Where agreement merges with disagreement: fMRI evidence of subject–verb integration

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Abstract

Language comprehension is incremental, involving the integration of information from different words together with the need to resolve conflicting cues when unexpected information occurs. The present fMRI design seeks to segregate the neuro-anatomical substrates of these two processes by comparing well-formed and ill-formed sentences during subject–verb agreement computation. Our experiment takes advantage of a particular Spanish feature, the verb agreement phenomenon: a subject–verb agreement mismatch that results in a grammatical sentence (“Los pintores trajimos…” [The painters brought us…]). Comprehension of this construction implies a shift in the semantic interpretation of the subject from 3rd-person to 1st-person, enabling the phrase “The painters” to be re-interpreted as “We painters”. Our results include firstly a functional dissociation between well-formed and ill-formed sentences with Person Mismatches: while Person Mismatches recruited a fronto-parietal network associated to monitoring operations, grammatical sentences (both Unagreement and Default Agreement) recruited a fronto-temporal network related to syntactic–semantic integration. Secondly, there was activation in the posterior part of the left middle frontal gyrus for both Person Mismatches and Unagreement, reflecting the evaluation of the morpho-syntactic match between agreeing constituents. Thirdly, the left angular gyrus showed increased activation only for Unagreement, highlighting its crucial role in the comprehension of semantically complex but non-anomalous constructions. These findings point to a central role of the classic fronto-temporal network, plus two additional nodes: the posterior part of the left middle frontal gyrus and the left angular gyrus; opening new windows to the study of agreement computation and language comprehension.

Keywords: Agreement, fMRI, Left middle frontal gyrus, Angular gyrus.
However, this approach critically confounds the neurophysiological routines involved in agreement comprehension with the ones triggered by the detection of syntactically ill-formed constructions.

(1) *2El pintor trajiste los cuadros a la galería Person Mismatch
“The painter3sg brought2sg the paintings to the gallery
(2) Los pintores trajeron los cuadros a la galería Default Agreement
The painters3pl brought2pl the paintings to the gallery.
However, a new perspective in understanding these mechanisms is possible if we take advantage of “legal” agreement mismatches (i.e. agreement mismatches that are nevertheless *grammatically correct*) that are available in some languages. One such case is *Unagreement* in Spanish, an agreement pattern characterized by the presence of a morphosyntactic *Person Mismatch* between the subject and the verb (Höhn, 2012; Mancini et al., 2011a, 2013).

In (3) below, despite the fact that a third person plural subject is followed by a first person plural verb, a well-formed grammatical Spanish sentence is generated. This morphosyntactic mismatch is overcome by assigning to the 3rd person subject argument a 1st person plural interpretation (from “The painters” to “We painters”). From the point of view of the discourse representation of the sentence, this subject shift for the subject implies a covert integration operation through which the speaker underlying the 1st person plural verb is included in the group of individuals referred to by the subject argument (from “they” to “they + myself”). In contrast, no such integration operation can be performed in (1), where the non-participant status of the subject form (“he/she”) is incompatible with the addressee role invoked by the 2nd person verb (“you”).

(3) Los pintores trajimos los cuadros a la galería Unagreement
The painters3pl brought1pl the paintings to the gallery.

The uniqueness of the *Unagreement* pattern in (3) resides in the fact that it shares properties with both *Default Agreement* (i.e. grammaticality) and *Person Mismatch* (i.e. morpho-syntactic mismatch), but at the same time it differs from both (as illustrated in Table 1). On the one hand, *Unagreement* shares a subject–verb morpho-syntactic mismatch with person violations but differs from them because it can be successfully integrated. Thus, both person violations and *Unagreement* should trigger processing difficulties in the evaluation of the morpho-syntactic consistency of subject and verb, independently of the grammaticality of the utterance. On the other hand, *Unagreement* shares grammaticality with *Default Agreement*, but unlike this, it requires additional semantic-discourse analyses to overcome the morpho-syntactic incongruity and to perform the subject shift (from “they” to “they + myself”), a process referred to as “person anchoring” by Mancini et al., 2013.

From the perspective of sentence processing, the “grammatical mismatch” status of *Unagreement* offers therefore the opportunity to isolate the neural mechanisms supporting successful semantic integration that characterize correct sentences, from those underlying the evaluation of the morpho-syntactic subject–verb consistency. Importantly, these two processing steps cannot be disentangled using traditional contrasts between correct and agreement-anomalous sentences because of the impossibility of integrating two utterly mismatching values into a common and meaningful semantic representation.

In the following paragraph, we outline the main electrophysiological and functional neuroimaging findings emerging from the literature on agreement computation and explain the role of this study in filling the gaps of this literature.

Electrophysiological correlates of agreement processing

Agreement processing has been extensively studied using ERPs (Event-Related Potentials), highlighting two different time intervals that are sensitive to the presence of subject–verb agreement violations (see Molinaro et al., 2011 for a review). Specifically, in an earlier time interval (between 300 and 500 ms) two effects have been reported. The first is a negative effect with a typical left anterior topographical distribution (Left Anterior Negativity, LAN) (Kutas and Hillyard, 1983) that has been associated to the detection of morphosyntactic violations (Friederici, 2011, 2012; Molinaro et al., 2011; Silva-Pereyra and Carreiras, 2007). The LAN effect differs from a more posteriorly distributed component (N400) found in a similar time interval (Clements-Stephens et al., 2012; Kutas and Federmeier, 2000; Kutas and Hillyard, 1983) and is usually thought to reflect lexical-semantic processing difficulties, as well as contextual and world-knowledge predictability (Hagoort et al., 2004; Kutas and Hillyard, 1984; Molinaro et al., 2010, 2012).

In a subsequent temporal interval, agreement mismatch-related processing has normally been found to give rise to a positive deflection, arising about 600 ms post-stimulus onset (P600) (Barber and Carreiras, 2005; Mancini et al., 2011a,b; Silva-Pereyra and Carreiras, 2007). Several lines of evidence have indicated that the P600 is related to integration efforts between the presently-processed elements and the previous context, based on both semantic and syntactic information (Friederici, 2011; Kaan et al., 2000; Kim and Osterhout, 2005; Kolk et al., 2003; Kuperberg et al., 2007), re-analysis processes (Barber and Carreiras, 2005; Carreiras et al., 2004; Molinaro et al., 2011), or access to discourse-related information (Brouwer et al., 2012; Kaan and Swaab, 2003). From a domain-general perspective, the P600 has been functionally interpreted as indexing conflict-monitoring processes aimed at detecting errors, and triggering corrective actions when there is a mismatch between the predicted and the observed event (van de Meerenendonk et al., 2009, 2010, 2011).

While all these studies have investigated the process of subject–verb agreement by comparing anomalous and grammatically correct sentences, Mancini et al. (2011b) used *Unagreement* sentences and compared them to *Default Agreement* and ill-formed patterns (see examples 1, 2 and 3). These authors found an N400 component for both the *Unagreement* and the *Person Mismatch* conditions compared to *Default Agreement*. However, while the negativity elicited by the *Unagreement* extended between 350 and 750 ms mainly in the left posterior electrodes, the *Person Mismatch* elicited a widely distributed and larger negative effect between 350 and 500 ms that was evident also in bilateral frontal and posterior scalp regions. Mancini et al. (2011b) also reported that in contrast to *Unagreement*, person violations generated a P600 effect widely distributed over the scalp.

