Published in final edited form as:

Neuroimage. 2011 July 1; 57(1): 251–261. doi:10.1016/j.neuroimage.2011.04.021.

Language-Invariant Verb Processing Regions in Spanish-English Bilinguals

Joanna L. Willms^{a,b}, Kevin A. Shapiro^{a,b,c,d}, Marius V. Peelen^{a,e}, Petra E. Pajtas^{a,e}, Albert Costa^f, Lauren R. Moo^{b,d}, and Alfonso Caramazza^{a,e}

^a Harvard University

^b Massachusetts General Hospital

^c Children's Hospital Boston

^d Harvard Medical School

^e Center for Mind/Brain Sciences (CIMEC), University of Trento, Italy

^f Pompeu Fabra University and ICREA, Spain

Abstract

Nouns and verbs are fundamental grammatical building blocks of all languages. Studies of brain-damaged patients and healthy individuals have demonstrated that verb processing can be dissociated from noun processing at a neuroanatomical level. In cases where bilingual patients have a noun or verb deficit, the deficit has been observed in both languages. This suggests that the noun-verb distinction may be based on neural components that are common across languages. Here we investigated the cortical organization of grammatical categories in healthy, early Spanish-English bilinguals using functional magnetic resonance imaging (fMRI) in a morphophonological alternation task. Four regions showed greater activity for verbs than for nouns in both languages: left posterior middle temporal gyrus (LMTG), left middle frontal gyrus (LMFG), pre-supplementary motor area (pre-SMA), and right middle occipital gyrus (RMOG); no regions showed greater activation for nouns. Multi-voxel pattern analysis within verb-specific regions showed indistinguishable activity patterns for English and Spanish, indicating language-invariant bilingual processing. In LMTG and LMFG, patterns were more similar within than across grammatical category, both within and across languages, indicating language-invariant grammatical class information. These results suggest that the neural substrates underlying verb-specific processing are largely independent of language in bilinguals, both at the macroscopic neuroanatomical level and at the level of voxel activity patterns.

Keywords

grammatical class; bilingualism; verbs; fMRI; MVPA

© 2011 Elsevier Inc. All rights reserved.

Corresponding Author: Alfonso Caramazza, Department of Psychology, Harvard University, 930 William James Hall, 33 Kirkland Street, Cambridge, MA 02138, tel: (617) 495-3867, fax: (617) 496-6262, caram@wjh.harvard.edu. Reprint requests should be sent to Alfonso Caramazza, Department of Psychology, Harvard University, 930 William James Hall, 33 Kirkland St., Cambridge, MA 02138 or via caram@wjh.harvard.edu

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

1. INTRODUCTION

All human languages distinguish between grammatical categories of words. At a minimum, each language—with rare and controversial exceptions—differentiates between nouns (objects) and verbs (predicates) (Sapir, 1921; Meillet, 1926; Robins, 1952; Hopper and Thompson, 1984; Evans, 2000). The universal (or near-universal) occurrence of these categories suggests that the noun-verb distinction may reflect basic principles that govern the organization of language in the brain.¹ Indeed, there is a growing body of evidence, collected from speakers of several languages, that supports the hypothesis that nouns and verbs are processed by different neuronal mechanisms. However, most studies have examined noun and verb processing within a single language, making comparisons across languages problematic.

Much of what is known about the representation of knowledge about grammatical categories has been deduced from studies of aphasic patients. It has long been observed that brain damage can selectively affect the ability to produce or comprehend nouns or verbs (see Shapiro and Caramazza, 2009, for a review). Such dissociations have been reported in patients who speak a number of languages, including English (e.g., Caramazza & Hillis, 1991), Spanish and Catalan (Hernández et al., 2007; Hernández et al., 2008; Caño et al., in press), Greek (Tsapkini et al., 2002; Kambanaros, 2008), Italian (Miceli et al., 1984), and Chinese (Bates et al., 1991). Interestingly, in the few reported cases of bilingual speakers, the same pattern of noun-verb dissociation has always been found in both languages (e.g., Kambanaros and van Steenbrugge, 2006; Hernández et al., 2007; Hernández et al., 2008). These findings in monolingual and bilingual patients suggest not only that noun and verb processing are dissociable in many different languages, but also that the same neural substrates may underlie the noun-verb distinction across languages.

More recently, studies using functional neuroimaging techniques have demonstrated that several cortical regions are selectively engaged in the processing of verbs or nouns. Similar patterns of differential activation have been found in monolingual speakers of English (e.g., Shapiro et al., 2006; Bedny et al., 2008; Tyler et al., 2008), Japanese (Yokoyama et al., 2006), Hebrew (Palti et al., 2007), Finnish (Liljeström et al., 2008), Italian (Perani et al., 1999), and German (Shapiro et al., 2005; Khader et al., 2010), suggesting a common neural substrate (see Vigliocco et al., 2011, for a comprehensive review). However, these results are not conclusive, as differences in tasks, materials, and subjects render it impossible to compare the patterns of activation directly. A recent meta-analysis has pointed out numerous inconsistencies across studies, even going so far as to argue that the lack of consistency suggests that anatomical distinctions in noun and verb processing are either nonexistent or irresolvable using current techniques (Crepaldi et al., 2011). A neuroimaging study of noun and verb processing in bilingual participants would provide a direct comparison across languages, at least in the case of bilingual speakers. To the extent that the results are comparable with earlier studies, it would also support the view that neural circuits underlying the processing of nouns and verbs can be differentiated.

¹There is ongoing controversy in the field of comparative linguistics about whether certain languages do not have “nouns” or “verbs” as these categories are commonly understood (cf. Evans & Levinson, 2009). Such controversies are reflective of the more general argument that the ways in which different languages impose grammatical structure on the conceptual universe are varied and not necessarily isomorphic (e.g. Croft, 2001; Kemmerer & Eggleston, 2010). Space does not permit a full discussion of this argument, which in many ways parallels debates about the categorical perception of color and number concepts across cultures. Nevertheless, we take it as axiomatic (1) that all languages have grammatical categories, and (2) that the construction of these grammatical categories is not arbitrary, but rather constrained by underlying neurocognitive parameters. The fact that most, if not all, languages have categories that are roughly comparable to “noun” and “verb” suggests to us that it is reasonable to use these terms as shorthand for an as-yet-undiscovered common discriminant.

