(1, 40) = 9.84, $p < 0.005$], suggesting that the congruency differential effect (i.e., difference between *Gender Mismatch* and *Gender Match*) was different for transparent and opaque nouns. In order to test the source of this interaction, the experimental conditions were contrasted in a pair-wise manner. Planned comparisons demonstrated that the *Gender Mismatch* condition was harder (i.e., higher RTs and error rates) than the *Gender Match* condition, for both transparent [t(40) = 7.83, $p < 0.001$] and opaque nouns [t(40) = 8.90, $p < 0.001$]. However, the effect was larger for opaque than for transparent nouns [t(40) = 3.14, $p < 0.005$]. Additionally, the error rate analysis showed a main effect of Gender Congruency [F(1, 40) = 13.49, $p < 0.001$]: the percentage of error rates was higher for *Gender Mismatch* than for the *Gender Match* condition. In addition, there was a main effect of Gender Marking [F(1, 40) = 7.92, $p < 0.01$], indicating that the percentage of errors was higher for transparent than for opaque nouns. The interaction between these two factors did not reach the significance threshold ($p < 0.05$).

<u>fMRI results: Congruency effect (Difference between Gender Mismatch and Gender Match conditions).</u> We extracted the main effect of Gender Congruency to characterize the functional neuroanatomical network involved in the processing of grammatical relations. Significant effects included regions with higher responses for the *Gender Mismatch* condition than for the *Gender Match* condition and regions that exhibited the opposite pattern. Specifically, significant response increases in occipital, frontal, and parietal regions in both hemispheres emerged from the contrast *Gender Mismatch*>*Gender Match*. This response pattern also comprised regions exhibiting bilateral activation, such as the middle and medial superior frontal gyrus, the anterior cingulate, the pre- and postcentral gyrus, the supplementary motor area, and the lingual gyrus. This contrast also showed significant left-lateralized parietal responses, including regions such as the angular gyrus and the posterior cingulate cortex. Interestingly, the statistical activation map resulting from this contrast comprised also the right insula and the right dorsal striatum, including the putamen and the caudate nuclei (see Table II and Figure 1 for more details).

Insert here Table II

Insert here Figure 1

On the other hand, the contrast *Gender Match>Gender Mismatch* resulted in a bilateral response pattern. This pattern included brain regions such as the pars opercularis and triangularis within the IFG, the superior frontal gyrus, the middle cingulate cortex, the anterior part of the supplementary motor area, and the inferior and superior parietal gyrus. This contrast also showed significant response increases in the left posterior MTG –extended into the middle occipital cortex– and the right superior temporal gyrus (see Table III and Figure 1 for a detailed list of regions and response patterns).

Insert here Table III

fMRI results: Transparency effect (Difference between Transparent and Opaque Nouns). In order to explore whether transparent and opaque nouns would trigger different brain activation patterns, we extracted the main effect of Gender Marking. Several clusters were identified in the two hemispheres, showing a significant main effect. Similarly to the Gender Congruency effect, the main effect of Gender Marking included regions with higher responses for transparent than for opaque nouns and regions that exhibited the opposite pattern (i.e., higher response for opaque than for transparent nouns).

On the one hand, opaque nouns, compared to transparent nouns, produced increased responses in a widespread fronto-parieto-temporal network, bilaterally distributed (see Figure 2). This neuroanatomical network included regions such as the pars opercularis and triangularis within the IFG, the insula, the medial part of the superior frontal gyrus, the posterior part of the MTG, the hippocampus (including the parahippocampal region), the fusiform gyrus, and the thalamus (see Table IV for a detailed list of regions). On the other hand, transparent nouns compared to opaque nouns produced increased responses in a more restricted left-lateralized network (Figure 2). This network included parietal regions such as the left supramarginal and the left angular gyri, and occipital regions such as the left superior and middle occipital cortices, the cuneus, and the calcarine sulcus (see Table V for more details).

Insert here Figure 2

Insert here Table IV

Insert here Table V

fMRI results: Interaction between Gender Congruency and Gender Marking. Importantly, the main goal of the present study was to investigate whether agreement processing could be modulated by the morphological and/or lexical information embedded in our linguistic code. With this aim in mind, we tested the interaction between Gender Congruency and Gender Marking. Interestingly, we found significant interaction effects in five different left-lateralized clusters, including the supramarginal and angular gyri, the hippocampus, the posterior part of the MTG/STG, and the pars triangularis within the IFG. Planned comparisons revealed that the patterns of response resulting from each of these areas were different depending on the gender-to-ending regularities (Figure 3). Specifically, for *Transparent Nouns*, the hippocampus, the pars triangularis within the IFG, and the posterior MTG/STG exhibited higher responses for *Gender Mismatch* than for *Gender Match*. In contrast, for *Opaque Nouns* the neural responses of these three regions were more prominent for the *Gender Match* than for the *Gender Mismatch* condition. As for the parietal areas (i.e., the angular and the supramarginal gyri), the difference between *Gender Mismatch* and *Gender Match* conditions was not significant for *Transparent Nouns* as opposed to *Opaque Nouns*. While activity in the angular gyrus was maximally enhanced by the *Gender Match* condition, it was the *Gender Mismatch* condition which produced the greatest activity in the supramarginal gyrus (Figure 3 and Table VI).