As for the N400 effect, the differences found in the timing and the topographic distribution of the *Unagreement* and *Person Mismatch* effects could reflect a functional dissociation between the two conditions after around 350 ms. Mancini et al. (2011b) consider that the N400 could be associated in both conditions with the violation of the expectation about the morpho-syntactic verb feature, triggering semantic–pragmatic difficulties in the composition of the speech act participant representation. Nonetheless, these authors note that while in the case of *Person Mismatch* the speech participants underlying subject and verb cannot be integrated into one unitary discourse representation, integration clearly occurs in *Unagreement*. Here, the first person plural interpretation results from including a speaker within the group referred to by “The painters”. This functional dissociation possibly implies the engagement of different neural generators (underlying the topographically and temporally dissociable N400 effects) that are respectively
recruited by the reading of grammatical (Unagreement) and ungrammatical (person violations) mismatches (Mancini et al., 2011b). From a neuro-anatomical perspective, Lau et al. (2008) indicate the anterior temporal cortex and the angular gyrus as crucial areas for the integration of incoming information into contextual and syntactic representations (see Bemis and Pytlíčková, 2012 for experimental evidence). Thus, these two neuro-anatomical regions are plausible candidates responsible for the successful integration that takes place in Unagreement sentences. On the other hand, the subsequent positive effect for Person Mismatch has been attributed to re-analysis operations taking place when ungrammatical information is being processed (Barber and Carreiras, 2005; Bornkessel and Schlesewsky, 2006; Fiedrich, 2012), while the absence of the P600 effect for Unagreement was taken to indicate that no reanalysis operation was triggered, since the sentence is grammatical. Thus, Unagreement and Default Agreement sentences undergo the same processes in this later phase.

However, the proposed early (starting ~350 ms) dissociation between the neurophysiological processes elicited by person violations and Unagreement is not completely supported by the ERP data. In fact, the main difference between the negative effects elicited by those two conditions (compared to Default Agreement) is reflected in the amplitude of the 300–500 ms effect (larger for person violations compared to Unagreement; see amplitude–topography interaction for ERPs discussed by McCarthy and Wood, 1985). Thus, it could be argued that the same initial process is at work for both Unagreement and person violations (involving the same neural network) and that this process is more taxed by encountering person violations. Unfortunately, electroencephalographic measures suffer from low spatial resolution at the brain level, thus limiting possible inferences about the extent of the brain networks underlying a specific scalp-measured effect. However, defining whether different or similar neurophysiological processes are initially elicited by person violations and Unagreement is crucial, since the early stages of processing are the ones reflecting core agreement computations (Molinaro et al., 2013). The present study capitalizes on the Mancini et al. (2011b) design, to finely detail the neural networks involved in different aspects of subject–verb agreement comprehension using the high spatial resolution of fMRI (functional Magnetic Resonance Imaging).

Neuro-anatomical bases of agreement processing

In the last few years the neuro-anatomical mechanisms of agreement comprehension have also been investigated using neuroimaging techniques in attempts to disentangle syntactic and semantic processing correlates in the brain. However, only a few fMRI studies have investigated subject–verb agreement processing (Kuperberg et al., 2003, 2008; Newman et al., 2003; Ni et al., 2000). Although manipulations have always involved anomalies between subject and verb, contradictory conclusions have been reported across these studies. For instance, Ni et al. (2000) investigated whether the brain distinguishes between the processing of grammatical information and meaning. Participants listened to sentences that were either grammatically correct or contained a verb finiteness violation (e.g. “Trees can grow...”) or a semantic violation (e.g. “Trees can eat...”). A dissociation between syntactic and semantic processing was found: while the former violations triggered significantly increased activity in the left inferior frontal gyrus, the latter activated several other regions in both hemispheres including the middle and superior frontal gyri and the superior temporal and parietal regions.

On the other hand, a study by Newman et al. (2003) compared sentences with number mismatches between subject and the second verb of a coordinated structure (e.g. “The lady praises the sister and meet the artist in the night”) against sentences including an extra verb (e.g. “The woman thanked the barber and paid the receptionist knew at the desk”) in an attempt to specify the contribution of the inferior frontal cortex during syntactic and semantic processing of sentences in a grammaticality judgment task. They found increased activation in pars opercularis of the inferior frontal gyrus for the syntactic violation, whereas the pars triangularis was more sensitive to the semantic violation. Additionally, they observed increased activation in the left posterior temporal region for both types of processing. Nonetheless, since the nature of the violation involving the extra verb is difficult to determine, the activation observed in this study may not exclusively reflect subject–verb processing difficulties.

With the same goal, Kuperberg et al. (2003) carried out an fMRI study in which they presented the participants with three different types of sentences: grammatically correct (e.g. “We couldn’t sleep at night because the baby would cry”), finiteness anomaly (e.g. “…because the baby would cry.”), or pragmatic violation (e.g. “…because the baby would remember.”). These authors found that relative to the grammatically correct sentences, similar neural regions are recruited by morphosyntactic and pragmatic information, but with different activation patterns. Similar results were reported by these authors in a follow-up study (Kuperberg et al., 2008), where they used the same design but added a distinction between two different types of semantically anomalous sentences: real-world pragmatic violations (“Every morning at breakfast the boys would plant the flowers.”) and anisymy semantic–thematic violations (“Every morning at breakfast the eggs would eat toast and jam.”). The common neuro-anatomical network recruited by both finiteness and animacy semantic–thematic violations relative to grammatically correct sentences included a widespread bilateral fronto-parieto-temporal response. Some of these regions exhibited more activity in response to the finiteness violations than to the animacy semantic–thematic violations (left inferior parietal lobule, bilateral anterior cingulate cortex and medial frontal gyrus). In this study, the authors introduced the idea that this fronto-parietal network could reflect the detection of conflict monitoring processes that would prevent comprehension errors (Kolk et al., 2003; Kuperberg et al., 2008; Vissers et al., 2006). However, since they provided no explanation as to why the recruitment of this monitoring network is not triggered by animacy semantic–thematic violations, this hypothesis was only partially borne out.

Overall, these controversial results illustrate the idea that the regions implicated in the processing of subject–verb agreement computation and its specific role in sentence comprehension are still uncertain. Different factors can be identified that potentially contribute to these discrepancies. Firstly, although violations always involved the verb, different aspects of verb inflection and sentence structure have been manipulated to create anomalies across studies. While the finiteness of the verb following the modal auxiliary was violated both in the Ni et al. (2000) and Kuperberg et al. (2003, 2008) studies, Newman et al. (2003) introduced a number mismatch between the subject and the second verb of a coordinate structure. It follows that differences in the nature of the subject–verb grammatical violation may generate the involvement of divergent neural regions concerned with different aspects of sentence processing.