What differences in brain activation might we expect to find between the two languages of a bilingual? In a review, Perani and Abutalebi (2005) conclude that when bilinguals learn both languages early, and they have comparable exposure and proficiency in both languages, the same regions are activated when a task is performed in either language. Further meta-analyses support this view (Indefrey, 2006; Abutalebi and Green, 2007). Thus, we might expect that a noun or verb production task would yield identical patterns of activity across languages.

Thus far, only one imaging study in bilinguals has attempted to characterize the differences between noun and verb processing in two languages. In Chan et al. (2008), Chinese-English bilinguals performed a lexical decision task with noun and verb stems in both languages. No regions showed a difference between nouns and verbs in Chinese, and few regions showed a difference in English. This result may not be surprising given previous work that shows regional patterns of activation for verbs, compared to nouns, only when grammatical category is explicitly marked. For example, Tyler et al. (2008) showed that contrasting verb phrases/sentences (e.g., *I sing*) to noun phrases (e.g., *the cereal*) elicits clusters of greater activity for verbs, but contrasting verb stems (e.g., *sing*) to noun stems (e.g., *cereal*) yields no differences in activation. In Chinese, characters denoting nouns and verbs are not explicitly marked for grammatical category (Li et al., 2004). Thus, the task used in that study might not be expected to show differences in activation between nouns and verbs by its design, and therefore does not necessarily address the question of noun and verb processing differences across languages.

We have previously hypothesized that morphosyntactic processes may be a key determinant of the differences in representing knowledge about nouns and verbs in the brain (Shapiro and Caramazza, 2009). Given this hypothesis, if two languages differ in morphosyntactic complexity, their respective patterns of grammatical class-specific processing might also be expected to differ. The inflectional system for verbs in English, for example, is relatively impoverished: in the present tense there are only two basic inflectional forms for person and number agreement—a null morpheme (as in *they walk-Ø*), and the -s agreement form (as in *he walk-s*). There is a single regular past tense form (*walk-ed*) and the future tense is indicated by the use of a modal auxiliary (*will walk-Ø*). By contrast, Spanish has a richer system of verbal inflectional morphology; in the present indicative alone, six agreement forms are possible (*yo and-o, tu and-as, el and-a, nosotros and-amos, vosotros and-ais, ellos and-an*); across tenses and moods each verb stem has approximately 50 distinct inflected forms. In addition, regular Spanish verbs may fall into any of three conjugation paradigms, with phonologically distinct inflectional forms within each paradigm.²

Differences in morphosyntactic complexity such as those illustrated here could translate into different patterns of verb-specific processing across languages. Such differences might manifest in two ways: 1) in the location of verb-specific processing, or, 2) in the activity patterns within common verb-specific regions. (For examples in other cognitive domains where this has been the case, see Peelen et al., 2006; Downing et al., 2007). The second model could easily accommodate the extant neuropsychological data. On the other hand, we might find that some regions are activated commonly and indistinguishably by verbs in both languages. This could reflect either experimentally imposed constraints on the variability of morphosyntactic processing (a task-specific effect), or it might identify regions that are involved in processing words of a given category irrespective of morphosyntactic complexity (a category-specific effect).

²Nominal inflection is of similar complexity in English and Spanish. In English, only the plural marker is used (*window-s*), while in Spanish, both the plural and gender markers are used (*niño-s*, boys, vs. *niña-s*, girls)

Which brain regions might exhibit different responses to noun and verb processing tasks? Evidence from aphasic patients suggests that noun deficits tend to arise from lesions to the left middle-to-anterior temporal lobe (Miceli et al., 1984; Tranel et al., 2001; Aggijaro et al., 2006). In imaging studies with healthy subjects, noun-specific activation has been observed in the left fusiform gyrus during a morphosyntactic task (Shapiro et al., 2006) and during a task in which grammatical content was assigned to pseudowords (Mestres-Misse et al., 2009). Verb deficits resulted from lesions in left inferior frontal regions, premotor regions, or in posterior temporal to inferior parietal regions (Miceli et al., 1984; Tranel et al., 2001; Aggijaro et al., 2006). Many imaging studies have found greater activation for verbs compared to nouns in the left prefrontal cortex (Perani et al., 1999; Shapiro et al., 2006; Palti et al., 2007; Bedny et al., 2008; Mestres-Misse et al., 2009) and in left posterior temporal regions (Perani et al., 1999; Kable et al., 2002; Shapiro et al., 2006; Yokoyama et al., 2006; Palti et al., 2007; Bedny et al., 2008; Liljeström et al., 2008; Tyler et al., 2008; Mestres-Misse et al., 2009). The convergence of lesion patterns in cases of grammatical category-specific deficits and functional activation patterns in neuroimaging studies leads us to predict noun-specific activation in the left inferior temporal lobe and verb-specific activation in left posterior mid-temporal and left prefrontal regions.

In this functional magnetic resonance imaging (fMRI) study, we sought to characterize brain activity for nouns and verbs in two languages within a study population of highly proficient (self-rated) Spanish-English bilinguals. For this purpose, we adapted a morphosyntactic processing task that has been used successfully to elicit noun-verb differences in earlier functional neuroimaging studies (Shapiro et al., 2006) and studies using transcranial magnetic stimulation (Shapiro et al., 2001; Cappelletti et al., 2008). Specifically, we presented noun and verb stimuli in the context of short phrases/sentences (*one building, he whistles, una iglesia, él fuma*). On each trial, participants completed a phrase/sentence by producing one word (e.g., given “*one building, two*”, participants said “*buildings*”; or given “*they walk, he*”, participants said “*walks*”) (see Fig. 1). The task was performed in both English and Spanish.