Insert here Figure 3

Insert here Table VI

Discussion

Taken together, the current findings indicate that a specific brain circuit responds to the agreement congruency between determiners and nouns and, more importantly, that the formal gender-to-ending cues impact the neural response of some specific nodes within this circuit. Firstly, we have demonstrated the critical role of the pars opercularis and triangularis within the left IFG and the posterior part of the left MTG/STG during gender agreement computation. But, critically, we also demonstrated that this circuit is not circumscribed to these regions. Bilateral areas such as the superior parietal cortex, the anterior cingulate cortex, and the superior frontal gyrus, as well as the left middle frontal gyrus, exhibited higher responses for incongruent than for congruent items. Secondly, we distinguished the brain regions engaged in the processing of transparent nouns from those recruited by opaque nouns. While the network related to transparent nouns is circumscribed to occipital and adjacent parietal areas in the left hemisphere, the network associated with opaque nouns involved temporal, parietal, and frontal regions, bilaterally distributed. Finally, we identified the regions involved in the interplay between syntactic and lexico-semantic features (i.e., regions involved in the processing of gender agreement that are also sensitive to gender-marking regularities). Specifically, significant interaction effects between Gender Congruency and Gender Marking emerged in five left-lateralized clusters, including the pars triangularis within the IFG, the posterior part of the MTG/STG, the hippocampus, and the angular and supramarginal gyri. Critically, the behavioral data is congruent with the fMRI results[2]: the subjects classified congruent determiner-noun pairs as grammatically correct more easily and accurately (i.e., with shorter decision times and lower error rates) than incongruent pairs (for similar behavioral results see Akhutina et al., 1999; Caffarra et al., 2014; Gollan and Frost, 2001; Holmes and Segui, 2004). This differentiation was evident for both transparent and opaque nouns. However, regarding the RTs, this congruency effect was larger for opaque than for transparent nouns, as evidenced by the significant interaction between Gender Congruency and Gender Marking. Overall, these results point out that the neural substrates of agreement processing could be constrained by the available form-based and/or lexico-semantic cues. The following paragraphs will discuss the relevance of these three main findings.

Which brain regions are sensitive to gender agreement within a noun phrase [Main effect of Gender Congruency]? In line with our hypothesis and in consonance with previous fMRI and ERP findings, we have demonstrated a clear distinction between the neural circuits

2 This congruency between behavioral and fMRI results could lead us to think that the engagement of these regions may reflect the recruitment of the conflict monitoring system, probably triggered by the detection of a gender grammatical error. In fact, activation of some of these brain areas (e.g., such as the middle frontal, the anterior and middle cingulate cortex, the inferior parietal cortex, and the cuneus/precuneus) has been previously reported, not only in the context of language processing but also for high visual attention demanding tasks (e.g. Stroop task). However, it is important to notice that the critical results here are not related with these bilaterally activated fronto-parietal areas. Importantly, similar activation of a left-lateralized fronto-temporo-parietal network have been previously reported for comprehension (Nieuwland et al., 2012) and passive reading tasks (Pallier et al., 2011), suggesting that these regions are crucial for the processing of linguistic information rather than attentional processing triggered by the detection of conflicting information. To further confirm that our critical effects were not biased by task difficulty effects, the same analyses were also run including the decision times as a covariate (see also Figure 1S and supplementary material). This analysis showed that the difficulty to detect gender grammatical errors impact the brain response. However, the regions resulting from this analysis are different from the ones we are focusing on (i.e., main effects and interactions).

involved in the processing of gender congruent and incongruent items. Namely, while a bilateral widespread fronto-parietal network was recruited for *Gender Mismatch* relative to *Gender Match* condition, a more circumscribed fronto-temporal network was engaged for *Gender Match* as compared to *Gender Mismatch*. In the former case, the circuit engaged by ungrammatical constructions included cortical and subcortical regions such as the dorsal striatum, the middle and medial superior frontal gyrus, the pre- and post-central gyrus, the anterior and middle cingulate cortices, the inferior and superior parietal cortices[3], and the left middle frontal gyrus. In the latter case, the pars opercularis and triangularis within the left IFG and the posterior part of the left MTG/STG were identified as critical areas for the processing of grammatically correct constructions. These results suggested that when incongruent information (e.g., a grammatical gender violation) is detected, the system certainly launches different mechanisms in an attempt to resolve the conflicting cues. Combining the current results with what previous findings suggest, it is possible to advance some hypotheses about the role of some of these regions.

Firstly, our results demonstrate that each type of construction evokes differentiated responses in the **left middle frontal gyrus**. This region showed similar effects for transparent and opaque nouns, with higher activation for incongruent than for congruent items (for similar results see Folia et al., 2009 [gender mismatch between pronouns and antecedents in Dutch]; Kuperberg et al., 2008; and Newman et al., 2003 [finiteness violations in English]; Nieuwland et al., 2012 [verb-object violations in Basque]). Interestingly, previous studies have demonstrated that the response of this area is independent of the type of morphosyntactic feature (Mancini et al., 2017 for a comparison between number and person mismatches) and the type of grammatical dependencies (Carreiras et al., 2015 for a comparison between determiner-noun and subject-verb relations). Based on these previous

[3]The anterior and middle cingulate cortices, as well as the inferior and superior parietal cortices, exhibited negative response (deactivation) compared to the fixation baseline condition, with greater deactivation for mismatching than for matching constructions. These areas are sensitive to the presence of morphosyntactic mismatches. Using different tasks (i.e., language-related or not), previous studies have shown a similar deactivation pattern in these regions. These effects have been frequently associated with the functioning of the default mode network (i.e., regions exhibiting high resting baseline responses) (Gusnard and Raichle, 2001; Kuperberg et al., 2003; Kuperberg et al., 2008; Lütcke and Frahm, 2008; Pardo et al., 1990; Raichle, 2015; Sohn et al., 2007). In particular, **the anterior cingulate cortex** has been identified as the neural epicenter of an amodal conflict-monitoring system responsible for distinguishing between a conflict associated with the input signal and a processing error (Du et al., 2013; Gunter et al., 2000; Mancini et al., 2017; Olichney et al., 2010; Quiñones et al., 2014; van de Meerendonk et al., 2011; van de Meerendonk et al., 2009; van de Meerendonk et al., 2010; Vissers et al., 2006; Ye and Zhou, 2009). This system seems to be reinforced after the detection of conflicting information such as the current gender agreement violation.

findings, it is possible to hypothesize that activity in this region could be reflecting morphosyntactic feature-checking mechanisms, which are equally enhanced regardless of the transparency of the nouns (see Quiñones et al., 2014 for a detailed discussion about this hypothesis).