Secondly, limitations and differences in the experimental designs adopted can be found. For instance, in the Ni et al. (2000) design, different types of violations (syntactic and semantic) were presented to the participants in separate scanning sessions, which may have caused a high degree of sentence structure predictability. This may have resulted in the adoption of different violation detection strategies in the Ni et al. (2000) study compared to the strategies developed in designs in which sentence structure is less predictable, as in the event-related design used by Kuperberg et al. (2003, 2008) and Newman et al. (2003).
Thirdly, the material presentation modality differs across studies: while in the study by Kuperberg et al. (2003, 2008) sentences were presented visually and word by word, in the Newman et al. (2003) study all the words were projected simultaneously. In contrast, Ni et al. (2000) used auditory presentation.

Finally, methodological differences concerning the fMRI analysis can also be found across studies in the way the comparisons between experimental conditions were carried out. For instance, while in Kuperberg et al. (2003, 2008) and Newman et al. (2003) the baseline for comparisons was always provided by linguistic material (correct version of the anomalous sentence), Ni et al. (2000) contrasted sentences with a non-linguistic baseline task (pitch judgment). In addition, only in the Kuperberg et al. (2003, 2008) studies were the comparisons between anomalous and well-formed sentences carried out considering both directions, making it possible to highlight the neural networks involved in the processing of grammatically correct sentences.

The present study

The experimental paradigm used in the present study attempts to isolate the neural substrates involved in agreement computation, with a special focus on both the evaluation of morpho-syntactic feature consistency and semantic integration complexity. To this end, we have improved on the methodological limitations mentioned above, using an event-related design in which the experimental manipulation always concerns a simple local subject–verb agreement configuration (e.g. “Los pintores trajeron/Los pintores trajimos/El pintor trajiste”). This type of manipulation therefore permits a cleaner observation of agreement processing, without the potential contamination from other confounds. In addition, we take advantage of the “intermediate” status of Unagreement between Default Agreement and person violation.

In light of the fMRI and ERP data reported above, we expect dissociation between the neural networks involved in the processing of correct grammatical sentences and the networks involved in the processing of anomalous sentences with a Person Mismatch. We predict that grammatical sentences (Default Agreement and Unagreement) in comparison to anomalous constructions should lead to increased activity within an extended left fronto-temporal network, including the anterior and posterior temporal cortex and the inferior and middle frontal gyri (Kuperberg et al., 2003, 2008). For the processing of grammatically anomalous constructions with a person violation, relative to grammatical ones (Default Agreement and Unagreement), we expect predominant activation of the anterior cingulate cortex and the posterior inferior or superior frontal cortices, brain regions previously related to conflict-monitoring operations (Kolk et al., 2003; Kuperberg et al., 2008; van de Meerendonk et al., 2011; Vissers et al., 2006).

Moreover, the present experimental design allows fine-grained discrimination of brain regions that are critically involved in core agreement processing. In fact, we should be able to report some region(s) associated to subject–verb morpho-syntactic mismatch detection showing increased activation for both Unagreement and Person Mismatch, irrespective of sentence grammaticality. Previous findings point to the Pars Opercularis within the left inferior frontal cortex and the anterior part of the left superior temporal gyrus as possible candidate regions for the processing of syntactic mismatches (Friederici, 2011; Hagoort, 2005).

Moreover, as indicated above, the successful integration of different speech roles in Unagreement sentences (speaker and non-participants) should involve the activation of areas related to semantic integration processes, reflecting the increased semantic-discourse complexity of these constructions compared to Default Agreement. In this sense, the angular gyrus and the anterior temporal cortex could be plausible candidates, and increased activation for the Unagreement compared to the other two conditions would confirm this. Among these two candidates, the angular gyrus could critically serve complex semantic integration operations (see also Bemis and Pykkänen, 2012). This would be supported by the neuro-anatomical localization of this region in the parietal cortex and its anatomical connectivity with different subsystems, including parietal (e.g. precuneus), temporal (e.g. inferior, middle and posterior temporal regions) and frontal networks (e.g. inferior frontal gyrus at the level of areas BA44 and BA45) (Catani and Mesulam, 2008; Catani and Thiebaut de Schotten, 2008; Catani et al., 2012; Thiebaut de Schotten et al., 2012). Recent meta-analyses have indeed emphasized the crucial role of the angular gyrus in the processing of different types of semantic complexity. Binder et al. (2009) proposed that this brain structure “occupies a position at the top of a processing hierarchy underlying concept retrieval and conceptual integration, thus suggesting that the angular gyrus mediates fluent conceptual combination, such as sentence comprehension, discourse, problem solving, and planning” (Binder et al., 2009, page 2776).

Materials and methods

Participants

Twenty-five right-handed healthy subjects participated as paid volunteers in the study. They were native speaker of Spanish and had normal or corrected to normal vision and no psychiatric or neurological records. Handedness was ascertained by an abbreviated Spanish version of the Edinburgh Handedness Inventory (Oldfield, 1971). All participants gave their written informed consent in accordance with guidelines approved by the Ethics and Research Committees of the Basque Center on Cognition, Brain and Language. The fMRI data of each individual subject were 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 following statistical analysis. A total of twenty-one participants (nine females), with ages ranging from 17 to 35 years (mean = 22.62, standard deviation = 4.43), were used to estimate the group effects.

Stimuli and experimental design

Each subject participated in a single session consisting of two pseudo-randomized repetitions of an event-related design functional scan. Each scan consisted in a serial presentation of sentences grammatically acceptable or not. Sentences were visually presented word by word and after each sentence a cue was shown instructing the participant to make a grammaticality judgment by pressing one of two different buttons (a go/no paradigm) (Fig. 1). Words were displayed in white letters on a black background. Each word was presented for 300 ms, followed by a 500 ms blank screen. In order to optimize the design
statistical efficiency, a fixation point (“+”) between successive sentences were presented in different (“jittered”) durations across trials (1.87, 3.56, 4.96 s, in the proportion of 57:28:15) (Dale, 1999).

The stimulation set consisted of 120 sentences which included three different conditions (in the proportion of 1:1:1): Default Agreement, Unagreement and Person Mismatch (see Fig. 1A). All sentences contained a lexical subject followed by a past tense verb (the critical word), which was always followed by at least two words. The two grammatical conditions included a plural subject, i.e. the Default Agreement and the Unagreement, whereas the ungrammatical condition (Person Mismatch) contained a singular subject. In the Default Agreement condition the third person plural subject is followed by a third person plural verb, while in the Unagreement condition the third person plural subject could be followed by both a first and a second person plural verb. Meanwhile, the Person Mismatch condition contained a third person singular subject followed by a second singular verb. The choice of past tense verbal forms was mainly motivated by the need to keep the length of the critical word balanced across conditions (Default Agreement: mean length = 9.66, SD = 2.5; Unagreement: mean length = 9.39, SD = 2.34; Person Mismatch: mean length = 9.38, SD = 2.34), which could not be done with other verb tenses.