We analyzed the blood oxygenation level-dependent (BOLD) response by grammatical category and by language to determine whether the same areas of differential activity for nouns and verbs could be observed across languages. Within regions that showed a differential response, we used multi-voxel pattern analysis (MVPA) to further investigate the degree to which grammatical class activity depends on language. This analysis technique exploits information contained in the pattern of activation across a set of voxels (Haxby et al., 2001). MVPA has previously been used to dissociate overlapping but functionally independent neuronal populations in extrastriate visual cortex (Peelen et al., 2006; Downing et al., 2007). By extension, MVPA was used here to test whether grammatical class-specific activations that overlap for the two languages reflect similar or distinct underlying neural processes.

In the present study, we tested the hypothesis that the same neural structures are involved in differentially processing the categories “verb” and “noun” in two different languages (language invariance). Therefore, we predict that the same regions will show noun- or verb-specific activation in both languages. We also predict that multi-voxel activity patterns within these regions will distinguish between nouns and verbs irrespective of language, although interactions within a region between language and grammatical category could reflect differences in morphosyntactic complexity and other uncontrolled (or uncontrollable) language-specific dimensions.

2. MATERIAL AND METHODS

2.1 Participants

Data from 16 right-handed participants (6 males, 10 females; mean age: 24 ± 3.3 years) were included in the fMRI analyses.³ Participants were recruited from the community through internet advertisements placed on the website Craigslist (<http://boston.craigslist.org>). Participants included in our analyses reported no history of neurological or psychiatric illness. All gave informed consent before participating and were compensated at the rate of \$50 per hour. The protocol was approved by all relevant institutional review boards.

All participants were fluently bilingual in Spanish and English. Thirteen subjects reported that their first language (L1) was Spanish; three subjects reported that they learned English and Spanish concurrently. The average reported age of first exposure to Spanish was 0.2 years ($SD = 0.7$, range: 0–2.5); the average age of first exposure to English was 3.1 years ($SD = 2.8$, range: 0–7). Participants estimated that they began speaking Spanish at 1.5 years ($SD = 0.7$, range: 1–2.5) and English at 3.9 years ($SD = 2.2$, range: 1–8). To control for the age of acquisition of English (AoA L2), this variable was included as a covariate in the whole-brain analysis.

Using a scale from one to ten, participants reported their current language proficiency in five areas. In three areas (comprehension, spelling, and pronunciation), participants rated their proficiency as equal in both languages (all $ps > 0.4$). In one area (writing), there was a trend toward higher proficiency ratings in English ($M = 9.69$, $SD = 0.48$) than in Spanish ($M = 8.81$, $SD = 1.64$), $t(15) = 2.00$, $p = 0.056$. In the fifth area (reading), participants rated themselves as having significantly higher proficiency in English ($M = 9.75$, $SD = 0.45$) than in Spanish ($M = 8.87$, $SD = 1.50$), $t(15) = 2.49$, $p < 0.05$. The difference in reading proficiency ratings indicated that subjects may have felt more comfortable using English in the context of the experiment. We controlled for the variation in Spanish reading (SR) proficiency by using SR as a covariate in the analyses.

Participants reported that they used both languages frequently throughout their lives, with an increasing reliance on English outside the home and as they grew older. Subjects reported that as children they used English approximately 40% of the time, while in adulthood they used English 75% of the time. As a control for dominance, the percentage English spoken in adulthood (EA) was included as a covariate in the analyses.

2.2 Material

Stimuli consisted of 24 words in each of the following categories: English Nouns (EN), English Verbs (EV), Spanish Nouns (SN), and Spanish Verbs (SV). Participants saw each word four times over the course of the experiment. Within both languages, nouns and verbs were matched (all $ps > 0.3$) on number of syllables, number of phonemes, number of letters, and frequency (Francis and Kucera, 1982; Sebastián-Gallés et al., 2000). Across languages, nouns and verbs were matched on number of phonemes and on frequency; Spanish nouns and verbs contained more syllables than their English counterparts ($ps < 0.05$), while English nouns and verbs contained more letters ($ps < 0.005$). Six words (5 verbs, 1 noun) were direct translations across languages (e.g., *wedding* and *boda*), while the remaining stimuli were semantically related (e.g., *deliver* and *manda* (order), *embroider* and *teje* (weave)). Among the verbs, argument structure was not strictly controlled: in English, 4 verbs were transitive and 5 were unergative; in Spanish, 5 were transitive and 1 was

³A total of 22 subjects had been scanned for this experiment; however, six subjects were excluded due to: technical difficulties while scanning (3); insufficient proficiency in Spanish (1); diagnosis of Attention Deficit/Hyperactivity Disorder (1); and ambidexterity (1).

unergative. The majority of words in both languages, however, were ambitransitive (15 in English, 18 in Spanish). For ambitransitive verbs, we did not have standardized ratings to determine the relative frequencies of transitive and intransitive uses (e.g., *he startles the horse* (transitive) vs. *the horse startles easily* (unaccusative)). We will return to this point in our interpretation of the results.

Five native speakers of Spanish with good knowledge of English were asked to rate whether they thought the words had a common origin; all the stimuli used were rated as non-cognates. The words across languages did not overlap phonologically more than 30%. All Spanish nouns were feminine (see Supplementary Materials), so that the number of cue types would be the same in both languages (one/two and una/dos, as opposed to un/una/dos) and so that the inflectional markers used in the Spanish task (see Procedures, below) were phonologically identical across categories (*a/-as*, *e/-es*).

In a behavioral paradigm, a separate group of 42 Spanish-English bilinguals rated the items for imageability. Nouns were more imageable than verbs $t(94) = 3.50$, $p < 0.001$ and Spanish words were more imageable than English words $t(94) = 2.20$, $p < 0.05$. To account for potential effects of imageability (IMG), we included this parameter as a regressor in our analyses.

2.3 Procedures

Participants completed the morphosyntactic task in Spanish and English during fMRI data acquisition. Stimuli from the two languages were not intermixed. The experiment was completed in four runs, which were organized by language in an ABBA fashion: The run order was counterbalanced across participants such that if runs 1 and 4 (A runs) were performed in English, runs 2 and 3 (B runs) were performed in Spanish, and vice versa.