Secondly, in consonance with previous evidence, we report that **the pars opercularis and triangularis within the left IFG and the posterior part of the left MTG/STG** distinguish between incongruent and congruent items. These regions have previously been identified as a crucial epicenter of the language-specific network (Friederici, 2011, 2012; Hagoort, 2005, 2013, 2014; Price, 2010, 2012). A harmonic engagement between these left-lateralized perisylvian regions seems to be critical for decoding linguistic information, not only in the context of sentence comprehension but also in the context of single word processing (Friederici and Kotz, 2003; Grodzinsky and Friederici, 2006; Lau et al., 2008; Petersson et al., 2012; Petersson and Hagoort, 2012; Zhu et al., 2012). However, despite the considerable amount of evidence concerning this topic, it has not been possible to reach a consensus about the functions carried out by each of these areas during sentence processing (Bornkessel-Schlesewsky and Schlesewsky, 2013; Friederici, 2011, 2012; Hagoort, 2005 for three different perspectives about this topic; 2013; Xu et al., 2013). In this particular case, where the syntactic gender consistency was manipulated between determiners and nouns, the engagement of these regions could be mediating the operations behind the integration of the two syntactic elements in a noun-phrase structure. While the MTG/STG seems to underlie the mechanistic procedures required for decoding the inputs (e.g., access/retrieval of morphosyntactic and lexical information, structure building processing and form-to-meaning mapping), the IFG seems to reflect a processing cost that shoots up when the system tries to integrate different sources of information (Baggio and Hagoort, 2011; see Hagoort, 2013; Hagoort, 2014 for a discussion about this topic; and see also Hagoort and Indefrey, 2014).

<u>*Does the brain process transparent and opaque nouns in the same way or differently [Main effect of Gender Marking]?*</u> Regarding the neural network sensitive to gender-to-ending regularities, the current fMRI results demonstrate a dissociation between transparent and opaque nouns. Interestingly, and in accordance with previous evidence, the statistical parametric map obtained from the main effect of Gender Marking revealed a bilateral pattern of activation including temporal, parietal, and frontal regions (Heim, 2008; Hernandez et al., 2004; Miceli et al., 2002; Padovani et al., 2005). On the one hand, *Opaque Nouns* compared

to *Transparent Nouns* produced increased responses in a widespread, bilaterally-distributed fronto-parieto-temporal network. On the other hand, we found higher neural responses for *Transparent Nouns* than for *Opaque Nouns* in left occipito-parietal regions. The difference in hemispheric lateralization is very salient: while the left hemisphere is more sensitive to transparent nouns, opaque nouns recruit regions in both hemispheres (Cacciari and Cubelli, 2003; see Friedmann and Biran, 2003 for contradictory results; and see also Laiacona et al., 2001; Luzzatti and De Bleser, 1999). From a theoretical perspective, transparent and opaque nouns differ in terms of gender information sources: while the gender information of transparent nouns could be accessed based on both form-based and lexical cues, the gender information of opaque nouns relies exclusively on lexical information. The differences in the neural responses characterizing transparent and opaque nouns provide conclusive evidence that the system can be fine-tuned depending on the available gender-related information sources.

As far as the processing of opaque nouns is concerned, our data parallel the neural responses that have previously been observed in other fMRI studies that analyzed the critical role of the left IFG in processing syntactic gender. However, our data extend this finding by suggesting that there is a coupling between the **IFG and other parietal and temporal regions** during the access/retrieval of gender information. This empirical finding supports the predictions of the neurocognitive model proposed by Heim (2008). Similarly, some authors have highlighted the posterior portion of the MTG as a hub for lemma selection and retrieval processes (Bemis and Pylkkänen, 2011, 2012; Braun et al., 2015; Choi et al., 2015; Gold et al., 2006; Hernandez et al., 2015; Indefrey and Levelt, 2004; Levelt et al., 1999; Pylkkänen et al., 2014; Rissman et al., 2003).

Concerning the processing of transparent nouns, increases in the activation of **left occipito-temporal regions** have previously been reported for Spanish determiner-noun pairs (but also see Dikker et al., 2010 for a different form-based effect in these posterior regions; see Molinaro et al., 2013). The involvement of these areas was considered as reflecting morphological decomposition processing (Božić and Marslen-Wilson, 2013; Božić et al., 2013; Gold and Rastle, 2007; Solomyak and Marantz, 2010). Interestingly, in the current experiment, the recruitment of these regions by transparent nouns is coupled with a significant response of the supramarginal gyrus. The selective engagement of this parietal area might reflect a processing cost associated with decoding the redundant morphological information. Crucially, this is the first time that such increased occipito-temporal activity is reported for transparent as compared to opaque nouns. Probably it is the combination of gender marking and agreement congruency that boosts the morphological decoding of transparent nouns. The gender morphosyntactic information of the determiners might enhance expectations concerning not only the gender morphosyntactic values of the nouns, but also the presence of a given morphological gender mark (i.e., canonical Spanish suffixes) (see Caffarra and Barber, 2015; Caffarra et al., 2014; Caffarra et al., 2015 for concomitant ERP result; and also see DeLong et al., 2005 for a discussion about this topic). In summary, both the hemispheric differential contributions and the distinctions regarding the areas involved in the processing of transparent and opaque nouns point in the same direction: the retrieval of gender morphosyntactic values required to compute the agreement relation relies on different sources of information, depending on the transparency of the nouns.

