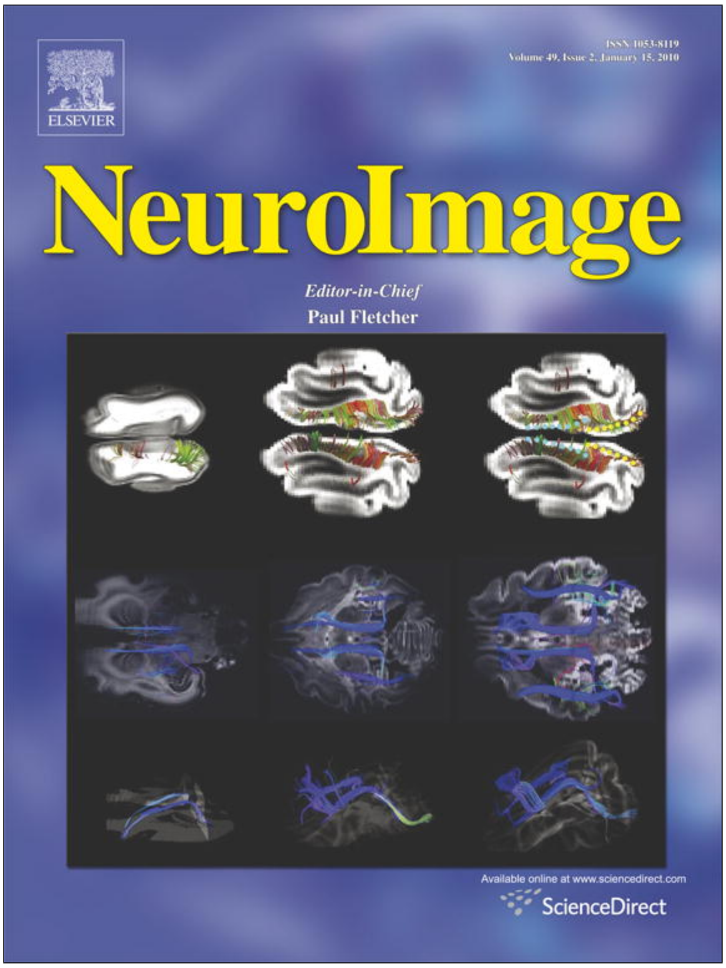
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Where syntax meets math: Right intraparietal sulcus activation in response to grammatical number agreement violations

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ABSTRACT

Previous research has shown that the processing of words referring to actions activated motor areas. Here, we show activation of the right intraparietal sulcus, an area that has been associated with quantity processing, when participants are asked to read pairs of words with number agreement violations as opposed to phrases with gender agreement violations or with no violation. In addition, we show activation in the left premotor and left inferior frontal areas when either gender or number agreement is violated. We argue that number violation automatically activates processes linked to quantity processing which are not directly related to language mechanisms.

Introduction

Models of phylogenetic human brain development assume that language emerged from neural structures dedicated to more basic cognitive functions. From this point of view, it is not surprising to find growing evidence from neuroimaging studies that language comprehension and production is not limited to left perysilvian areas (e.g., left inferior frontal and left superior temporal areas), as is commonly viewed in classic neuropsychology texts. Recent research has shown that areas associated with non-linguistic processing may reveal increased activity during language tasks. For instance, word processing related to actions involving different body parts, such as “pick” and “kick,” activate motor and premotor cortex in a somatotopic fashion (Hauk and Pulvermüller, 2004; Hauk et al., 2004; Shtyrov et al., 2004), reading words with strong olfactory associations in their meaning activated olfactory regions of the brain (Gonzalez et al., 2006), and generating colour words activated a region near brain areas involved in the perception of colour (Martin et al., 1995). Thus, evidence has begun to accrue that action and perceptual information associated with the reference of a word contributes in some way to its neural representation (see review in Vigliocco, Barber, Vinson, and Druks, submitted). Furthermore, these studies suggest a bridge between the semantic properties of words and their neural activity. To date, no study has shown a link between grammatical processing and underlying conceptual representations. Here we show that grammatical processing activates quantity processing areas in phrases with number agreement violations compared to phrases with gender agreement violations or that agree in both number and gender.

Agreement is an important mechanism for language comprehension and production. This is especially noticeable in romance languages, which are richly inflected. In Spanish, nouns are marked as either masculine or feminine, with a natural criterion for assigning gender to human beings (based on the biological sex of the referent) and an arbitrary criterion for objects, roles, and abstract entities (Corbett, 1991). They also carry explicit plural markers signalling one aspect of quantity of the semantic referent. The gender and number of determiners, adjectives, pronouns, and past participles must always agree with the entity to which they refer. Thus, agreement is a syntactic operation that reflects conceptual features (e.g., the sex of a referent, or the number of objects) and a syntactic relation that is realized through morpho-phonological markers. For instance, in “The woman saw the films last month. She remembers them well now,” the personal pronoun *She* agrees in gender and number with the antecedent and unambiguously co-refers to *the woman*, while the pronoun *them* agrees in number with the antecedent and unambiguously co-refers to *the films*. In romance languages such as in Spanish *them* and *films* should also agree in gender—morphosyntactic gender. Furthermore, this gender is not always directly related to masculine and feminine gender concepts. For example, the word for nose is masculine in Spanish (la nariz) but feminine in Portuguese (o nariz). Hence, gender is used as an agreement marker which aids the

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recognition of gender marked items. The alignment of the different agreement cues facilitates the computation of the co-referential relationship necessary to comprehend the sentence introduced by the personal pronoun contributing to discourse cohesion, as well as for computing the relations among elements within a sentence. In fact, empirical behavioural evidence showed that readers are sensitive to the use of gender and number cues in online agreement computation (e.g., Cacciari et al., 1997; Garnham et al., 1995; Carreiras et al., 1993).

The mechanisms of agreement computation have also been investigated in the last few years using electrophysiological and neuroimaging techniques. Event-related potentials (ERPs) studies have found effects of agreement violation mainly in two components: the Left Anterior Negativity (LAN) and the P600 (e.g., Barber and Carreiras, 2003, 2005; Barber et al., 2004; Deutsch and Bentin, 2001; Gunter et al., 2000; Kutas and Hillyard, 1983; Münte and Heinze, 1994; Osterhout and Mobley, 1995; Silva-Pereyra and Carreiras, 2007). In particular, Barber and Carreiras (2005) studied the agreement of gender and number mechanisms in Spanish between word pairs presented in isolation or embedded in sentences. Disagreement in word pairs formed by a noun and an adjective (e.g., faro–alto [lighthouse–high]) produced an N400-type effect, while word pairs formed by a determiner and a noun (e.g., el–piano [the-piano]) showed an additional left anterior negativity effect (LAN). Agreement violations with the same words inserted in sentences (e.g., El piano estaba viejo y desafinado [the$_{\text{masc-sing}}$ piano$_{\text{masc-sing}}$ was old$_{\text{masc-sing}}$ and off-key]) resulted in a pattern of LAN–P600.