Before the experiment, participants completed a practice task that consisted of ten trials in one language followed by ten trials in the other language. This order varied among participants to match the order in which they would complete the experiment. Responses during this task were monitored to ensure that participants understood the instructions and consistently produced correct responses. The task was not difficult, and most participants reached ceiling performance within a few practice trials. All participants reached ceiling performance well before the end of the practice session. Behavioral data were not collected during the scanning session. Stimuli used in the practice task were not included in the actual experiment. To minimize the potential for head movement, participants were instructed to keep their teeth lightly touching while speaking. Participants reported no difficulty in maintaining this technique, and their verbal responses were clear. No head movement in any axis exceeded 3.5 mm for any participant.

Participants completed each trial by producing a grammatically correct single word (spoken out loud) (Fig. 1). On each trial, the first screen (1 s) showed a phrase/sentence (e.g., English noun trial: *one window*; English verb trial: *he delivers*; Spanish noun trial: *una ventana*; Spanish verb trial: *él manda*); the second screen (1 s) showed a cue word (English noun trial: *one* or *two*; English verb trial: *he* or *they*; Spanish noun trial: *una* or *dos*; Spanish verb trial: *él* or *tú*). The task was to complete the second phrase/sentence using the same word as in the first phrase/sentence, but making any agreement necessary to correspond with the cue word. For example: *two windows, one...* “window”; *he delivers, he...* “delivers”; *dos ventanas, dos...* “ventanas”; *él manda, tú...* “mandas”. A fixation cross (+) with variable duration (2–8 s) appeared between trials. In each language, half of the trials involved the addition or removal of an “-s” suffix; the other half involved no change. Because the inflectional transformations for both word classes in both languages involve adding or removing the same phoneme (/s/), any differences that emerge in patterns of activity across categories or

languages cannot be attributed to phonological differences. At the same time, the constraints placed on the kinds of operations used might have the effect of limiting or suppressing any differences that might be attributable to differences in morphosyntactic complexity.

Trial types were pseudo-randomly ordered in an event-related design (no more than four consecutive trials of the same type). The trials were jittered with a fixation period ranging from 2 to 8 seconds. The next trial began when a new stimulus phrase/sentence replaced the fixation cross on the screen. Each of the four functional runs contained 96 trials; half were noun trials and half were verb trials. Each word appeared twice within a run and four times over the course of the experiment. In each of these four instances, the word appeared in a different arrangement of stimulus phrase/sentence and cue word; for instance, the English verb *to agree* appeared as *he agrees*, *he... “agrees”*; *he agrees, they... “agree”*; *they agree, they... “agree”*; *they agree, he... “agrees.”*

2.4 fMRI Measurement

Data were collected with a 3-Tesla Siemens Magnetom scanner using a 12-channel head coil. Due to a change of scanners at the facility, the first 10 subjects were scanned on an Allegra model and the last 6 subjects were scanned on a Trio model. The change of scanner did not appear to affect the main findings. Functional data were acquired using an echoplanar imaging sequence (TR 2000ms, TE 30ms, flip angle 90°, FOV 256mm, matrix 64×64, voxel size 4×4×4mm, slices acquired in interleaved order, 35 slices with Allegra scanner and 33 slices with Trio scanner). Four dummy scans were acquired at the beginning of each run. Imaging took place at Massachusetts General Hospital Athinoula A. Martinos Center for Biomedical Imaging in Charlestown, MA.

Stimuli were projected into the scanner using E-Prime presentation software (v1.1, Psychology Software Tools, Pittsburgh, PA). Participants viewed the screen via a mirror mounted on the head coil. Stimuli appeared as white lettering on a black background.

2.5 Data Analysis

The acquired DICOM files were converted to NIfTI format using the program MRICConvert (v2.0, Lewis Center for NeuroImaging, University of Oregon). Preprocessing and univariate analyses were conducted using SPM5 (Wellcome Department of Imaging Neuroscience, University College London, UK). Images were slice-time-corrected, realigned and unwarped (motion-corrected), and normalized to the standard SPM5 EPI template in Montreal Neurological Institute (MNI) coordinates. Voxels were resampled to 2×2×2mm. For the univariate analyses, data were smoothed with a Gaussian kernel (FWHM = 8mm). No smoothing was applied for the multi-voxel pattern analysis.

The preprocessed images were entered into subject-specific first level models. Each trial type was modeled as a separate boxcar function; the onset and duration of each square wave matched the onset and duration of the cue phrase/sentence. Each trial thus had a fixed duration of 1 second. Fixation was modeled as a separate function in the first level models. In addition to these five variables of interest (four trial types plus fixation), we included imageability as a parametric modulator. The onsets and durations for each trial type were entered into SPM, where the square waves were convolved with a canonical hemodynamic response function. Time-series data were filtered at 128 s. The model was estimated and β -weights corresponding to each trial type were extracted from each voxel against an implicit baseline. Contrasts for each trial type were then combined in a group-level model for univariate whole-brain analysis.

2.6 Univariate Analysis

The group-level univariate model was based on a flexible factorial design. A subject factor with equal subject variance was included along with four trial conditions: EN, EV, SN, and SV. The effects of including three covariates (*AoA L2*, *SR*, and *EA*) and imageability were also assessed. We performed whole-brain *F*-contrasts to look for main effects of Language (Spanish/English) and Grammatical Class (Noun/Verb). Where significant effects were observed, the direction of these effects was determined using *t*-contrasts. For follow-up analyses, we defined regions of interest (ROI) according to these group-level clusters (MarsBaR toolbox, Brett et al. 2002). Subject-wise activation levels were extracted from each ROI for each trial type. These values, for each ROI separately, were entered into a 2×2 Language × Grammatical Class repeated-measures ANOVA in SPSS (v17.0).