Is our brain sensitive to gender-marking cues during the computation of determiner-noun agreement relations [Interaction effect]? The interaction between Gender Congruency and Gender Marking revealed a functional coupling between **the pars triangularis within the left IFG, the hippocampus, and the posterior part of the left MTG/STG**. The neural activity of these areas follows the same pattern across conditions: the differences between congruent and incongruent items for transparent and opaque nouns were significant in these three regions. In the former case –transparent nouns– incongruent determiner-noun pairs exhibited greater response than congruent pairs, whereas in the latter case –opaque nouns– it was the congruent condition which produced the more conspicuous signal. This is an important result as, in contrast with the large number of previous studies that have demonstrated the engagement of this left fronto-temporal activity during sentence comprehension, there has been little empirical evidence so far reporting this coupling during gender agreement processing (see Heim, 2008 for a review of this topic; Miceli et al., 2002; Padovani et al., 2005).

The interaction effect emerging in these areas could be reflecting a lexical processing cost that affects differently the decoding of gender features and the building of local syntactic units (i.e., noun phrases) in transparent and opaque nouns. Therefore, the difference between conditions emerging in these regions can be explained by referring to studies and models that assume pMTG involvement in the extraction of morphosyntactic information from the morphological or lexical representation of a noun to build syntactic structure (Hagoort, 2005;

Lau et al., 2008; Molinaro et al., 2015; Pallier et al., 2011). The deeper the processing system must go to extract the gender specification of a noun (Levelt et al., 1999), the greater the processing cost over this temporal region. The divergence in the congruency differential response found for transparent and opaque nouns could be explained by the hierarchical organization of the lexicon. Activity in these particular regions seems to be sensitive to both the building of the local syntactic unit (i.e., as the difference between congruent and incongruent items suggests) and the "lexical load" distinguishing transparent and opaque nouns. The similarities in the response patterns shown by the hippocampus and the posterior MTG/STG constitute a critical piece of evidence supporting the contribution of these regions during the retrieval of gender-related information[4] (see Duncan et al., 2012 for a discussion about hippocampus function; see also Nieuwland and Martin, 2017; Nieuwland et al., 2012 for previous evidence about the hippocampus implication during sentence processing).

In addition to this fronto-temporal system, the interaction effect also showed that the engagement of **the supramarginal and angular gyri** depends on both Gender Marking and Gender Congruency factors. While in the case of transparent nouns, the neural responses for incongruent and congruent determiner-noun pairs did not differ in amplitude, in the case of opaque nouns, the incongruent items produced greater responses than the congruent ones. As mentioned above, the functional characterization of parietal regions during sentence processing has received much less attention than the role played by inferior frontal and temporal areas. This situation becomes critical when we review the literature on agreement computation. For instance, Hagoort and colleagues (Hagoort, 2013; Hagoort and Indefrey, 2014) defined parietal regions as critical nodes engaged for the retrieval of different types of linguistic information (e.g., morphological, phonological, lexico-semantic, and/or syntactic

[4] Some authors have proposed that the hippocampus computes the correspondence between the expected and the encountered signals (Duncan et al., 2012; Hasselmo et al., 1995; Kumaran, 2008; Kumaran and Maguire, 2005, 2006, 2007; Lisman and Grace, 2005). In line with this claim, Duncan et al. (2012) labeled one specific subregion within the hippocampus (i.e., CA1) as a mismatch/match detector. However, the role this region plays in language comprehension has received much less attention than its general involvement in memory functions. Indeed, patients with hippocampal impairment show problems in the on-line comprehension of sentences (see Duff and Brown-Schmidt, 2012 for a review of this topic; see also Duff and Kurczek, 2013; Kurczek, 2014; Kurczek et al., 2013). Specifically, Kurczek et al. (2013) demonstrated that hippocampus damage disrupts the pronoun referential processing (e.g. *"Melissa is playing violin for Debbie/Danny… She*$_{[target]}$ *is …"*) during sentence comprehension, suggesting its critical role in maintaining and integrating language information. Interestingly, Ullman and colleagues (Ullman, 1999; Ullman, 2004; Ullman et al., 1997) proposed that a declarative memory system sub-served by medial temporal regions (including the hippocampus) underlies lexical processing (i.e., learning, storage, and retrieval) (see also Lum et al., 2012; Lum et al., 2015). Empirical evidence from clinical populations has shown that impairments in this declarative system worsen performance in converting irregular verbs (i.e., relative to regular verbs) to their past tense forms (Ullman, 1999; Ullman, 2004; Ullman et al., 1997).

information). In contrast, Bornkessel-Schlesewsky and Schlesewsky (2013) highlighted the critical role played by parietal areas during syntactic combinatorial operations. According to the current data, both theoretical accounts seem to be plausible. Activity in parietal regions seems to depend on both Gender Congruency and Gender Marking, suggesting that these areas are sensitive to lexical and syntactic combinatorial processes. During the establishment of local grammatical relations, opaque nouns appear to impose a processing cost in the integration of the morphosyntactic information. This could be affected by different "lexical loads" associated with transparent and opaque nouns, respectively. It is important to stress that this is the first time the engagement of parietal regions has been reported during agreement computation as a function of different lexical and morphosyntactic factors.