Some recent fMRI investigations (e.g., Miceli et al., 2002; Hernandez et al., 2004) indicate that gender features are processed in a network that involves frontal (BA 45 and BA 9) and temporal (BA 20/21 and BA 21) areas of the left hemisphere. For instance, Hernandez et al. (2004) investigated the neural correlates of grammatical gender decisions in Spanish. Participants were visually presented with transparent and opaque words and were required to make a gender decision while being scanned. The gender of the word can be easily derived from the ending in transparent words (e.g., masculine when the word ends in –o, such as *faro* "lighthouse" and feminine if they end in –a, such as *mesa* "table"), but it cannot be derived from the ending in opaque words (e.g., *reloj* "watch"). The comparison between opaque and transparent words revealed increased activity in the left inferior frontal gyrus in BA 44/45, a more superior locus near BA 44/6 and, bilaterally in the insula (near BA 47) and the anterior cingulate gyrus for opaque items with respect to transparent ones. The authors argued that the gender decision for opaque words requires additional morphological processing as compared to transparent ones and confirmed the critical role played by the left inferior frontal gyrus in processing grammatical information. Many fMRI studies, using different tasks, stimuli, languages, and paradigms have found activation of left inferior frontal areas in syntactic processing (e.g., Fiebach et al. 2001; Friederici et al., 2003; Heim et al., 2002; Indefrey et al., 2001, 2004; Moro et al., 2001; Ni et al., 2000). In particular, Hammer et al. (2007) found increased activation in left inferior frontal areas when morphosyntactic agreement between pronouns and antecedents was violated, as compared to when it was not; i.e., when antecedents were things, which only carries morphosyntactic gender, and therefore only a syntactic violation is involved. However, it is unclear whether different brain areas will be recruited when agreement involves not only a grammatical relationship, but broken agreement has conceptual consequences, such as in the case of number agreement.

The "triple-code model" of number processing assumes three distinct systems of representation: a quantity system, a nonverbal analogical–semantic representation of the size and distance relations between numbers; a verbal system, where numerals are represented lexically, phonologically, and syntactically, much like any other type of word; and a visual system, in which numbers can be encoded as Arabic numerals (Dehaene, 1992; Dehaene and Cohen, 1995; Dehaene et al., 2003). These authors proposed that the three circuits coexist in the parietal lobe and capture most of the observed differences between numerical processing tasks: a bilateral intraparietal system associated with a core quantity system, a region of the left angular gyrus associated with verbal processing of numbers, and a posterior superior parietal system of spatial and nonspatial attention, strongly engaged in visual attention processes that may contribute to the visual processing of numbers. Thus, the "triple-code model" assumes that there are modality-specific symbolic codes in the visual Arabic and auditory verbal domain, but that there is also a supramodal abstract "number sense" that conveys semantic, i.e., magnitude, information, and contributes to mathematical performance (Dehaene, 1992). Thus if, as suggested by Dehaene and Cohen (1995), a region of intraparietal cortex underlies this abstract "number sense," then it should respond to numbers even when the task itself does not explicitly require processing of numerical magnitude. Interestingly, Eger et al. (2003) have found bilateral activation in the intraparietal sulcus in the absence of explicit magnitude processing when they compared non-arithmetical processing of number with that of letters and colors using a target-detection task across the visual and auditory modalities. They proposed that these intraparietal responses to numbers reflect access to an abstract supramodal representation of numbers that codes magnitude (see, however, Cohen Kadosh et al., 2007a,b; Cohen Kadosh and Walsh, 2009, for a proposal that numerical representation is notation-dependent and thus includes non-abstract representations). Here, we asked whether numerical processing can be activated by the processing of grammatical number in a reading task in which agreement of grammatical gender and number is manipulated.

Some previous research has investigated relationships between number sense and quantifiers understanding in natural language. It has been shown that patients with corticobasal degeneration performed significantly worse on quantifier processing than Alzheimer disease patients (Clark and Grossman, 2007). This is thought to be due to the fact that corticobasal degeneration patients have a specific impairment of number sense associated with right hemisphere parietal lobe disease (Halpern et al., 2004). In addition, McMillan et al. (2005) carried out an fMRI study in which they presented participants two consecutive events. In the first event, they presented sentences containing quantifiers expressions (e.g., some, less than half, etc.), and in the second event, the sentences were presented accompanied by a stimulus array which contained eight randomly distributed familiar objects (women, balls, flowers, cars, and dinosaurs). The participants were asked to judge the truth of the sentences with respect to the visual array. They found that first-order (some, all) and high-order (less than half, odd) quantifiers both activated the right inferior parietal cortex, and suggested that processing of numerosity is involved in quantifier comprehension. In addition, they found that only high-order quantifiers activated the right dorsolateral prefrontal cortex, and suggested that this could be caused by the contribution of executive resources such as working memory to understand these more complex quantifiers. Since the right intraparietal sulcus has been shown to be involved in number comparison, a task calling for internal manipulation of numerical quantity (Chochon et al, 1999), these results are consistent with the view that numerosity is involved in quantifier comprehension. However, since the present results are based on the contrasts between activation for sentences plus array plus response minus activation of sentences alone, the effects may be caused not necessarily by processes occurring at the comprehension stage but by later processes triggered by the need to compare the two representations (sentences and arrays) as well as by the need to give a an explicit response.

The aim of the present fMRI study was to identify the cortical areas involved in agreement processing during comprehension when this is a pure grammatical operation and when it has conceptual consequences. To that end, we presented the determiner–noun and noun–adjective pairs used by Barber and Carreiras (2005) in three conditions: agreement in number and gender, number agreement violation, and gender agreement violation. If agreement in gender and number involves a stage of syntactic processing irrespective of what cues (purely syntactic or syntactic and semantic) are intervening in the processing (as suggested by Barber and Carreiras, 2005), we should be able to find activations in similar regions when gender and number agreement was violated. In particular, we should expect activation of the left inferior frontal areas based on gender-related previous studies. However, taking into account the "triple-code model" as well as previous findings (e.g., Chochon et al., 1999; Eger et al., 2003; Halpern et al., 2004; McMillan et al., 2005) showing activation of the intraparietal sulcus for quantity processing, we should expect activation in the intraparietal sulcus for number disagreement.