2.7 Multivariate Analysis

Multi-voxel pattern analysis was performed in the ROIs defined by the univariate whole-brain analysis (see above). For each subject, β -weights were extracted for each run separately using unsmoothed data. Each of the 4 conditions (EN, EV, SN, SV) was presented in 2 out of the 4 runs (see Procedures), resulting, for each voxel, in 2 β -weights per condition (e.g., EN1, EN2). For each subject, the voxelwise patterns of betas of the first half of the data (e.g., EN1) were correlated with the voxelwise patterns of betas of the second half of the data (e.g., EN2). For each ROI and subject, we constructed a 4×4 correlation matrix reflecting the similarity of multi-voxel activity patterns between the 4 conditions. Correlations were Fisher transformed [$0.5 \times \ln((1+r)/(1-r))$] at this stage. The resulting 16 correlations were grouped into 4 categories: 1) within-language, within-grammatical class (EN1-EN2, EV1-EV2, SN1-SN2, SV1-SV2); 2) within-language, across-grammatical class (EN1-EV2, EV1-EN2, SN1-SV2, SV1-SN2); 3) across-language, within-grammatical class (EN1-SN2, EV1-SV2, SN1-EN2, SV1-EV2); 4) across-language, across-grammatical class (EN1-SV2, EV1-SN2, SN1-EV2, SV1-EN2). Note that all eight trial/run types appeared in each of these groups, differing only in their pairing. The four groups were compared in a 2×2 repeated-measures ANOVA: Language Comparison (within-language, across-language) × Class Comparison (within-class, across-class).

Comparing these groups of correlations measures the degree to which multi-voxel activity patterns carry information about language (main effect of Language Comparison: (1) + (2) vs. (3) + (4)) and grammatical class (main effect of Class Comparison: (1) + (3) vs. (2) + (4)). For example, a main effect of Language Comparison with greater correlation within-language than across-language would indicate that the multi-voxel patterns in English differ significantly from the multi-voxel patterns in Spanish. In the same way, a main effect of Class Comparison showing greater correlation within-class than across-class would indicate that the multi-voxel patterns of Nouns can be differentiated from the multi-voxel patterns of activity of Verbs. Furthermore, the interaction between language and grammatical class (Language × Class: (1) – (2) vs. (3) – (4)) indicates the extent to which grammatical class information depends on language. It should be noted that all ROIs showed, by definition, a univariate difference between verbs and nouns. Although correlations are (computationally) not influenced by mean values, the main effect of Class Comparison could, in principle, be related to such differences in mean activity values. Most importantly for present purposes, the main comparisons of interest were those involving language (main effect of Language Comparison and interaction between language and grammatical class). These comparisons were not influenced by differences in mean activity.

3. RESULTS

3.1 Univariate Analyses

Our whole-brain univariate analyses ($p < 0.01$, corrected for false discovery rate (FDR), minimum cluster extent ($k = 40$) revealed a main effect for Grammatical Class (all verbs vs. all nouns) in four regions, but they revealed no main effect of Language (all English trials vs. all Spanish trials) and no interaction between Language and Grammatical Class. Neither the main effect of Language nor the interaction showed any active voxels (at $k = 0$) at this threshold or at a reduced threshold of $p < 0.05$ (FDR-corrected). The inclusion of four regressors (imageability, age of acquisition of English (*AoA L2*), Spanish reading proficiency (*SR*), and the percentage of time participants used English as adults (*EA*)) did not significantly alter the observed activity or significance levels. The areas activated during the task, as shown by the contrasts Noun > Fixation and Verb > Fixation, included, bilaterally, the posterior superior frontal gyrus, the precentral gyrus and superior temporal gyrus, parts of the cerebellum, and parts of the parietal lobe (see Figs. S1a and S1b in Supplementary Material).

To visualize the direction of the main effect of Grammatical Class, we performed two t -contrasts: Noun > Verb and Verb > Noun ($p < 0.01$, FDR-corrected, $k = 40$). The Verb > Noun contrast contained all four clusters observed in the main effect (Fig. 2 and Table 1), while the Noun > Verb contrast yielded no voxels above threshold. Thus, the main effect of Grammatical Class was driven by greater activity for verb trials than for noun trials. In decreasing order of significance, these clusters were: left posterior middle temporal gyrus (LMTG, BA 22 and 39), left middle frontal gyrus (LMFG, BA 9, 46, and 6), pre-supplementary motor area (pre-SMA, BA 6 and 8), and right middle occipital gyrus (RMOG, BA 18). At a lower threshold in the Noun > Verb contrast, the most significant region of activity (voxel-level $p < 0.001$, uncorrected) appeared in the right post-central gyrus and inferior parietal lobule; however, due to the low significance of regions showing greater activation for nouns than for verbs, no further analyses were performed.

Next, we performed several analyses that approached the same question in different ways; with each analysis, the goal was to determine whether the verb effect in LMTG, LMFG, pre-SMA, and RMOG was driven by both languages. At the whole-brain level, we tested the interaction between Language and Grammatical Class at a threshold that was purposefully much lower than would be used to report significant results ($p < 0.05$, uncorrected). Large regions of activation appeared for the interaction at this low threshold. This activation was compared to our four regions of interest as previously defined. The two maps did not overlap (Fig. 3). Of 24,768 voxels active for the interaction at low threshold and 2,174 voxels more active for verbs than for nouns, only seven voxels overlapped. Six of these voxels were located close to one another at the anterior edge of LMTG; the seventh was located in the RMOG. This small degree of overlap visually suggests the consistency of the Verb > Noun effect across the two languages.

To further test the consistency of the Verb > Noun effect, we performed an ROI analysis, entering individual subject data into a Language $\times$ Grammatical Class repeated-measures ANOVA for each ROI. The results of this analysis were not corrected for multiple comparisons. As the ROIs were defined by the contrast Verb > Noun, the main effect of Grammatical Class was significant in all ROIs. The main effect of Language was significant in the RMOG ($F(1,15) = 5.5$, $p < 0.05$), indicating a higher average response to Spanish stimuli ($M = 0.6$, $SD = 2.9$) than to English stimuli ($M = -0.5$, $SD = 3.5$). The main effect of Language approached significance in the pre-SMA ($F(1,15) = 4.0$, $p = 0.064$) but was not significant in either LMTG or LMFG ($ps > 0.1$). In this analysis, we were primarily interested in the interaction between Language and Grammatical Class. A significant

interaction could indicate that one language is driving the main effect of Grammatical Class. The interaction between Language and Grammatical Class was significant in the LMTG ($F(1,15) = 5.6, p < 0.05$) but not in other regions (all $ps > 0.1$). Further tests of the interaction in LMTG showed that the effect of Grammatical Class was significant in each language individually (English: $t(15) = 7.1, p = 0.0000035$; Spanish: $t(15) = 3.4, p = 0.0037$) and strongest in English; the comparison of Spanish verbs to English nouns was also significant, $t(15) = 2.6, p < 0.05$, which may be unsurprising given the greater response to verbs in this region. There was no significant difference between English verbs and Spanish verbs or between English nouns and Spanish nouns (all $ps > 0.2$). The results confirm that, in these four regions, higher activity for verbs, compared to nouns, is driven by both languages (see Fig. 4 for a comparison of Verb > Noun activity in English and Spanish in each ROI).