In order to balance the proportion of acceptable/unacceptable sentences and avoid expectations concerning the morphological form of the verb, 120 filler sentences with a similar sentence structure were added to the material. Ungrammatical sentences contained both person and number mismatches between subject and verb. Importantly, since unacceptable experimental sentences (Person Mismatch condition) always involved a third person singular subject followed by a second person singular verb, incorrect fillers comprised both a third person singular subject followed by a third person plural verb (40 sentences, e.g. “El pinto3.sg trajo3.sg un cuadro…”), and a third person plural subject followed by a third person singular verb (40 sentences, e.g. “Los pintores3.pl trajeron3.sg un cuadro…”). Forty additional correct fillers of the type “El pinto3.sg trajo3.sg un cuadro…” were also added to balance the overall number of correct and incorrect sentences. This was in order to avoid expectations concerning the morphological form of the verb, especially for the ungrammatical sentences (see also Mancini et al., 2011b for additional methodological details and examples).

Despite the fact that the Unagreement pattern represents a marked agreement construction compared to the full agreement counterpart, its frequency of use is very high, above all in spoken Spanish. Due to the lack of an adequate corpus of spoken Spanish from which to draw the frequency of this pattern, in preparing the experimental materials we relied on the naturalness judgment task provided by a group of native speakers of Spanish, who did not take part in the experiment. Their task was to read all of the sentences in the three experimental conditions and judge how natural each of them sounded on the basis of a 1-to-7 point scale. When we debriefed them, they reported awareness only of the Person Mismatch manipulations; while they rated Unagreement and Default Agreement sentences as being equally natural (see Mancini et al., 2011b; Perez et al., 2012 for the methodological details and statistical results of this task).

Image acquisition

Scanning was carried out on a Siemens MAGNETOM Trio™, a Tim System 3-T scanner, using a standard thirty-two channel phased-array surface coil (Siemens, Erlangen, Germany), which provided high spatial resolution and signal-to-noise ratio. In all subjects BOLD-contrast-weighted echoplanar images for functional event-related scans consisted of 32 axial slices of 3 mm thickness (with 3.75 mm between slices) that covered the whole brain. In-plane resolution was 3 × 3.75 mm, with the following parameters: field of view (FOV) = 1152 × 1152 mm; matrix = 64 × 64; echo time (TE) = 30 ms; repetition time (TR) = 2 s with no time gap; flip angle = 78°. The first six volumes of each run were discarded to allow for T1 equilibration effects. Subsequently, a MPRAGE T1-weighted structural image (1 × 1 × 1 mm resolution) was acquired with the following parameters: TE = 2.97 ms, TR = 2530 ms, flip angle = 7° and FOV = 256 × 256 × 160 mm³. This yielded 176 contiguous 1 mm thick slices.

Functional 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, coregistered with the anatomical T1, normalized to the MNI space using the unified normalization segmentation procedure and smoothed using an isotropic 8 mm Gaussian kernel. Resulting time series from each voxel were high-pass filtered (128 s cut-off period).

Statistical parametric maps were generated by modeling univariate linear model, using for each stimulus type a regressor obtained by convolving the canonical hemodynamic response function with delta functions at stimulus onsets, and also including the six motion-correction parameters as regressors. Parameters of the GLM were estimated with a robust regression using weighted-least-squares that also corrected for temporal autocorrelation in the data (Diedrichsen & Shadmehr; http://www.bangor.ac.uk/~ps412/Imaging/RobustWLS.html). A pairwise contrast comparing activity to each phrase type relative to every other phrase type was performed (Unagreement > Default Agreement, Person Mismatch > Default Agreement, Default Agreement > Person Mismatch, Unagreement > Person Mismatch and Person Mismatch > Unagreement). Resulting contrast images were then entered into a second level design analysis to enable population inferences. Additionally, contrast images for each of the four conditions compared to the fixation baseline were submitted into a second level One-way ANOVA including three experimental conditions (Default Agreement, Unagreement and Person Mismatch). This analysis would allow us to determine whether differences between experimental conditions were due to activation or deactivation with respect to the fixation baseline condition. Population-level inferences were tested using the SPM8 random effects model that estimated the second level t statistic at each voxel. 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 reported in the tables of results. All local maxima were reported as MNI coordinates (Evans et al., 1993).

Results

Behavioral results

Percentage of correct response and mean reaction times (RT) for Default Agreement, Unagreement and Person Mismatch are presented in Table 2, with the corresponding standard error between parentheses.

4 The stimuli onsets include six different components. The first one corresponded to the onset of each sentence trial and was modelled as a single regressor, independently of the experimental conditions. The next four corresponded to each experimental condition (Full Agreement, Unagreement, Person Mismatch and Fillers) and lasted from the onset of the critical verb. In the last component the response time was included, lasting from the onset of the response mark.

5 The head movement of the participant is one of the most common sources of fMRI data noise, but other factors such as physiological responses or motion related to behavioral motor responses can also produce artefactual signals. While some pre-processing steps of the data analysis (e.g. realignment procedure) attempt to resolve the effects of this noise in the estimation of the BOLD signal, significant residual effects often remain in the data. The robust regression using weighted-least-squares is an algorithm that estimates the variance of the noise for each volume included in the functional time series. These variance parameters are used to obtain a weighted least-squares estimate of the regression parameters of a linear model, resulting in a significant increase of the model sensitivity to detect emerging activation sources (Diedrichsen, J., Shadmehr, R., 2005. Detecting and adjusting for artifacts in fMRI time series data. Neuroimage 27, 624–634).
Table 2
Percentage of correct response and mean decision times (in ms) for the three types of sentences with standard error between parentheses.

<table>
<thead>
<tr>
<th></th>
<th>RT</th>
<th>Hits</th>
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<tr>
<td>Standard agreement</td>
<td>629.32 (38.06)</td>
<td>90.37 (1.80)</td>
</tr>
<tr>
<td>Unagreement</td>
<td>664.28 (39.29)</td>
<td>87.50 (1.60)</td>
</tr>
<tr>
<td>Person agreement violation</td>
<td>568.03 (34.53)</td>
<td>90.00 (2.68)</td>
</tr>
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Percentage of correct responses was above 85% for all experimental conditions, indicating that the participants judged the sentences corresponding to the Default Agreement and Unagreement conditions as grammatically acceptable in contrast to the Person Mismatch sentences that were judged as grammatically unacceptable.

One-way ANOVAs on mean response times and accuracy were performed using the conditions (Default Agreement, Unagreement and Person Mismatch) as factor. This analysis showed no significant difference in accuracy among the three conditions. However, for RTs, a significant main effect of condition was found (F (2, 40) = 9.11, p < 0.001, ε = 0.99). Planned comparisons demonstrated that the detection of Person Mismatch was faster (lower RT) than the detection of grammatically acceptable sentences, including Default Agreement (t (20) = 2.60, p < 0.05) and Unagreement (t (20) = 4.48, p < 0.001) conditions. This result is consistent with previous ones (Kuperberg et al., 2003; Mancini et al., 2011a,b; Nevins et al., 2007; Nieuwland et al., 2012) and may reflect the additional time required for the syntactic–semantic integration processes triggered by grammatical sentences relative to the grammatical error detection processes evoked by ill-formed constructions (see Molinaro et al., 2013 for a discussion of this behavioral pattern of results). It is important to note that although Unagreement processing entails more processing difficulties in constructing sentence meaning than the Default Agreement pattern, the time required to judge the grammaticality of these two conditions was not statistically different (t (20) = 1.50, p > 0.05).