Methods

Participants

A total of 15 right-handed volunteers (7 women) undergraduate students, native speakers of Spanish, aged between 20 and 35 years participated in the study. Each participant received $45 for participating. Language proficiency was assessed with the Boston Naming Test–Spanish. Participants all received a score of at least 80% (48/60) correct on the Boston Naming Test. They were all either monolingual or had not learned English until adulthood (later than 16 years of age). Participants were assessed for handedness with an abridged Spanish version of the Edinburgh Handedness Inventory (Oldfield, 1971) and completed a language history questionnaire. The participants were also asked about claustrophobia or any other criteria which could exclude them from participating in an fMRI experiment. All subjects had normal or corrected vision with no history of neurological disorders or reading impairments. This project was approved by the Institutional Review Boards responsible for the treatment of experimental subjects at both Baylor College of Medicine and the University of Houston. Informed consent was obtained from each participant in accordance with the approval of both institutions. One subject was discarded for the data analysis because of movement artifacts.

Design and task

The 2×3 factorial design included four different types of word pairs (determinant–noun pairs vs. noun–adjective pairs) and three disagreement conditions (gender agreement violation vs. number agreement violation vs. baseline: agreement). In each trial participants were presented with two words one after the other. The pairs of words could be determinant–noun (el carro) or noun–adjective pairs (carro-negro), which could agree or disagree in gender or number. Specifically, each trial began with a "+" as a visual cue, presented for 100 ms, followed by the first word (either a determiner or a noun) for 300 ms, followed by a blank screen for 200 ms, followed by a second word (either a noun or an adjective) for 300 ms. They were instructed to judge each pair for grammatical congruency using the buttons in their hands, pressing one of two buttons whether the two words agree (i.e., were grammatically correct) or disagree in gender or number (i.e., were grammatically incorrect). Participants completed the grammatical task, while undergoing simultaneous and continuous whole brain functional imaging. They were given a button-press device for each hand and instructed which hand should press for grammatically correct and incorrect. The assignment of hands was counterbalanced across participants. During the task, stimuli were presented visually to the participant via a rear projection video screen and a series of mirrors, which allowed the participant to view the screen placed behind their head. Jython software (Reston, Virginia) was used to present the stimuli to the participant every 6.0–8.0 seconds (average interstimulus interval = 7.01 seconds, SD = 0.72 seconds). The interstimulus interval was varied in order to counteract expectation effects which might diminish or change participants' strategies. In addition, varying these times also helped to ensure that brain activity was sampled at different points of the BOLD response. An event-related design was used in which a different ramdomization of trials was used for each participant.

Stimuli

The stimuli consisted of 266 word pairs used by Barber and Carreiras (2005) of which 192 word pairs were experimental pairs (96 determiner–noun pairs, and 96 noun–adjective pairs) and the other 64 were fillers. The 192 experimental trials were divided in six experimental conditions (see below): determiner–noun agreement phrases; determiner–number violation phrases; determiner–noun gender violation phrases; noun–adjective agreement phrases; noun–adjective number violation phrases; noun–adjective gender violation phrases. Stimuli in the remaining 64 trials were fillers (determiner–noun and noun–adjective word pairs) in which the nouns and adjectives used were opaque; that is, their gender was not identifiable by looking at the word ending. There were 32 word pairs in each of 6 conditions, plus the 64 fillers. Thus, the contrasts involved the 6 phrase types described above, divided first by word condition (e.g., determiner–noun or noun–adjective) and then by violation type (e.g., congruent, gender, or number).

Determiner–noun word pairs:

(a) Agreement, e.g., *El piano* ($the_{m\text{-}s}$ $piano_{m\text{-}s}$).
(b) Gender disagreement, e.g., *La piano* ($the_{f\text{-}s}$ $piano_{m\text{-}s}$).
(c) Number disagreement, e.g., *Los piano* ($the_{m\text{-}p}$ $piano_{m\text{-}s}$).

Noun–adjective word pairs:

(d) Agreement, e.g., *Faro alto* ($lighthouse_{m\text{-}s}$ $high_{m\text{-}s}$).
(e) Gender disagreement, e.g., *faro alta* ($lighthouse_{m\text{-}s}$ $high_{f\text{-}s}$).
(f) Number disagreement, e.g., *faro altos* ($lighthouse_{m\text{-}s}$ $high_{m\text{-}p}$).

Three lists of 266 experimental word pairs each were generated. Assignment of word pairs to conditions in each list was counterbalanced across participants. Thus, each pair occurred three times across subjects, once in each condition, so that each subject only saw one form of each pair during the experiment. In Spanish, it is mandatory that determiners, nouns, and adjectives agree in gender and in number. In the present stimuli, gender was always a strictly morphosyntactic feature without semantic significance. All nouns and adjectives were morphologically marked in gender and number, that is, they ended with the canonical suffixes in Spanish for gender ("–o" for masculine and "–a" for feminine) and number ("–s" or "–es" for plural). This way, both gender and number agreement were similar in terms of transparency cues for agreement. Although there are some exceptions (e.g., tesis "thesis") in which ending does not change for singular and plural, number is almost always transparent, while gender is not. All words were of medium lexical frequency according to the Spanish database (Sebastian et al., 2000) and of 3 to 7 letters long. In the noun–adjective pairs the mean frequency for adjectives was 23.27 per million, and the differences of frequency for the masculine, feminine, singular and plural forms were balanced across the counterbalancing conditions. Length was also balanced across conditions. In the article noun pairs, the target (mean frequency of 20.19 per million) was always the same in the three conditions (agreement, gender violation, and number violation). (See Appendix A for the list of experimental materials.)

In addition, a list of 64 filler trials was introduced. Some fillers had opaque gender (e.g., the word "*reloj*" [clock] lacks any explicit

Table 1
Percentage of correct responses and mean decision times (in ms) (standard deviations within parentheses) for agreement, gender violation, and number violation conditions in determiner–noun and noun–adjective pairs.

	Agreement	Gender	Number
Determiner–noun	1113 (306)	1276 (369)	1282 (378)
	.99 (.02)	.98 (.03)	.97 (.02)
Noun–adjective	1284 (353)	1416 (429)	1466 (417)
	.94 (.05)	.96 (.06)	.90 (.08)

morphological marking) and some other fillers were irregular words (e.g., "*mano*" [hand] ends with the letter "–o" but is feminine). This type of filler was included to prevent participants from using a superficial strategy for solving the task such as, for example, attending only to the suffixes or tracking whether there were the same number of grammatically correct and incorrect sentences. This way, participants had to respond *yes* and *no* the same number of times. All the filler word pairs agreed in gender and number. Each subject received a different randomization order of the trials.