3.2 Multivariate Results

In each of the four verb-selective ROIs described above, a multi-voxel pattern analysis was performed comparing the similarity (voxelwise correlation) of activity patterns between the conditions of the experiment (see Methods). This analysis compared fine-grained activity patterns in each ROI without regard to the average level of activation (average levels of activation were compared in the univariate analysis).

Of interest was the extent to which activity patterns were influenced by language (comparing within- vs. across-language correlations) and grammatical class (comparing within- vs. across-class correlations). The effect of Language Comparison was non-significant in all ROIs (all $ps > 0.5$), indicating that the activity patterns for English and Spanish phrases were statistically indistinguishable; this implied that similar processing occurred for both languages in these regions. The effect of Class Comparison was significant in LMTG, $F(1,15) = 17.6, p < 0.001$, and in LMFG, $F(1,15) = 8.8, p < 0.01$, indicating that verb patterns could reliably be distinguished from noun patterns. In other words, LMTG and LMFG showed evidence of processing nouns and verbs as separate entities. This was not the case in pre-SMA or RMOG (all $ps > 0.1$): in pre-SMA and RMOG, the multi-voxel patterns for nouns and verbs were not statistically separable, suggesting that these regions process nouns and verbs in a similar manner.

In the multivariate analysis, the interaction between Class Comparison and Language Comparison indicated the extent to which the differential pattern for grammatical categories depended on the language in which the task was performed (Fig. 5). The interaction was significant in LMFG ($F(1,15) = 4.7, p < 0.05$). In this region, the effect of Class Comparison was stronger when multi-voxel patterns for nouns and verbs were compared across languages than when multi-voxel patterns for nouns and verbs were compared within-language. This effect is the opposite of what one would expect to see if grammatical class were processed differently in the two languages. The interaction was not significant in LMTG, pre-SMA, or RMOG (all $ps > 0.2$).

4. DISCUSSION

This experiment investigated the neural regions engaged in processing grammatical information about nouns and verbs in bilingual speakers. Specifically, we sought to determine whether bilinguals process nouns and verbs in the same brain regions across languages, and if so, whether finer-grained patterns of activity within these regions show any differences across languages. We found that Spanish-English bilinguals who rated themselves as being highly proficient in both languages showed the same regions of increased activity for verbs compared to nouns in Spanish and English. Four brain regions (LMTG, LMFG, pre-SMA, and RMOG) showed a greater response to verbs than to nouns in

both languages. Within these regions of interest, a univariate analysis showed that the interaction between Language and Grammatical Class was significant only in the LMTG, where the effect of Grammatical Class was stronger in English, though it remained significant in Spanish as well. As in many previous studies, we did not find any regions where noun activity was greater than verb activity. This continues to be a perplexing finding and will require further investigation.

Multi-voxel pattern analysis showed that activity in these four regions was just as strongly correlated across language as within language, indicating that similar processing occurred in the two languages. Furthermore, activity patterns were more similar within than across grammatical category in LMTG and in LMFG, indicating that verb processing in these regions can be differentiated reliably from noun processing. These results suggest that the neural structures and types of processing recruited for verbs as a grammatical category seem independent of language in proficient bilinguals, both at the macroscopic neuroanatomical level and at the level of fine-grained neural activity patterns. Other aspects of language that were not systematically manipulated—such as morphophonological complexity or proficiency differences—could have language-dependent effects.

4.1 Grammatical organization in bilingual speakers

The finding that bilingual speakers show reliable patterns of activation for noun and verb processing across languages is consistent with studies of bilingual patients with aphasia, who show similar patterns of grammatical impairment across languages (de Diego Balaguer et al., 2004; Hernández et al., 2007; Hernández et al., 2008; Caño et al., in press). These findings have been interpreted as consistent with the proposal that similar organizational principles apply to multiple languages acquired under similar conditions (Paradis, 1994; Ullman, 2001).

We are not aware of neuroimaging studies that have directly compared grammatical processes across the languages of balanced bilingual (or multilingual) speakers. However, the lack of any observed differences in activation between languages in a grammatical processing task fits with a series of previous studies that have also shown similar patterns of activity across languages for early, highly proficient bilingual speakers (for comprehensive reviews, see Abutalebi et al., 2001; Indefrey, 2006; Abutalebi and Green, 2007).

What principles might underlie the organization of information about grammatical categories across languages? As previously mentioned, human languages universally distinguish between nouns and verbs.⁴ In general, this distinction relies on two kinds of criteria: lexical-semantic criteria (nouns typically refer to entities, while verbs typically refer to actions or events), and syntactic or distributional criteria (nouns and verbs play different roles in sentences and occur in conjunction with different sets of grammatical morphemes). These different criteria are not necessarily isomorphic; for example, in some instances words that refer to actions (e.g., *run*) may occur syntactically and morphologically as nouns (e.g., *the running of the bulls*). However, all languages must have a mechanism for mapping lexical items with particular semantic structures to specific syntactic roles (Pinker, 1984; O'Grady, 1997), which in some languages are marked morphologically.⁵ We might therefore expect to find that common neural substrates underlie the mechanisms for categorizing lexical items and processing category-specific morphosyntactic information.

⁴Again, we qualify this statement by referring to the controversies discussed in footnote 1.

⁵In some languages, there are cases in which words may be morphologically in one class and syntactically in another (Evans 2000). Analysis of these cases is beyond the scope of the present discussion, but see (Evans 1995).