All sentences versus fixation

To characterize the functional neuro-anatomical network that was recruited by the processing of sentences, independently of the experimental manipulation, we performed a One-way ANOVA comparing each sentence type with the fixation point condition. The statistical parametric map resulting from the main effect is displayed in Fig. 2, overlaid on the surface of the MNI single-subject T1 image (for more details see Supplementary Fig. 1S). This network includes brain regions such as the left pars opercularis, triangularis and orbitals within the inferior frontal gyrus, as well as the anterior and posterior part of the left middle temporal cortex, the left superior temporal sulcus, the supramarginal cortex, the inferior parietal gyrus and the angular gyrus, typically related to different stages of language processing. Additionally, the left and right fusiform gyri and the left and right inferior and middle occipital cortex, associated to early stages of visual word perception, showed significant activation for all sentences compared to the baseline condition. Also, regions involved in the planning and execution of motor behavioral responses, such as the supplementary motor area and the precentral and postcentral cortex in both hemispheres exhibited a higher response pattern in this comparison.

Person Mismatch versus grammatical sentences

To dissociate the neural correlates corresponding to morpho-syntactic mismatch detection and conflict-monitoring from those related to the integration of meaningful information, we compared the response pattern between Person Mismatch and the grammatical sentences (Default Agreement and Unagreement). A significant increase of activation for the Person Mismatch relative to the Default Agreement condition was observed in a bilateral fronto-parietal network (see Table 3 and Fig. 3). This network included the middle frontal, the anterior and middle cingulate cortex, the inferior parietal cortex and the cuneus/precuneus. All these neural regions showed a similar activation pattern in both cerebral hemispheres. In addition, we found a significant increase of activation for the supramarginal cortex exclusively in the right hemisphere. Furthermore, significant difference in the response pattern of the rectus within the ventro-medial orbitofrontal cortex was found, although this region exhibited deactivation when the three types of sentences were compared to the base line fixation condition. In the same way, the recruitment of a similar pattern of activation was found when comparing Person Mismatch and Unagreement (see Table 3).

Grammatical sentences versus Person Mismatch

The Default Agreement relative to Person Mismatch condition showed a significant increase of activation with a left hemisphere lateralization, including temporal and frontal regions (see Table 3 and Fig. 4A). The frontal activation patch comprised inferior frontal regions (pars triangularis and pars orbitalis) and the precentral/postcentral cortex. The increase of activation in the temporal areas recruited by Default Agreement included the superior temporal cortex, anterior and posterior

![Fig. 2. Significant activation clusters resulting from the contrast All sentences vs. Fixation baseline were projected on the surface of the MNI single-subject 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; FB: Fixation baseline.](image-url)
part of the middle temporal cortex and the inferior temporal cortex, as well as the fusiform area and the lingual cortex.

Similarly to the Default Agreement versus Person Mismatch contrast presented above, when comparing Unagreement and Person Mismatch (see Table 3 and Fig. 4B), the activation of a similar fronto-temporal network was found, highlighting that the processing of grammatical substrates emerged. Figs. 15 (A and B) summarize this result. Note that the activation pattern evoked by Unagreement and Default Agreement was restricted to the left hemisphere, contrary to the activation pattern elicited by Person Mismatch that comprised regions in both hemispheres. Interestingly, if we observe the activation pattern of the Unagreement and Full Agreement sentences compared to the Person Mismatch (bar graph in the right side of Fig. 4) we can note differences between Unagreement and Full Agreement in the pars orbitalis and the most anterior part of the middle temporal cortex. These regions appear to be more activated by the Unagreement sentences.

![Fig. 3](image-url)  
**Fig. 3.** Significant activation clusters resulting from the contrast Person Mismatch vs. Default Agreement are represented in red. Statistical maps were overlaid on the surface (A) of the MNI single-subject T1 image. The bar graph in (B) displays the contrast estimates and 95% of confidence intervals for the three experimental conditions compared to the fixation baseline (DA: Default Agreement; U: Unagreement; PM: Person Mismatch) at different maximum peaks representative of the significant activated clusters. The three experimental conditions are represented in (B) with different colors (Default Agreement in blue; Unagreement in green; Person Mismatch in red). L: left; R: right.
Unagreement versus Default Agreement

The Unagreement response compared to Default Agreement evoked significant increases of activation in the left angular gyrus, the left middle frontal and the right superior frontal cortex (see Table 3 and Fig. 5A). Within this network it is possible to detect the regions involved in morphosyntactic mismatch detection and also regions recruited by the increased semantic complexity of the Unagreement construction. To disentangle between these different qualitative processes, we superimposed this response (Unagreement versus Default Agreement) on the Person Mismatch versus Default Agreement contrast (Fig. 5B, where the common response is represented in yellow). The posterior part of the left middle frontal gyrus is commonly activated by both Unagreement and Person Mismatch, suggesting that this region is involved in morphosyntactic mismatch detection (see Table 1).

On the other hand, the left angular gyrus is specifically activated by the Unagreement sentences (represented in green in Fig. 5B). The mean of the contrast estimates between subjects for each condition (Default Agreement, Unagreement and Person Mismatch) in both regions (the left angular gyrus and the left middle frontal cortex) are shown on the right side of Fig. 5. The engagement of the angular gyrus in subject–verb agreement comprehension is a relatively novel finding (see Discussion). When we explored the single-subject activation response of this region we observed a large variability in the activation pattern across the participants.

In an attempt to clarify this finding and explore the behavioral consequence of this activation variability, we estimated the correlation between the signal change in this region and the corresponding reaction time and percentage of accuracy per condition (Default Agreement, Unagreement and Person Mismatch). Remarkably, a significant correlation was obtained between the activation pattern of the left angular gyrus and the performance scores of the Unagreement grammaticality judgment (see Fig. 6). Participants with greater activation in left angular gyrus showed faster reaction time ($\beta = -0.0003$ [t(19) = -2.17, $p < 0.05$], $R^2 = 0.20$, adjusted $R^2 = 0.16$, $F(1, 19) = 4.69, p < 0.05$) and higher percentage of accuracy ($\beta = 0.011$ [t(19) = 2.82, $p < 0.01$], $R^2 = 0.30$, adjusted $R^2 = 0.26$, $F(1, 19) = 7.96, p < 0.01$). The recruitment of this region thus seems critical for the successful integration of the Unagreement pattern: the activation pattern of the left angular gyrus does not show any relation with the behavioral measures associated to the other two conditions.
The main goal of the present study was to dissociate the neuro-anatomical substrates of the different processing steps involved in subject–verb agreement comprehension in Spanish by taking advantage of the Unagreement construction. First of all, we isolated the brain network involved in subject–verb morpho-syntactic integration from the ones related to conflict-monitoring triggered by the detection of agreement grammatical errors. On the one hand, all sentence types (Unagreement, Default Agreement and Person Mismatch relative to baseline) evoked increase of activation in a left lateralized fronto-temporal network, with higher activation for grammatical than anomalous sentences (grammatical sentences relative to Person Mismatch). This network includes the inferior frontal gyrus, the precentral/postcentral cortex, the superior temporal cortex, anterior and posterior part of the middle temporal cortex and the inferior temporal cortex, as well as the fusiform area and the lingual cortex. On the other hand, an additional bilateral fronto-parietal network was recruited exclusively by the Person Mismatch condition (Person Mismatch relative to baseline; Person Mismatch relative to grammatical sentences), including the anterior part of the middle frontal gyrus, the rectus, the anterior and middle cingulate cortex, the inferior parietal cortex and the cuneus/precuneus.