Data acquisition

Participants were scanned using a 3.0 T Siemens Allegra scanner at Baylor College of Medicine. Anatomical imaging parameters were: 192 transversal slices at 0.89 mm, voxel size = 0.96 mm × 0.96 mm × 0.89 mm, TR = 1200 ms, TE = 2.93 ms, FOV = 245 mm × 214 mm; in-plane resolution = 256 × 208, flip angle = 12°. The functional images were EPI gradient echo, using 26 transversal slices at 4 mm thickness (0 mm overlap), voxel size = 3.44 mm × 3.44 mm × 4.00 mm, TR = 2000 ms, TE = 40 ms, in-plane resolution = 64 × 64, flip angle = 90°. A total of 1200 volume images were taken. The first 2 (dummy) volumes of each run were discarded to allow for T1 equilibration effects.

Data analysis

Data were analyzed with statistical parametric mapping (SPM2: Wellcome Department of Imaging Neuroscience, London, UK. http://www.fil.ion.ucl.ac.uk), running under Matlab 6.5.1 (Mathworks, Sherbon, MA, USA). All volumes from each participant were realigned and unwarped (Jesper et al., 2001), adjusting for residual motion-related signal changes. The average of the motion-corrected images was co-registered to each individual's structural MRI using a 12-parameter affine transformation. The images were then spatially normalized to the Montreal Neurological Institute (MNI) template by applying a 12-parameter affine transformation, followed by a nonlinear warping using basis functions following the method of Friston et al. (1995a). Functional data were spatially smoothed with an 8-mm full-width half-maximum isotropic Gaussian kernel, to compensate for residual variability after spatial normalization and to permit application of Gaussian random field theory for corrected statistical inference (Friston et al., 1995b). At the first level, data were analyzed in a participant-specific fashion, with each of the six experimental conditions (gender violation, number violation, and agreement for both the determiner–noun and the noun–adjective pairs) and the filler condition modelled separately and convolved with the canonical hemodynamic response function (HRF). The data were high-pass filtered using a set of discrete cosine basis functions with a cutoff period of 128 seconds. The significance threshold was set at $p < 0.001$ uncorrected. Clusters smaller than 20 contiguous voxels were omitted from the results.

Statistical analysis

The contrasts of interest were each of the 4 violation conditions [2 type of violation: (gender violation vs. number violation) × 2 type of word pair: (determiner–noun vs. noun–adjective)] relative to its corresponding specific baseline condition (agreement in the determiner–noun pairs and agreement in the noun–adjective pairs). This would help us determine whether differences between the four experimental violation conditions were due to increases or decreases in activation—i.e., of the BOLD signal with respect to the baseline condition. These contrast images were then entered into a second level ANOVA to permit inferences about condition effects across participants (i.e., a random-effects analysis; Holmes and Friston, 1998). Only correctly responded trials were included in the fMRI and in the behavioural analyses. In addition, responses that exceeded 4 seconds beyond the presentation of the second word were eliminated from both analyses.

The second level analysis focused on the effects of disagreement vs. agreement (i) over number and gender, and for each type of phrase separately (ii) over determiner–noun pairs and noun–adjective pairs and for each pair separately. Details of the relevant interactions are reported in the tables. Activation over and above the baseline conditions is illustrated in the figures.

Results

Behavioural data

Percentage of errors and mean response times for agreement, gender violation, and number violation in determiner–noun and noun–adjective pairs are presented in Table 1. ANOVAs on mean response latencies and error rates were conducted based on the 2 (word

Table 2
Brain activation for type of violation (number and gender) and type of word pairs (determiner–noun and noun–adjective).

Region and effect	*x*	*y*	*z*	Violation > agreement		Number violation > agreement		Gender violation > agreement		Number > gender		Gender > number		Interaction type of violation by type of word	
				Z	Vx	*Z*	Vx	*Z*	Vx	*Z*	Vx	*Z*	Vx	*Z*	Vx
Premotor cortex	**−40**	**4**	**36**	4.2	**262**	3.2	121	**4.6**	**166**	n.s.		*2.0*		n.s.	
	−48	4	22	3.3	**	3.8	**	3.1	**	*2.6*		n.s.		n.s.	
Inferior frontal gyrus	**−58**	**12**	**22**	4.1	**	3.8	**	3.9	17	*2.6*		n.s.		n.s.	
Right intraparietal sulcus	**40**	**−48**	**40**	3.1	*1*	3.6	**306**	*2.1*		3.4	**91**	n.s.		3.4	11
	42	**−50**	**48**	n.s		3.5	**	n.s.		3.9	**	n.s.		*2.4*	
Superior parietal gyrus	**24**	**−70**	**46**	*2.6*		4.4	**	n.s		3.4	17	n.s.		*3.0*	

x, y, z = coordinates of local maxima. *Z* = *Z* scores. Vx = number of voxels at $p < 0.001$ uncorrected. *Z* scores and cluster size are reported in **bold** if they are significant in height or extent at $p < 0.05$ after family-wise correction for multiple comparisons across the whole brain. Those in *italics* were reported at $p < 0.05$ uncorrected. All others are significant at $p < 0.001$ uncorrected. When activation foci are part of the same cluster to that of the coordinates reported with the highest peak for the cluster in the upper cell, the corresponding cells below contain two asterisks (**). When the *Z* scores do not surpass the threshold of $p > 0.0001$ uncorrected, the corresponding cells for number of voxels are empty.

condition: determiner–noun vs. noun–adjective pairs) by 3 (type of violation: agreement vs. gender violation vs. number violation) design.

Reaction times

Incorrect responses were excluded from the latency analysis. In addition, in order to avoid the influence of outliers, reaction times more than 2.0 standard deviations above or below the mean for that participant in each condition were excluded.

The ANOVA showed a main effect of word condition [$F(1,13)=40.3$, $p<0.0001$], indicating that reaction times were slower in the noun–adjective pairs than in the determiner–noun pairs. The main effect of violation type was also significant [$F(2,26)=9.3$, $p<0.001$]. The interaction was not significant [$F<1$]. Pairwise comparisons showed that there were no differences between the gender and number violation conditions. However, both gender violation and number violation were slower than the agreement condition.