4.2 Brain regions engaged in verb processing across languages

In the present study, the LMTG showed the strongest grammatical class selectivity both in the univariate and multivariate analyses. In the univariate analysis, but not the multivariate analysis, the effect of grammatical class in LMTG was stronger in English than in Spanish. The origin of this effect is not obvious and could possibly include factors such as proficiency, language dominance, or morphosyntactic complexity. Nevertheless, given that a significant verb effect was present in both languages in LMTG and that the multivariate analysis showed language-invariant grammatical class-specific patterns, the same neural structures appear to be involved in processing verbs in both languages in LMTG.

This region has been consistently implicated in the processing of verbs (compared to nouns) across a variety of tasks including semantic judgment (Bedny et al., 2008), grammaticality judgment (Burton et al., 2009), lexical decision (Perani et al., 1999), picture naming with objects and actions (Liljeström et al., 2008)⁶, and morphosyntactic tasks (Shapiro et al., 2006). We would also expect to find verb-specific activation in the LMTG if the present task were performed by either Spanish or English monolinguals. This expectation is borne out by Shapiro et al. (2006) in which English monolinguals performed several variations of the present task and showed greater activation for verbs in this region. The verb-specific effects reported in this region are not restricted to English; they have been observed in Hebrew (Palti et al., 2007), Italian (Perani et al., 1999), German (Khader et al., 2010) Finnish (Liljeström et al., 2008), and Japanese (Yokoyama et al., 2006). Furthermore, the LMTG is one of the regions lesioned in patients who are more impaired for verb than noun processing (Tranel et al., 2001; Aggujaro et al., 2006).

In English, greater activation for verbs in LMTG has been shown to depend on the presentation of stimuli in unambiguous grammatical context, where the category of stimulus words is specified either by morphological inflection (Tyler et al., 2008) or by strong semantic constraints (Burton et al., 2009). In most of the other languages that have been investigated, morphosyntactic rules require that the grammatical category of a lexical item be overtly specified (e.g. by markers for case, number, gender, agreement, tense, etc.). In these studies the finding of increased activity for verbs in the LMTG does not depend on the explicit engagement of morphosyntactic processes as such.

It is therefore possible that the LMTG is engaged specifically in the lexical-semantic processing of verbs. The term “lexical-semantic” is deliberate here, and is meant in opposition to “conceptual-semantic”: as noted above, the LMTG seems to be activated selectively for verbs irrespective of the extent to which they refer to concrete actions (Bedny et al., 2008; Shapiro et al., 2006) and is even activated by pseudowords when used as verbs rather than nouns (Shapiro et al., 2006). Lexical-semantic variables may include such attributes as argument structure, which has indeed been shown to modulate the neural response to verb processing in various brain regions, including the LMTG (Assadollahi & Rockstroh, 2008; den Ouden et al., 2009; Shetreet et al., 2010). In this context, we speculate that the interaction of language and grammatical category in our study may be attributable in part to uncontrolled differences in verbal argument structure.⁷ The LMFG, like the LMTG, showed significantly greater overall activation for verbs across languages and significantly higher multi-voxel correlations within- than across-grammatical category. Verb-specific activity in LMFG has been reported in a number of studies (Perani et al., 1999; Palti et al., 2007; Liljeström et al., 2008) including when the present task was performed by English monolinguals (Shapiro et al., 2006), while other studies show greater activation for verbs

⁶Actions were named in inflected form (e.g., “barks”).

⁷We would like to acknowledge David Kemmerer for this suggestion.

more ventrally in the posterior inferior frontal gyrus (IFG) (Yokoyama et al., 2006; Longe et al., 2007; Bedny et al., 2008; Khader et al., 2010) or in both regions (Palti et al., 2007). This left prefrontal verb-specific activation converges with the finding that lesions in left prefrontal cortex are frequently associated with impaired verb processing (e.g., Miceli et al., 1984; Tranel et al., 2001; Aggujaro et al., 2006). Activation of the left MFG for verb processing has been demonstrated in studies that involve either production of verbs with category-specific morphosyntactic marking (Perani et al., 1999; Shapiro et al., 2006; Liljeström et al., 2008) or lexical decision-making with explicit focus on morphological features (Palti et al., 2007).

By contrast, activation of the IFG without activation of the MFG is shown in studies using comprehension paradigms that do not specifically require attention to morphological features of verbs, even if verbs are presented in morphologically marked forms (Yokoyama et al., 2006; Longe et al., 2007; Bedny et al., 2008). The IFG also shows increased activity in grammatical decision tasks when the grammatical category of the stimulus word is ambiguous (Burton et al., 2009). Finally, some studies have demonstrated that the IFG shows greater activity for nouns when the task at hand renders noun processing more demanding, for example, in the production of irregular forms (Sahin et al., 2006) or in a grammatical class switching paradigm (Berlingeri et al., 2008). Together, these results suggest that the left IFG may be involved in category-general aspects of lexical or morphological processing, showing greater activity in contexts that impose a greater information processing burden. This may be due to factors such as strength of stimulus-response association and selection between competing responses, which have been shown to affect activation of the inferior frontal cortex during the production of verbs (Crescentini et al., 2010).

Here, we showed that left MFG, but not IFG, activity is elicited by morphosyntactic processing of verbs in both English and Spanish and that multi-voxel patterns of activity in MFG carried information about grammatical category. These results suggest that this area is involved in category-specific morphosyntactic processing of verbs across languages with explicit morphological markings.

Two additional regions (pre-SMA and RMOG) showed a higher overall BOLD response to verbs than to nouns. In the multivariate analysis, however, neither of these regions carried significant information about grammatical category. The RMOG showed the least significant effect of grammatical class in the univariate analysis, although several investigators have described similar activation for the Verb > Noun contrast in the right (Tyler et al., 2008; Khader et al., 2010) and left (Perani et al., 1999) hemispheres. In patients, there is scant evidence to support any role for the right occipital lobe in verb production, although the left occipital lobe has been associated with deficits for both verbs (Tranel et al., 2001) and nouns (Aggujaro et al., 2006). In this experiment, however, the multivariate analysis suggests that activation in the RMOG was driven by factors unrelated to grammatical category. Among other processes, the middle occipital gyri have been implicated specifically in letter recognition (Ellis et al., 2009). One possibility might be that the greater activation for Spanish was driven by the presence in the Spanish stimuli of letters not found in English, namely those with an acute accent (as in *tú* and *él*).