The engagement of this bilateral fronto-parietal network associated to anomalous sentences has been previously reported, not only in the context of subject–verb agreement computation (Kuperberg et al., 2003, 2008; Ni et al., 2000), but also related to the processing of other aspects of language perception (Bambini et al., 2011; Kerns et al., 2004; Lauro et al., 2008; Novick et al., 2005; van de Meerendonk et al., 2009, 2010; van de Meerendonk et al., 2011; Ye and Zhou, 2009). It is possible that this network reflects the engagement of the conflict monitoring system, probably triggered by the grammatical subject–verb agreement error (for instance, “The painter3.sg brought2.sg” (for alternative viewpoints see the Discussion Section of Kuperberg et al., 2008). The involvement of this monitoring system in the processing of the Person Mismatch condition is consistent with Mancini et al. (2011b). Their ERP results demonstrated a clear distinction in the electrophysiological responses associated to ungrammatical and grammatical sentences: only Person Mismatch evoked the P600 component. As outlined in the Introduction, the P600 effect could reflect monitoring processes triggered by the conflict between the expected and the unexpected linguistic event (for a discussion of this topic see van de Meerendonk et al., 2009, 2010, 2011). Supporting this hypothesis, different authors have demonstrated the contribution of the anterior cingulate cortex (the hub of the conflict monitoring system, Carter and van Veen, 2007; Taylor et al., 2007) in...
the generation of this late positive effect (Du et al., 2013; Olichney et al., 2010). Previous studies have emphasized the amodal nature of this brain system that prevents behavioral mistakes by monitoring the presence of possible conflicts between the expected and the perceived representation of an input: critically, the anterior cingulate cortex plays a pivotal role (Carter and van Veen, 2007; Taylor et al., 2007; van de Meerenendonk et al., 2009, 2010, 2011).

The activation of this bilateral fronto-parietal network is plausibly task-dependent. For instance, Kolk et al. (2003) demonstrated that while anomalous sentences evoked a P600 effect when participants were required to make an acceptability judgment task, an N400 effect was found for the same sentences when participants passively read the sentences. Compared to natural sentence processing or passive reading, both acceptability and grammaticality judgment tasks are well known to enhance brain activity related to conflict-monitoring processes (see task-dependent P600 amplitude discussion also in Kuperberg et al., 2007; van de Meerenendonk et al., 2009). Thus, these tasks require extra attentional and working memory resources. Probably, the variable difficulty of the behavioral tasks employed in different studies is partially responsible for the controversial results illustrated in the Introduction section related to the neuro-anatomical correlates of the subject–verb agreement processing. In order to minimize this factor, future research should include in the statistical estimation of the BOLD responses the behavioral measures (e.g. reaction time), a methodological procedure that has previously been successfully used by other authors (Binder et al., 2004).

The brain network involved in successful integration

As indicated above, the three conditions (Default Agreement, Unagreement and Person Mismatch) recruit a left lateralized fronto-temporal network irrespective of their grammaticality. However, some regions within this network exhibited a different sensitivity to grammatical than anomalous sentences (see Fig. 4). In fact, while the pars opercularis and the pars orbitalis within the inferior frontal gyrus respond similarly to both grammatical and ungrammatical sentences, the pars triangularis and the precentral/postcentral cortex dissociate between grammatical and ungrammatical conditions, with Default Agreement and Unagreement generating greater activation compared to Person Mismatch. A similar dissociation was found in the temporal regions. In fact, while the anterior and posterior part of the middle temporal gyrus and the inferior temporal cortex exhibited a greater response for grammatical sentences than ungrammatical ones, the superior temporal cortex a similar increased response was found for the three conditions, irrespective of the grammaticality of the sentence.

This left fronto-temporal network has been the focus of attention of the sentence comprehension research community during the last decade (see Bornkessel-Schlesewsky and Schlesewsky, 2013; Friederici, 2011 for two recent and divergence points of view). However, the specific processing role played by each node of this network is still controversial. For example, regarding the inferior frontal gyrus, some authors have proposed a functionally-defined anterior–ventral to posterior–dorsal gradient: with BA 44 supporting syntactic local-structure building, BA 44/45 supporting thematic role assignment and BA 45/47 supporting semantic processes (Friederici, 2002, 2011). Other approaches consider Broca’s region (BA 44/45) as the space for the unification of different aspects of language, mapping semantic, syntactic and phonological integration processes from anterior to posterior regions (Bookheimer, 2002; Hagoort, 2005; Hagoort et al., 2004) or define Broca’s area (BA 44/45) as the region supporting the computation of syntactic movement (Grodzinsky and Friederici, 2006).6

Similarly, a controversial scenario emerges for the temporal regions, with a similar posterior-to-anterior functional gradient. As for the anterior temporal cortex, some authors argue that this region plays a particular role in storing and activating semantic associative, categorical and contextual information (Kuperberg et al., 2008), while the posterior temporal cortex subserves syntactic structure building processes (see Bornkessel-Schlesewsky and Schlesewsky, 2013 for a review). A completely different view emphasizes the involvement of anterior temporal regions in the initial syntactic composition of sentence level constituents processes (Bermis and Pylkkänen, 2012; Brennan and Pylkkänen, 2012), while the posterior temporal regions would play a crucial role in the storage/retrieval of lexico-semantic information or combinatorial semantic processes (Rogalsky and Hickok, 2009). In contrast, an intermediate and less specific view has suggested that the ventral part of the anterior temporal region is sensitive to multiple types of syntactic and semantic information rather than to only one and may be involved in integrating these multiple sources of information to construct higher order propositional meaning (Lau et al., 2008).

In the context of the present experimental design, we cannot isolate which of these proposals fits better with our data. For instance, the activation of the left inferior frontal gyrus for all the sentence types independently of grammaticality is compatible with the most recent model of sentence comprehension proposed by Bornkessel-Schlesewsky and Schlesewsky (2013). This new perspective suggests that the functional role of the frontal regions (including the inferior frontal gyrus) is not specifically related to language per se, but serves to integrate different linguistic information with behavior, due to its role in cognitive control mechanisms (in an experimental context this would be reflected in the task responses). This idea is highly appealing and consistent with previous evidence (for an extensive revision of this topic see Bornkessel-Schlesewsky and Schlesewsky, 2013). However, the higher activation level of the pars triangularis exhibited by grammatical sentences (Default Agreement and Unagreement) as compared to ungrammatical ones (Person Mismatch) fits well with the model proposed by Friederici (2011, 2012), suggesting that this inferior frontal sub-region is part of a (larger) semantic network (see Newhart et al., 2012 for a double dissociation between working memory/cognitive control mechanisms and sentence processing in the inferior frontal gyrus).