Future Directions. The comparison between grammatical and ungrammatical constructions allows researchers to characterize different aspects of agreement and sentence comprehension in a fine-grained way. However, it critically confounds the neurophysiological routines involved in agreement and sentence comprehension with those triggered by the detection of syntactically ill-formed constructions. Critically, a new perspective in understanding these neural mechanisms would be possible by testing agreement in a more ecological and naturalistic way. For instance, by focusing on grammatically correct sentences, we can parametrically manipulate the syntactic and semantic dimensions, namely, from simpler to more complex syntactic structures (i.e., from determiner-noun to noun-verb agreement) and from semantically simpler to more complex agreement relations (i.e., from determiner-noun transparent grammatical gender relations to conceptual gender agreement relations). In addition, in order to reconcile the different theoretical accounts for gender and agreement processing, the comparison between written and spoken language comprehension should be addressed in further studies.

Conclusions. The current fMRI study demonstrated the preferential role of different left-lateralized perisylvian regions in the establishment of syntactic gender agreement. Crucially, these data illustrated, for the first time, how our brain is sensitive to formal gender-to-ending cues during the computation of determiner-noun agreement relations: different sources of gender information associated with nouns affect the neural circuits involved in the computation of local agreement dependencies. When gender orthographical/morphological cues are available (i.e., as in the case of transparent nouns), both formal and lexical information is used to establish grammatical relations. The circuits underlying these mechanisms involve regions associated with morphological decomposition (i.e., occipito-temporal and parietal regions exhibiting a main effect of Gender Marking) but also regions associated with lexical processing (i.e., activity in fronto-temporal and parietal regions depending on both Gender Marking and Gender Congruency). In contrast, when no formal cues are available (i.e., as in the case of opaque nouns), gender information is retrieved from the lexicon. These processes seem to be mediated by the posterior part of the MTG/STG, the pars triangularis within the IFG, and the hippocampus. In addition, parietal areas seem to be critical for the processing of opaque nouns, since they interact with the fronto-temporal loop (i.e., posterior MTG/STG and pars triangularis within the IFG). It is important to highlight that this is the first time that such a clear functional relation between the posterior MTG/STG, pars triangularis within the IFG, and parietal regions has been observed during agreement computation. Critically, these results build upon the previous neuroanatomical models proposed in the context of both gender processing (Heim, 2008) and sentence comprehension (Bornkessel-Schlesewsky and Schlesewsky, 2013; Friederici, 2011, 2012; Friederici and Gierhan, 2013; Hagoort, 2003, 2005, 2013). More importantly, they point out that the processing of formal and conceptual cues during the establishment of grammatical relations depends on a complex and dynamic fronto-temporo-parietal system that is bilaterally distributed, challenging the deep-rooted idea about the left perisylvian circuit decoding grammatical information.

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Table 1

Table I. Error rates and mean decision times (in ms) for both agreement patterns (match and mismatch) in the two types of nouns (transparent and opaque) with the corresponding standard error between parentheses.

	Mean decision times		**Error rates**	
	Match	**Mismatch**	**Match**	**Mismatch**
Transparent	714.85 (26.92)	809.42 (32.29)	4.31 (0.49)	8.62 (1.16)
Opaque	689.30 (26.83)	825.00 (34.96)	3.23 (0.66)	6.66 (0.96)

Table 2

Table II. Significant activation clusters resulting from the contrast Mismatch > Match, including both Types of Nouns (Transparent and Opaque).

Hemisp.	Region	x,y,z {mm}	Peak level	Cluster level
			Z	Vx
Left	Medial Orbitofrontal	-4 52 -2	**5,69**	653
	Middle Frontal Gyrus	-26 24 50	**6,42**	839
	Ant Cingulate	-6 38 -6	**4,56**	
	Paracentralobule	-6 -22 60	**5,92**	269
	Precentral Gyrus	-42 -6 32	**4,55**	231
	Postcentral Gyrus	-44 -16 34	4,39	
	Angular Gyrus	-48 -66 42	**5,27**	528
	Precuneus	-4 -48 10	**6,71**	1439
	Post Cingulate	-8 -40 26	**6,11**	
	Sup Occipital/Cuneus	-16 -82 28	**5,78**	
	Lingual	-4 -74 -2	**5,12**	317
Right	Medial Sup Frontal Gyrus	10 52 2	**6,88**	653
	Middle Frontal Gyrus	26 54 6	**5,14**	
	Precentral Gyrus	50 12 42	**5,24**	279
	Insula	34 -2 16	**6,14**	280
	Caudate	14 14 12	**4,69**	
	Putamen	26 8 10	**4,56**	
	Supp Motor Area	2 -16 68	**4,47**	269
	Lingual	8 -70 -4	**4,49**	317

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 cluster level after FWE or FDR correction, if indicated in bold and underline are significant at the peak level after FWE or FDR correction. Post: Posterior; Ant: Anterior; Sup: Superior; Supp: Suplementary.

Table 3

Table III. Significant activation clusters resulting from the contrast Match > Mismatch, including both Types of Nouns (Transparent and Opaque).