Error rates

The ANOVA showed a main effect of word condition [$F(1,13)=24.5$, $p<0.0001$], indicating that the percentage of errors was larger in the noun–adjective pairs than in the determiner–noun pairs. The main effect of violation type was not significant [$F(2,26)=2.7$, $p<0.09$]. Importantly, the interaction was significant [$F(2,26)=3.8$, $p<0.05$]. Pairwise comparisons showed that there were no differences between the three violation type conditions in the determiner–noun pairs. However, in the noun–adjective conditions, the number of errors was larger in the number violation pairs than in the agreement and in the gender violation conditions.

fMRI data

A main effect of increase of activation for number and gender violation agreement relative to the agreement baseline was observed in the left premotor cortex and in the left inferior frontal areas (see Table 2 and Fig. 1 for details). In addition, an increase of activation of number violation relative to the agreement baseline and to the gender violation was observed in the right parietal areas (right intraparietal sulcus and right superior parietal gyrus) (see Table 2). Importantly, this effect was mainly driven by the determiner–noun pair conditions which showed an increase of activation in number violation as compared to gender violation and as compared to agreement in the right intraparietal sulcus and the right superior parietal gyrus (see Table 3 and Fig. 2). Interestingly, the same contrast in the left homologue areas of the parietal cortex did not show any effect significant even at $p<0.05$ uncorrected threshold. Laterality analyses were performed for the two parietal regions (intraparietal sulcus and superior parietal gyrus) extracting the signal for the two main coordinates $+-40$, -48, 40 and $+-24$, -70, 46) within a 6 mm sphere. The ANOVA including Region and Hemisphere as factors on the BOLD signal for number violation relative to agreement showed a

Table 3
Brain activation for number agreement violations only in determiner–noun pairs.

Region and effect	*x*	*y*	*z*	Number violation > agreement		Number > gender	
				Z	Voxels	*Z*	Voxels
Right intraparietal sulcus	**40**	**−48**	**40**	3.9	**77**	**4.7**	**727**
	42	**−50**	**48**	3.5	**	**4.6**	**
Superior parietal gyrus	**24**	**−70**	**46**	3.9	**124**	4.4	**

x, *y*, *z* = coordinates of local maxima. *Z* = *Z* scores. Voxels = number of voxels at $p<0.001$ uncorrected. *Z* scores and cluster size are reported in **bold** if they are significant in height or extent at $p<0.05$ after family-wise correction for multiple comparisons across the whole brain. All others are significant at $p<0.001$ uncorrected. When activation foci are part of the same cluster to that of the coordinates reported with the highest peak for the cluster in the upper cell, the corresponding cells below contain two asterisks (**). When the *Z* scores do not surpass the threshold of $p>0.0001$ uncorrected, the corresponding cells for number of voxels are empty.

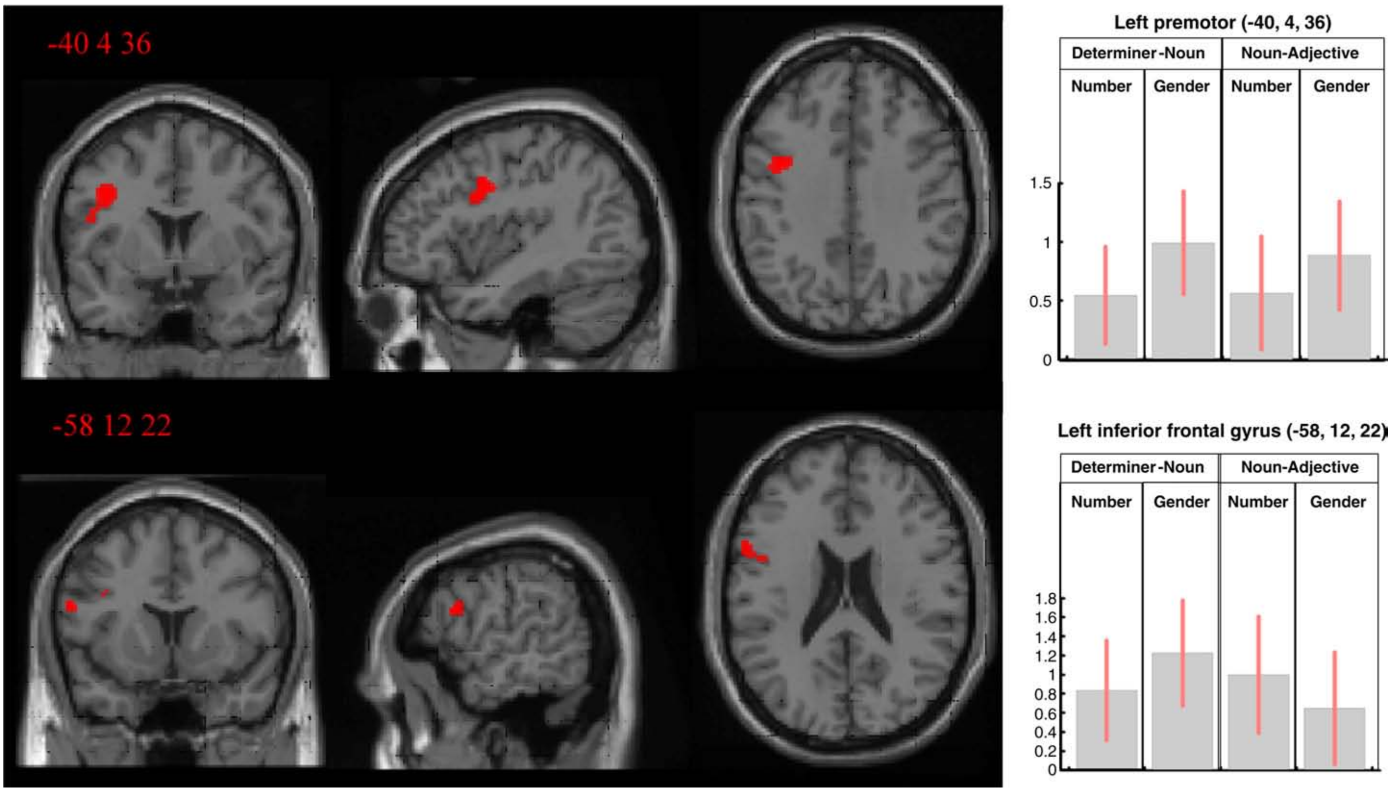

Fig. 1. Left part: Axial, coronal, and sagittal sections (left part) for the contrast violation > agreement. All contrasts depicted at $p<0.001$ uncorrected. Right part: Graphs of contrast estimates and 90% confidence intervals. Number: number violation > agreement; Gender: gender violation > agreement.