More interestingly, the experimental design used here can shed light on the neural correlates of two different processing stages: a) the evaluation of subject–verb morphosyntactic consistency recruits the posterior part of the left middle frontal gyrus and b) discourse-semantic integration processes critically rely on the involvement of the left angular gyrus as part of the more domain-general semantic network. In the following paragraphs we will detail these two major points.

Morpho-syntactic detection processing

One of the main results of the present study is the dissociation found in the middle frontal cortex, where a differential response is shown for the two morpho-syntactic subject–verb mismatches (Unagreement and Person Mismatch). On the one hand, in a posterior portion of the middle frontal gyrus we found activation for both Person Mismatch and Unagreement. On the other hand, a more anterior part of the middle frontal cortex responds only to Person Mismatch (see Fig. 3). Importantly, both types of stimuli involve a Person Mismatch, although with a different grammatical status.

The similarity in the activation pattern of Person Mismatch and Unagreement sentences is consistent with the results obtained in the ERP experiment showing that both Person Mismatch and Unagreement evoke a posterior negative effect between 300 and 500 ms compared to Default Agreement sentences (Mancini et al., 2011b). It is therefore possible that the posterior portion of the middle frontal gyrus contributes to the generation of this early negative component, although this hypothesis requires further evidence. This finding is also consistent with previous fMRI results from a variety of languages and agreement

6 Broca’s area typically comprises three different cytoarchitectonically defined Brodmann areas, BA 44, BA 45 and BA 47, that are partially overlapping with the Pars Opercularis, Triangularis and Orbitalis (according to Tzourio-Mazoyer et al., 2002, Automated Anatomical Labeling (AAL)) within the inferior frontal gyrus.
dependencies: pronoun gender mismatches in Dutch (Nieuwland et al., 2007), article–noun gender violations in Dutch (Folia et al., 2009); finiteness violations in English (Kuperberg et al., 2003, 2008; Newman et al., 2003); verb–object number violations in Basque (Nieuwland et al., 2012).

There are two different points of view that can explain this common activation in the posterior part of the middle frontal cortex recruited by Person Mismatch and Unagreement. First (from a more domain-general perspective), it may be that this common activation reflects the involvement of more general working memory mechanisms (see Katsuki and Constantindis, 2012 for a review about the role of this dorsolateral frontal regions in working memory processes) associated to the evaluation of the morpho-syntactic relation between the person feature of the (subsequently presented) subject (“El pintor/The painter.sg” and verb (“trajiste/ broughtt.z.”). In this sense, Murray and Ranganath (2007) explored the functional brain activity during a sequential encoding of word pairs while the participants either made a semantic judgment related to the second word or a semantic judgment that involved a comparison between the second word and the previous word. This experiment demonstrated activity increases of dorsolateral prefrontal regions during relational compared with item-specific encoding, suggesting that this frontal region play a critical role for building relationships between items during on-line processing (see also Blumenfeld and Ranganath, 2006; Murray and Ranganath, 2007). This idea is consistent with previous studies that have reported the activation of this frontal region in association with more general aspects of language processing: verbal fluency tasks (Abrahams et al., 2003) and visual Stroop congruency tasks (Ye and Zhou, 2009).

As the second plausible explanation (from a more language-specific domain), this sub-region within the middle frontal gyrus would be crucially engaged in checking the morpho-syntactic match between two sentence constituents, irrespective of its grammaticality. Several models of sentence comprehension consider morpho-syntactic checking as an initial critical step for building up the syntactic structure of a sentence that depends on agreement relations (Friederici, 2011, 2012). The low temporal resolution of fMRI does not clarify the chronology of the brain regions involved in the processing of these two experimental conditions (Person Mismatch and Unagreement): thus, we cannot temporally determine if the posterior part of the left middle frontal gyrus is activated earlier compared to the other brain regions that are significantly activated for these conditions. Nonetheless, the fact that Unagreement and Person Mismatch only share the morpho-syntactic subject–verb incongruity (Unagreement differs from person violations because it can be successfully integrated) supports the idea that this common brain activation for the two conditions would reflect processes involved in the evaluation of morphosyntax consistency.

These two apparently different perspectives are not necessarily exclusive. On reading Unagreement and Person Mismatch sentences, the system detects the presence of a morpho-syntactic mismatch between subject and verb, a process that is reflected in the common activation of the posterior portion of the middle frontal cortex. However, the system subsequently recognizes that while Unagreement verbal and nominal information can be further integrated, the person feature violation included in the Person Mismatch condition cannot be integrated into the current sentence context. The posterior part of the middle frontal cortex can mediate the processing of agreement computation via a) afferent connections providing information to regulate the detection of a morpho-syntactic mismatch, and b) efferent projections sending such information to regions involved in subsequent processing stages for resolving the grammaticality of the sentence (see Xiang et al., 2010 for a functional connectivity study; an also see Veyetian et al., 2012, for a description of the anatomical connectivity of this frontal region in the primate brain). Despite the fact that this hypothesis needs further investigation (for instance, to establish the directionality of the information flow between the different nodes within this fronto-parieto-temporal network), the activation of the left middle frontal gyrus associated to sentences with morpho-syntactic incongruities points to the important role of this region during sentence comprehension and more specifically in the processing of agreement computation, probably as part of a more general (not-language specific) hub.

Additional discourse-semantic integration processing

According to the feature anchoring hypothesis (Mancini et al., 2013), successful integration of the different speech roles in Unagreement sentences (speaker and non-participants) requires the activation of regions related to semantic integration processes, to overcome the feature mismatch between subject and verb (“Los pintores trajimos/The painters.ptcl broughtt.despl.”). Based on previous findings, we identified the angular gyrus and the anterior temporal cortex as plausible candidates for this processing stage. Our experimental design has allowed us to discriminate between these two neuro-anatomical candidates: a) The anterior part of the left middle temporal gyrus and the left anterior temporal cortex exhibited a greater response to grammatical sentences compared to the anomalous ones without differences between Unagreement and Default Agreement; b) The left angular gyrus is selectively activated only by Unagreement sentences (both for Unagreement relative to Default Agreement and for Unagreement, Person Mismatch and Default Agreement relative to the baseline condition); c) Participants with greater activation in the left angular gyrus showed faster reaction time and a higher percentage of accuracy. These results suggest that both the left angular gyrus and anterior temporal regions mediate semantic-integration processes during the computation of subject–verb agreement. However, only the left angular gyrus is activated for the more semantically complex condition that can be successfully integrated (i.e., in the case of Unagreement, where the person value of the referent shifts from third to first person plural (from “they” to “they + myself”).