Hemisp.	Region	x,y,z {mm}	Peak level	Cluster level
			Z	Vx
Left	Oper Inf Frontal Gyrus	-48 14 22	**4.36**	359
	Tri Inf Frontal Gyrus	-41 16 30	3,61	
	Sup Frontal Gyrus	-24 -4 72	**6,06**	264
	Supp Motor Area	-10 14 68	**4.85**	
	Inf Parietal Gyrus	-50 -28 50	**4,52**	193
	Post Middle Temporal	-38 -64 16	**4.40**	319
	Middle Occipital	-42 -70 14	**6,2**	
Right	Oper Inf Frontal Gyrus	44 10 22	**4,75**	196
	Middle Frontal Gyrus / IFG	36 -2 60	**5,28**	513
	Sup Frontal Gyrus	22 2 66	**6,26**	922
	Supp Motor Area	10 16 68	**5,74**	
	Middle Cingulate	10 12 34	**5,26**	
	Sup Parietal Gyrus	16 -48 56	**5,18**	158
	Sup Temporal Gyrus	66 -36 14	**5,05**	221
	Calcarine	12 -78 18	**4,86**	132

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 cluster level after FWE or FDR correction, if indicated in bold and underline are significant at the peak level after FWE or FDR correction. Sup: Superior; Ant: Anterior; Inf: Inferior; Supp: Suplementary; Tri: Triangular; Oper: Opercular.

Table 4

Table IV. Significant activation clusters resulting from the contrast Opaque Nouns > Transparent Nouns, including both grammatical patterns (Mismatch and Match).

Hemisp.	Region	x,y,z {mm}	Peak level	Cluster level
			Z	Vx
Left	Oper Inf Frontal Gyrus	-44 14 10	**7,55**	2921
	Insula	-36 20 8	**7,17**	
	Medial Sup Frontal Gyrus	-6 48 20	**5,88**	3446
	Sup Frontal Gyrus	-20 4 48	**4,92**	303
	Precentral	-28 -16 56	**4,73**	
	Paracentralobule	-12 -38 72	**4,64**	284
	Thalamus	-4 -24 6	**4,7**	299
	Post Middle Temporal	-58 -8 -10	**4,56**	176
	Fusiform	-36 -38 -16	**7,44**	341
	ParaHippocampal	-22 -28 -16	**5,29**	
	Lingual	-12 -40 -8	**5,04**	
	Hippocampus	-22 -22 -10	**6,65**	
Right	Tri Inf Frontal Gyrus	40 38 6	**6,93**	1871
	Insula	36 4 14	**6,69**	
	Oper Inf Frontal Gyrus	50 16 20	**5,86**	
	Meiddle Frontal Gyrus	28 22 38	**5,95**	3446
	Middle Cingulate	10 22 40	**5,85**	
	Supp Motor Area	2 6 58	**5,69**	438
	Sup Parietal Gyrus	20 -58 62	**6,15**	629
	Postcentral	34 -42 62	**5,52**	
	Thalamus	4 -24 4	**6,33**	299
	Sup Temporal Gyrus	62 -32 16	**5,93**	1803
	Precentral	54 -2 48	**5,9**	
	Lingual	6 -68 6	**4,93**	481
	Calcarine	10 -80 8	4,16	

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 cluster level after FWE or FDR correction, if indicated in bold and underline are significant at the peak level after FWE or FDR correction. Sup: Superior; Post: Posterior; Inf: Inferior; Supp: Suplementary; Tri: Triangular; Oper: Opercular.

Table 5

Table V. Significant activation clusters resulting from the contrast Transparent Nouns > Opaque Nouns, including both grammatical patterns (Mismatch and Match).

Hemisp.	Region	x,y,z {mm}	Peak level	Cluster level
			Z	Vx
Left	Supp Motor Area	-4 16 64	**5,15**	237
	SupraMarginal	-44 -44 32	**5,5**	689
	Angular Gyrus	-60 -58 30	**4,76**	
	Middle Occipital	-44 -72 36	4,29	
	Sup Occipital	-12 -86 22	**6,33**	189
	Sup Occipital	-18 -86 12	**6,14**	
	Calcarine	-22 -60 14	**6,3**	220
	Precuneus	-20 -50 14	**4,57**	
Right	Supp Motor Area	6 18 64	**5,3**	237
	Cuneus	8 -72 36	3,75	220
	Middle Occipital	40 -66 26	**5,51**	221

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 cluster level after FWE or FDR correction, if indicated in bold and underline are significant at the peak level after FWE or FDR correction. Sup: Superior; Supp: Suplementary.

Table 6

Table VI. Significant activation clusters resulting from the interaction effects between Gender-marking and Gender Congruency.

Region (Left Hemisp.)	x,y,z {mm}	Interaction		Simple effects	
		Peak level	Cluster level	Tansparent	Opaque
		Z	Vx	Z	Z
Tri Inf Frontal Gyrus	-48 20 10	5.58	276	+4.11	-6.09
Post MTG/STG	-62 -26 -2	4.17	316	+5.43	-4.22
Hippocampus	-28 -34 -12	3.24	26	+5.27	-3.32
Supramarginal Gyrus	-64 -30 28	3.61	59	n.s	+4.9
Angular Gyrus	-52 -66 38	4.18	80	n.s	+6.64

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 cluster level after FWE or FDR correction, if indicated in bold and underline are significant at the peak level after FWE or FDR correction. The sign of the Z scores indicates the direction of each interaction. The positive sign indicates that the neural response for the Mismatch condition was higher than for the Match condition. Whereas the negative sign indicates the opossite pattern, higher neural response for Match than for Mismatch. Tri: Triangularis; Inf: Inferior; Post: Posterior; MTG/STG: Middle and superior temporal gyrus;Trans: Transparent.