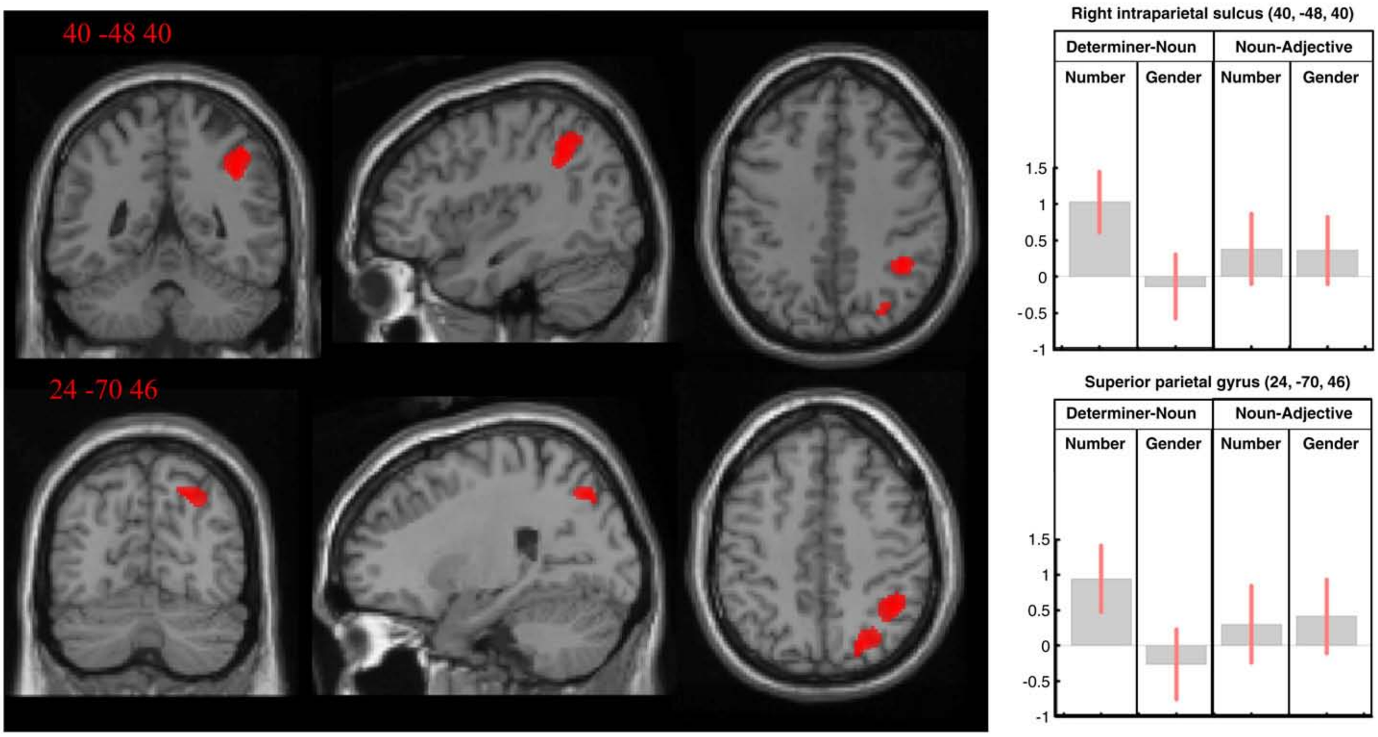

Fig. 2. Left part: Axial, coronal, and sagittal sections for the contrast number violation>gender violation in determiner–noun pairs. All contrasts depicted at $p<0.001$ uncorrected. Right part: Graphs of contrast estimates and 90% confidence intervals for a right frontal middle area. Number: number violation>agreement; Gender: gender violation>agreement.

main effect of Hemisphere, $F(1,13)=4.96$, $p<0.05$. Neither the main effect of Region nor the interaction between Region and Hemisphere was significant (both F values<1).

No further increases of activation were observed when agreement was compared to the violation conditions or when gender violation was compared to number violation or to agrement. In addition, no effects were observed for the contrasts relative to the type of word (determiner–noun vs. noun–adjective and vice versa).

Finally, singular vs. plural contrasts were performed for the two parietal regions extracting the signal of the coordinates within a 6 mm sphere. No significant effects were found either in the singular>plural or in the plural>singular contrasts.

Discussion

Grammatical violations of gender and number agreement produced similar and distinct effects on regional brain activation. Activation in the left premotor and left inferior frontal regions was higher for the two ungrammatical conditions as compared to the grammatical condition, both in the case of determiner–noun and noun–adjective pairs. However, the activation in the right parietal areas (intraparietal sulcus and superior parietal gyrus) was higher for number disagreement than for gender disagreement and agreement conditions, but this effect was mainly driven by the determiner–noun pairs. Thus, we have identified brain areas that are modulated by both gender and number agreement violations. Furthermore, we have identified neural activity unique to number agreement violation. Finally, the behavioural data showed that it was easy and faster to judge the determiner–noun pairs than the noun–adjective pairs and the agreement than the disagreement conditions.

Increased activation for number and gender agreement violations over agreement

The left premotor and left inferior frontal areas that we found to be more active for number and gender violations relative to congruent pairs are very close to the areas other authors have previously associated with gender computation (Hammer et al., 2007; Hernandez et al., 2004; Miceli et al., 2002) as well as to areas involved in different types of grammatical processing of different structures in different languages (Fiebach et al. 2001; Friederici et al., 2003; Heim et al., 2002; Indefrey et al. 2004; Moro et al., 2001, Ni et al., 2000). These results suggest that agreement violation processing during visual word processing tasks modulates activation in regions that are also engaged during syntactic processing. The similarity in the effects of agreement violation and syntactic processing is also consistent with the results obtained in ERPs showing that both gender and number violation modulated the LAN and the P600 (Barber and Carreiras, 2005). These two components were found to be sensitive to other grammatical violations and did not differ in early stages of processing. Thus, the present results add evidence to consider that these left frontal areas are involved in morphosyntactic processing. Number and gender violation seem to require additional morphosyntactic processing in order to determine the nature and cause when two words do not agree in morphosyntactic features.