Language-related neuroimaging findings have pointed to the involvement of this region during semantic processing (see reviews in Binder et al., 2009; Lau et al., 2008; Price, 2012; Seghier, 2013; Seghier et al., 2010; Vigneau et al., 2006), particularly in tasks that require concept retrieval and conceptual integration (Bemis and Pykkänen, 2012), as well as sentence integration into discourse (Bambini et al., 2011; Friederici and Kotz, 2003; Kuperberg et al., 2003, 2008; Luke et al., 2002; Menenti et al., 2009). These findings have been replicated across multiple studies with different semantic tasks and stimuli (for meta-analysis reviews, see Binder and Desai, 2011; Binder et al., 2009; Vigneau et al., 2006). For instance, Binder et al. (2009) found that the most consistent semantic activation across 120 functional neuroimaging studies was located within the left angular gyrus, strengthening the heteromodal character of this region (for Binder et al., 2009, “posterior heteromodal association cortex” i.e. not-language specific). Using magnetoencephalography, Bemis & Pykkänen (2012) measured neural activity elicited by the comprehension of adjective–noun pairs to highlight the neural substrates involved in basic linguistic composition across different modalities (auditory and visual). Interestingly, they found significant angular gyrus activation for compositional (e.g. red-boat) vs. non-compositional stimuli (e.g. xhq-boat) in both modalities, and interpreted this result as evidence for the crucial role of this region in conceptual integration processes.7

At the sentence level, Kuperberg et al. (2006), found activity increases in the left and right angular gyr in association with reading sentences that were partially related to their preceding contexts, relative to highly related or unrelated sentences. In their study, participants were asked to evaluate the semantic relation between subsequent sentences. These authors found that the greater the difficulty in judging the semantic

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7 It is important to note that the functional interpretation of this magnetoencephalography result is mediated by the temporality of the effects, based on the available models of sentence comprehension that assume initial syntactic composition followed by later semantic combinatorial operations. These authors found that the increased left anterior temporal cortex activity always preceded increased left angular gyrus activity in both auditory and visual modality (p. 10–11).
relationship between sentences, the greater the activity of the angular gyrus (the effect only emerged for intermediate semantic relation, Kuperberg et al., 2006). Similarly, Nieuwland et al. (2007) manipulated the referential ambiguity between a pronoun and its referent in a sentence comprehension paradigm (e.g. "Ronald told Frank that he had a positive attitude towards life/ Rose told Emily that he ... ": the right and left angular gyri were strongly activated with higher amplitude for referential ambiguities than referential anomalies. These findings highlight the specificity of the angular gyrus in dealing with high-level discourse representation. Interestingly, similar activity increases of the angular gyrus have been also found in fMRI studies that explored the neuro-anatomical correlates of metaphor processing (Bambini et al., 2011; Mashal et al., 2007; Shibata et al., 2012), which requires accessing a metaphorical meaning that extends beyond the literal meaning expressed by the linguistic input. This additional semantic processing recalls the additional semantic resources required to interpret Unagreement patterns: in fact, comprehension of both metaphors and Unagreement requires integrating the subject and verb forms at a higher conceptual level, overcoming the literal (discordant) meaning. Finally, neurological lesions in the angular gyrus have been previously associated with difficulties in processing complex sentences such as "It was the niece that the father kicked" (Dronkers et al., 2004; Newhart et al., 2012). Thus, it appears that the angular gyrus plays a crucial role in the processing of semantic complexity, whatever its source (both within sentences and beyond the sentence processing domain). In the present study we additionally show that this region is activated even when an agreement-relevant morphosyntactic scenario is the source of semantic complexity. Possible replications of our findings could therefore have strong implications for neuro-anatomical models of sentence processing.

Taking into account these coherent findings, it seems plausible that neuro-cognitive models of sentence comprehension should take this parietal region as a key node for semantic integration processing. Currently, no existing neuro-cognitive models of sentence comprehension have considered parietal regions as mediating semantic functions (but see Binder et al., 2009; Binder and Desai, 2011 for a neuro-anatomical model of semantic processing). For instance, Bornkessel-Schlesewsky and Schlesewsky (2013) proposed that parietal regions are part of a dorsal pathway that mediates different aspects of syntactic processing: time-dependent segmentation, constituent combination into well-formed syntactic structure, and assessment of the elements in this structure in action-related terms. On the other hand, these authors pointed to the anterior middle temporal cortex as a key region mediating semantic integration processes. In contrast, Friederici (2011) argued that the role of inferior parietal regions as part as a dorsal stream ("dorsal pathway I mediating syntactic operations dealing with complex sentence structures") is an open issue and suggests phonological working memory storage as the most likely function of these regions. This author considers that semantic processing engages middle and posterior superior temporal gyrus and BA 45/47 in the inferior frontal cortex ("ventral pathway II ").

In this sense, the correlation between the behavioral results and the angular gyrus activity is a crucial piece of evidence: participants with greater activation in this region were more efficient (faster and more accurate) in the Unagreement grammaticality judgment. The neural response pattern of this region with respect to the baseline condition varied between participants: only the participants who exhibited activation in the angular gyrus during the Unagreement grammaticality judgment showed high task performance, while the ones exhibiting either no activation or deactivated showed lower performance. This inter-subject variability in the functional recruitment of parietal neural regions during reading processes has been previously reported (Bolger et al., 2008a,b; Levy et al., 2009; Seghier et al., 2008), and may reflect their association with the default network (see Seghier, 2013 for a review).

The fact that only the angular gyrus shows task-related modulation, as opposed to the frontal regions that did not show such variability, casts doubts on the theoretical proposal of Bornkessel-Schlesewsky and Schlesewsky (2013) indicating that only frontal regions are involved in domain-general cognitive control. The present correlation between the activation pattern for the angular gyrus and its relation with behavioral measures suggests that this parietal region influences the observed behavior of the participants in the experimental task.

Conclusions

Taken together, the present findings suggest that different brain networks are involved in language comprehension depending on i) the grammaticality of the sentence (Unagreement/Default Agreement vs. Person Mismatch) and the subsequent possibility of integrating morpho-syntactic information at a semantic-discourse level; and ii) overcoming (or not) an apparent morpho-syntactic mismatch (Person Mismatch vs. Unagreement).

Many accounts of subject–verb agreement fMRI findings derive from studies on the processing of feature mismatches and the results have provided a very fragmented scenario. Here, we used an experimental design that allowed us to distinguish the fine-grained neural circuitry within a fronto-temporal-parietal network recruited by different aspects of subject–verb agreement computation. The results indicate that the evaluation of morpho-syntactic subject–verb match correlates with activity in the posterior part of the left middle frontal gyrus, while syntactic-semantic integration is pursued by an extended left fronto-temporal network. Additional semantic complexity due to the re-interpretation of speech-act participants at the discourse level was observed to increase activity in the left angular gyrus. Overall, the present findings open new windows to the study of agreement computation and language comprehension, pointing to a central role of activity and interactivity between the classic fronto-temporal network and two additional nodes: the posterior part of the left middle frontal gyrus and the left angular gyrus.

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