Figure 1
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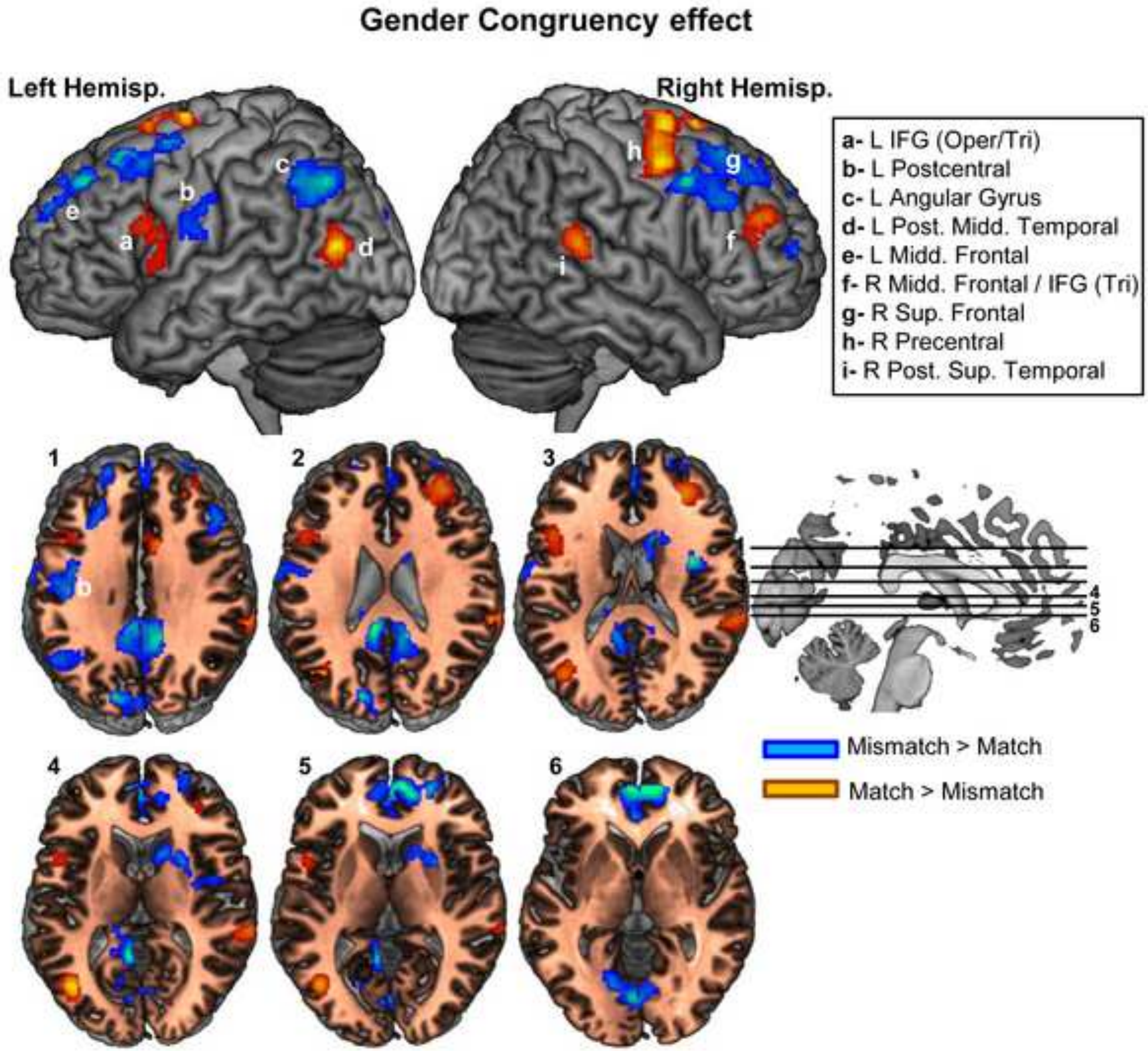

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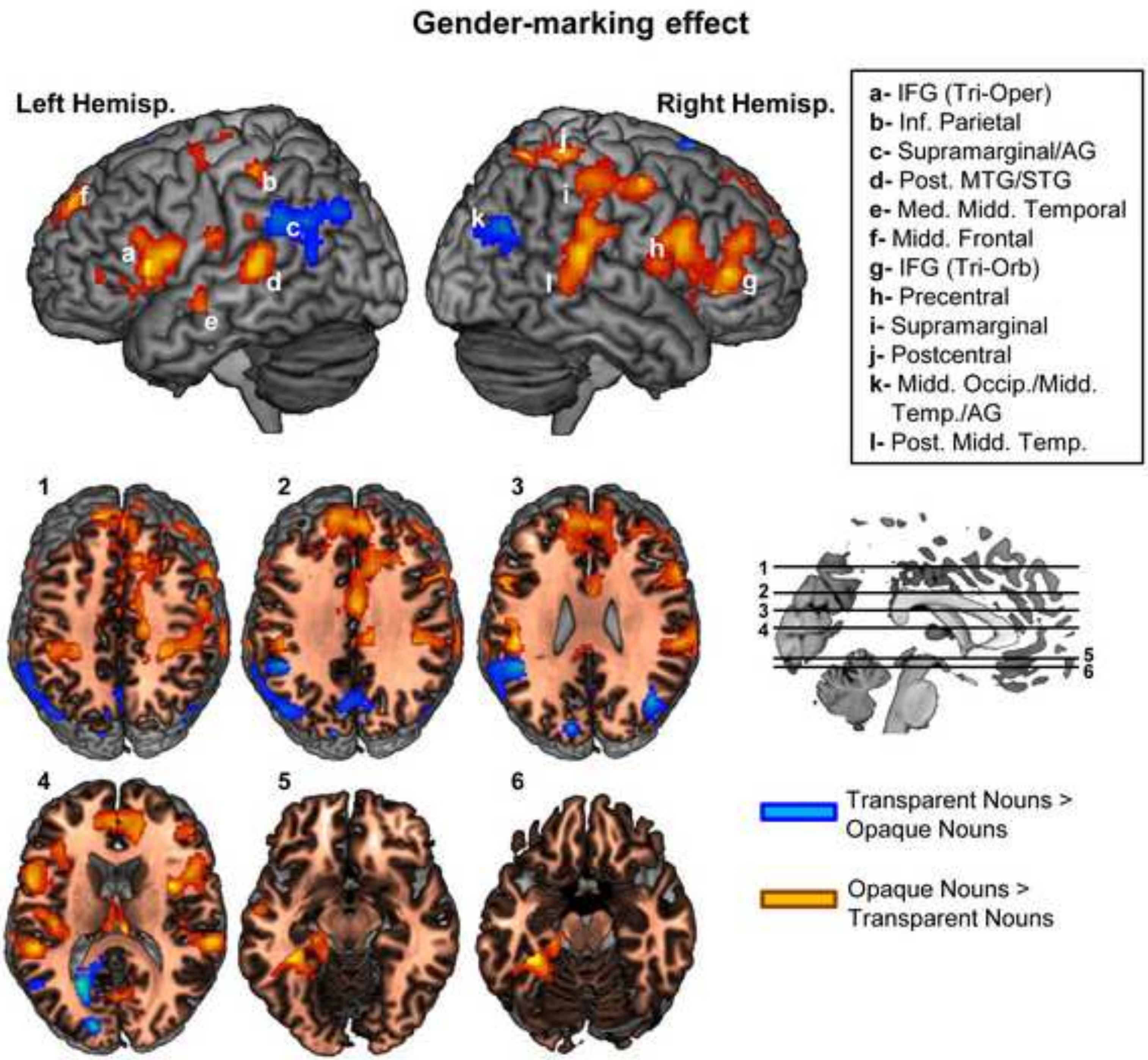