Increased of activation for number violation relative to gender violation and agreement

Interestingly, number agreement violation activated the right intraparietal sulcus and the right superior parietal gyrus, this effect being mainly driven by the determiner–noun pairs. The "triple-code model" and several fMRI studies have suggested a crucial role of regions situated along the horizontal segment of the intraparietal sulcus of both hemispheres for the representation of numerical quantities (e.g., Dehaene et al., 2003). The present results only showed right but not left IPS activation, what seems to be partially inconsistent with the "triple-code model" predictions. However, recent studies have suggested that left and right IPS seem to play a different role. Briefly, the right intraparietal sulcus has been implicated in several tasks related to quantity processing (e.g., Dehaene et al., 2003; Piazza et al., 2002, 2006; Piazza et al., 2007;

Pinel et al., 2004). Independent lines of research have pointed to parietal cortex as crucial for coding numerical quantity both when it is conveyed by number symbols (digits, number words; Eger et al., 2003; Pinel et al., 2001) or by nonsymbolic displays of dot patterns (Ansari et al., 2006; Cantlon et al., 2006; Piazza et al., 2004), which suggests that is involved in computing an abstract code for numerical magnitude (see however, Cohen Kadosh et al., 2007a,b; Cohen Kadosh and Walsh, 2009, who recently challenged the idea of abstract representation and suggested that numerical representation in the intraparietal sulcus (IPS) is notation-dependent). Activation of the more posterior dorsal parietal areas has been observed whenever subjects count, which relates also to movements of spatial attention (Dehaene et al., 2003). However, we did not observe activation in the left angular gyrus, the most likely candidate a priori in case number violation triggered some verbal numerical code of numerical computation. Nonetheless, the lack of activation in the left angular gyrus could be due to the fact that our control condition is also a linguistic task. All three conditions (number disagreement, gender disagreement and agreement) involve verbal stimuli, so effects of verbal decoding and comprehension would be cancelled out since they are present in all three conditions. If expectations about several or a single entity is what makes number agreement (specially in determiner–noun pairs) different from the other two conditions, and other results involving numerical comparison or magnitude estimations have found mainly right IPS activation, it is quite likely instead that we have only found right IPS activation.

A comparison between correct plurals and singulars was performed because linguistic and psycholinguistic theories have debated about differences between singulars and plurals in terms of markedness. Although the most common view in the psycholinguistic literature assumes that singular is unmarked and plural marked (Eberhard, 1997), the linguistics literature is very much more nuanced. Thus, Greenberg's (1966) Number Hierarchy (singular before plural before dual before trial) establishes the typological unmarkedness of the singular based on the fact that (a) more languages have singulars than plurals, (b) more languages use the singular more than the plural, and (c) whenever languages have both numbers, there will be more nouns in the singular than in the plural. However, that ordering does not cover the case of facultative number (Corbett, 2000) and in fact it does not even apply to the full to languages with obligatory singular/plural contrasts in the sense that, for specific nouns (like arms), the plural may actually be the unmarked term (Tiersma, 1982). Additionally, plurality interacts closely with (in)definiteness and this in turn with whether NPs have specific determiners, and whether such NPs project kinds or properties (see Dayal, 2004). Note also Chierchia's idea (1998) that nouns in numeral classifier languages (like Chinese or Japanese) will exhibit neutralization of the singular/plural distinction. Since we have neither manipulated (in)definiteness nor the inherent specificity of unmarked plurals like arms in any way, we prefer to remain agnostic on the issue of plurality. For the linguistic view that plural number is the unmarked term, see Krifka (1989) and Sauerland et al. (2005). We looked for differences of activation between correct singulars and plurals in the regions of interest in which we have find an increase of activation for number violation, but we did not find differences (either increase of activation for singulars or for plurals).

Importantly, the effect of number violation relative to gender violation and agreement was mainly specific to determiner–noun pairs. Fig. 2 shows that number violation in the determiner–noun pairs led to increased activation of the right intraparietal sulcus and the superior parietal gyrus compared to the agreement baseline and to the gender violation conditions. It is quite unlikely that the right intraparietal sulcus and the right superior parietal gyrus are brain regions specifically involved in language processing. In contrast, the increased right parietal activation for number violation is more likely to reflect the automatic activation of a quantity computation while participants were performing a grammatical judgment task: is this pair of words grammatically correct or incorrect? When reading the determiner, participants trigger expectations about whether the noun would be singular or plural, that is, whether it should refer to only one or many entities. Such expectations about quantity could be fulfilled or not when they read the noun. Therefore, the number mismatch leads to an increase of activation in areas involved in computing quantity. The fact that the effect is negligible for the noun–adjective pairs alone may be accounted for by the fact that plural or singular nouns do not create such important expectations (see Barber and Carreiras, 2005). Determiners must be followed by nouns, but nouns may be followed by many other possible constituents (verbs, adjectives, prepositions, adverbs, etc.) some of which do not need to agree in number with the noun. In addition, in the case of noun–adjective pairs, the noun creates a concrete representation with a particular number and the adjective qualifies the noun; however, the determiner creates an expectation of number that will be confirmed with the representation of the noun that follows.

The human intraparietal sulcus is systematically activated in all number tasks and could host a representation of quantity (see, however, Göbel et al., 2004; Shuman and Kanwisher, 2004). There is considerable evidence from neuroimaging studies to indicate that the parietal lobes are involved in the processing of symbolic and non symbolic numerical information (e.g., Cappelletti et al., in press; Castelli et al., 2006; Dehaene et al., 2003; Dehaene et al., 2004; Zago et al., 2001; Piazza et al., 2006, 2007). However, the left and right intraparietal sulcus may play slightly different roles. The left parietal region is critical for most calculation deficits, it is involved in tasks requiring access to verbal memory, such as verbal coding of numbers, in exact computation, comes into play as a result of education and symbolic acquisition and provides the interconnection of the quantity representation with the linguistic code (see Dehaene et al., 2003; Dehaene and Cohen, 1995). In contrast, the right intraparietal sulcus is engaged when recognizing numerosity (the number of objects in a set), which provide us with a basic intuition that guides the acquisition of formal arithmetic, and it is present from infancy/early childhood (see Cantlon et al., 2006; Dehaene, 1997; Dehaene et al., 2003). In fact, activation of the right intraparietal sulcus only or activation higher than the left intraparietal sulcus has been observed when subjects estimate the numerosity of a set of concrete visual or auditory objects (Piazza et al., 2002, 2006, Piazza et al., 2007). Approximate judgments (in both the visual and auditory domain) correlate with stronger activation in the right than in the left IPS, while exact judgments correlate with more activation in the left versus right IPS (Piazza et al., 2006). For instance, Piazza et al. (2002) demonstrated right lateralized activation of inferior parietal cortex associated with determining and manipulating the numerical quantities of a set. Chochon et al. (1999) demonstrated greater right hemisphere activation in a magnitude comparison task, but greater left hemisphere activation in a multiplication task. Cantlon et al. (2006) reported that the only region showing overlapping activation in preschool children and adults during processing of numerosity was the right IPS. In addition, Cappelletti et al. (in press) found that right parietal activation was number-selective. They compared activation to numbers and object names during the same conceptual and perceptual tasks while factoring out activations correlating with response times. Activation was higher for conceptual decisions of numbers relative to the same tasks on object names only in right parietal areas.

Interestingly, recruitment of the right inferior parietal cortex was also observed when assessing quantifiers (Clark and Grossman, 2007; McMillan et al. (2005). The fact that processing of quantifiers involves the right inferior parietal cortex, an area associated with number sense which is not typically associated with language, suggests an involvement of number knowledge in quantifiers processing. This link between number processing and quantifiers processing is further supported by the finding that patients with corticobasal degeneration performed significantly worse on quantifier processing than Alzheimer disease patients (Clark and Grossman, 2007). This is thought to be due to the fact that corticobasal degeneration patients have a specific impairment of number sense associated with right hemisphere parietal lobe disease (Halpern et al., 2004). In addition, this finding of right parietal activation and damage associated with quantifiers' comprehension is consistent with the previously mentioned neuroimaging literature investigating the neural basis of number knowledge. Finally, Cohen Kadosh et al. (2007b) applied TMS to disrupt left or right IPS activation clusters in order to induce dyscalculic-like behavioral deficits in healthy volunteers. They found that automatic magnitude processing was impaired only during disruption of right IPS activity. Thus, it seems that the right, but not the left, IPS is functionally necessary for automatic magnitude processing. It might well be that the right IPS is used for coding magnitude in general (Walsh, 2003), whether numerical or non-numerical.

While we cannot completely assure that the intraparietal activation reported here is due to numerical processing, there are two facts that seem to suggest that this is the case (1) differences between the two disagreement conditions are limited to agreement in number or in gender. The same determiners and nouns are used across the two conditions (gender and number agreement). Since both gender and number lead to increased activity in the left inferior frontal and left premotor regions, but only number disagreement led to activity in the intraparietal sulcus, it can be inferred that the purely grammatical effects common to the two disagreement conditions are leading to the common activation in left frontal and premotor regions, whereas the conceptual number effects due to the number disagreement condition are leading to the intraparietal activation. Gender and number conditions are equated in syntactic complexity (in fact they showed equivalent response times in the syntactic judgment task), but they differ mainly at the conceptual level in the semantic representation of numerosity. In addition (2) the coordinates revealed in the present study overlap with those reported in other studies looking at numerosity processing. The coordinates in the present paper (40, −48, 40) fall within the area that is associated with numerical processing (37, −46, 42, in a meta-analysis of 14 fMRI studies of magnitude comparisons (Cohen Kadosh et al., 2008). Thus, the overlap of coordinates with numerosity processing and the fact that gender and number disagreement most likely differ only in numerosity have led us to conclude that grammatical number disagreement involves numerosity computation which in turn leads to increased activity in the right intraparietal sulcus.

In sum, the results of the present experiment add evidence to the suggestion that the quantity processing would be a function implemented in intraparietal regions of the right hemisphere and reinforces the assumption of a nonverbal system for numerosity judgments. It is striking that the right intraparietal sulcus has been activated by a verbal task for which quantity processing, at least on the surface, is not required. In addition, the results are in line with the general proposal that claim that language processing is not restricted to the classical “languages areas.” In this regard, motor and sensory areas may be involved in some aspects of semantic language processing. The present study provides evidence that syntactic processes can also involve cerebral areas not directly related to the language processing.

Conclusion

The present results converge on the conclusion that the human brain is equipped with a shared mechanism to compare numbers and other magnitudes. In addition, the present research suggests that semantic representation is distributed in a large number of different networks which extend beyond perisylvian areas. Results show that number violation specially when processing determiner–noun phrases correlates with increased activity of a right lateralized frontoparietal cortical network, which is recruited during tasks which involve quantity processing. In sum, the current findings show the involvement of the right parietal lobe for automatic activation of magnitude processing during language processing. These results add evidence to the growing view of language as a complex process that is not restricted to the classical cerebral areas of language.

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Appendix A

Determiner–noun pairs: El techo, el puerto, el saco, el hierro, el sábado, el premio, el pozo, el gobierno, los dedos, los lagos, los arros, los labios, los lavabos, los litros, los metros, los hornos, la costa, la saliva, la capa, la sopa, la rama, la cola, la pierna, la danza, las risas, las orejas, las letras, las navajas, las páginas, las espadas, las sierras, las reglas, la receta, la boda, la colcha, la plata, la luna, la aguja, la taza, la selva, las perlas, las abejas, las flautas, las gomas, las palas, las cuadras, las iglesias, las alarmas, el pico, el banco, el piano, el circo, el martillo, el rebaño, el campo, el espejo, los hielos, los rayos, los besos, los torneos, los clavos, los frenos, los cocos, los votos, los hígados, los daños, los hombros, los arcos, los rollos, los caldos, los cercos, los sótanos, el trueno, el cráneo, el engaño, el mérito, el ahorro, el vidrio, el código, el trofeo, las vueltas, las gotas, las pausas, las ondas, las aldeas, las burlas, las minas, las retinas, la deuda, la pasta, la prisa, la misa, la duda, la urna, la rueda, la bandera.

Noun–adjective pairs: cuerpo moreno, número mínimo, mundo justo, caso cierto, pelo rizado, fruto ácido, fuego flojo, llanto amargo, tiempos pasados, grupos serios, tipos listos, ídolos sabios, hilos finos, quesos agrios, huevos fritos, caminos anchos, cabeza menuda, lucha épica, vida sana, basura nociva, zona rara, suela gorda, piedra áspera, visita rápida, puertas seguras, mañanas futuras, cartas vacías, casas ajenas, ropas caras, citas médicas, blusas viejas, novelas baratas, pueblo bélico, estado sereno, libro único, lado turbio, ruido brusco, museo bello, vuelo largo, dibujo bonito, rostros pálidos, cambios súbitos, brazos tensos, juegos lícitos, autos rojos, discos buenos, barcos lentos, sonidos lejanos, guerra mítica, lengua humana, bolsa usada, droga tóxica, cena mala, tarea ardua, sábana blanca, sombra oscura, alturas idóneas, mantas raídas, cosas opacas, hojas pegadas, telas sosas, tumbas hondas, maderas blandas, plantas quietas, verano cálido, juicio severo, deseo mutuo, estilo maduro, piso pagado, cielo claro, plato llano, equipo entero, asuntos íntimos, cuellos rígidos, suelos planos, relatos amenos, muros duros, gestos lindos, anillos dorados, abrigos gruesos, fiesta loca, dama culta, copa tapada, mesa baja, tabla curva, falda negra, papaya fresca, tierra remota, semanas previas, medidas válidas, cintas atadas, aguas tibias, comidas jugosas, etapas cortas, jarras llenas, figuras famosas.

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