Figure 3

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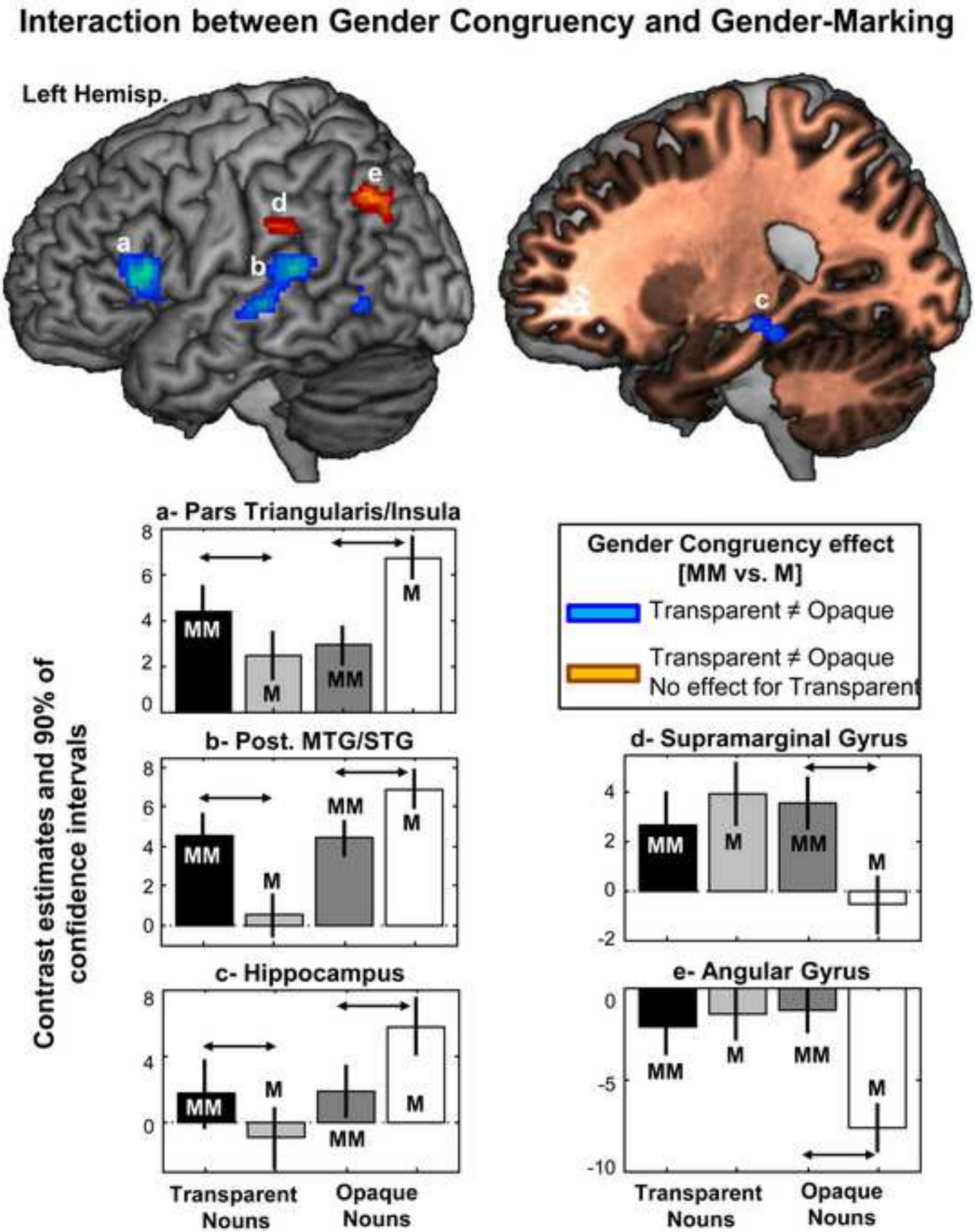

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