In contrast to the RMOG cluster, the cluster of voxels in pre-SMA was much more strongly activated for verbs more than nouns in the univariate analysis. However, the multi-voxel patterns in pre-SMA did not show greater consistency within than across grammatical categories, indicating that it may be involved in processes that are not grammatical class-specific. The pre-SMA has been found to play a role in a wide range of language processes including single-word reading (Turkeltaub et al., 2002), lexical decision (Carreiras et al.,

2006), generation of semantically-related words (e.g., Alario et al., 2006), and sentence generation (Haller et al., 2005). Others have found that the pre-SMA may be involved in representing action words as cues for motor planning (Postle et al., 2008). Consistent with the interpretation that the pre-SMA is involved in non-category-specific processes, studies have shown that the pre-SMA is active during covert selection of nouns, verbs, and adjectives (Blackler et al., 2006) and that rTMS applied to this region results in reaction time delays that do not vary by word category (Tremblay and Gracco, 2010).

Thus, one potential role of the pre-SMA in this experiment is in selection of a particular word form from among a defined set of alternatives. The correct response on verb trials was one of several grammatically correct potential answers (e.g., present tense, past tense), but participants were restricted to one response by task instructions. The pre-SMA is consistently activated during general selection/inhibition of verbal or motor responses (for a review, see Nachev et al., 2008). Since verbs in both English and Spanish require more complex morphosyntactic agreement than do nouns, selection of the correct verb response may engage the pre-SMA.

Our results diverge from those of Chan et al. (2008), who found different patterns of verb vs. noun activation across languages in Chinese-English bilinguals. Chan et al. reported no verb- or noun-specific activation in Chinese, whereas in English several verb-selective regions were found, although only at a relatively lenient (uncorrected) threshold. As noted in the Introduction, this discrepancy could be related to the use of noun and verb stems in Chan et al., whereas in the present study grammatical category was explicitly marked.

Finally, it should be noted that although behavioral data were not collected during this study, such data would not alter our main conclusions. The goal of our study was not to establish the existence of verb-selective regions, as this has been the focus of much previous research (e.g., Perani et al., 1999; Shapiro et al., 2006). Rather, the main goal of the present study was to establish the correspondence of these previously identified regions across languages. As such, if the participants exhibited differences in behavioral performance across languages during the study, these differences would only have acted against our hypothesis of language invariance in proficient bilinguals.

Our results with Spanish-English bilinguals provide support for language-invariant cortical organization with respect to the noun/verb distinction, as operationalized in terms of inflectional number and tense marking. It should be noted that, even if the circuits were identical for Spanish and English, these languages are relatively close in phylogeny, and while they differ in many important respects, they are similar in grammatical and semantic structure when jointly compared to languages like Hungarian, Basque, Chinese, or Kiswahili. Nevertheless, the presence of the same pattern of verb-specific activity across languages suggests that the core principles governing the differential processing of nouns and verbs could be as universal as their occurrence in human language.⁸

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

⁸To those who reject the contention that the noun-verb distinction (or something like it) is a universal feature of human language, this may seem to be begging the question. We would rather argue that it is a first step at addressing the question empirically: *if* there are universal principles of grammatical categorization, surely they can only be discovered by comparing commonalities among similar languages as well as dissimilar languages. With similar languages, of course, it is easier to control for confounding variables like phonology and morphosyntactic complexity. Thus the finding that there are some commonalities among similar languages, after extraneous variables are controlled, suggests that the enterprise may be a viable one—even if it has a long way to go.

Acknowledgments

FUNDING

This work was supported by the National Institute on Deafness and Other Communication Disorders, National Institutes of Health (R01 DC006842) and Consolider-Ingenio 2010 Programme (CSD2007-00012 and PS12008-01191).

The authors wish to thank Talia Serrecchia for assistance with data collection and Scott Fairhall for assistance with data analysis in SPM. We also thank Edu Navarrete for his invaluable help in selecting Spanish stimuli.

References

- Abutalebi J, Cappa SF, Perani D. The bilingual brain as revealed by functional neuroimaging. *Biling-Lang Cogn*. 2001; 4:179–190.
- Abutalebi J, Green D. Bilingual language production: The neurocognition of language representation and control. *J Neurolinguistics*. 2007; 20:242–275.
- Aggujaro S, Crepaldi D, Pistarini C, Taricco M, Luzzatti C. Neuro-anatomical correlates of impaired retrieval of verbs and nouns: Interaction of grammatical class, imageability and actionality. *J Neurolinguistics*. 2006; 19:174–194.
- Alario FX, Chainay H, Lehericy S, Cohen L. The role of the supplementary motor area (SMA) in word production. *Brain Res*. 2006; 1076:129–143. [PubMed: 16480694]
- Assadollahi R, Rockstroh BS. Representation of the verb's argument structure in the human brain. *BMC Neurosci*. 2008; 9:69. [PubMed: 18644141]
- Bates E, Chen S, Tzeng O, Li P, Opie M. The noun-verb problem in Chinese aphasia. *Brain Lang*. 1991; 41:203–233. [PubMed: 1718531]
- Bedny M, Caramazza A, Grossman E, Pascual-Leone A, Saxe R. Concepts are more than percepts: the case of action verbs. *J Neurosci*. 2008; 28:11347–11353. [PubMed: 18971476]
- Berlingeri M, Crepaldi D, Roberti R, Scialfa G, Luzzatti C, Paulesu E. Nouns and verbs in the brain: grammatical class and task specific effects as revealed by fMRI. *Cogn Neuropsychol*. 2008; 25:528–558. [PubMed: 19086201]
- Blackler D, Byrnes ML, Mastaglia FL, Thickbroom W. Differential activation of frontal lobe areas by lexical and semantic language tasks: A functional magnetic resonance imaging study. *J Clin Neurosci*. 2006; 13:91–95. [PubMed: 16410203]
- Brett, M.; Anton, J-L.; Valabregue, R.; Poline, J-B. Region of interest analysis using an SPM toolbox. the 8th International Conference on Functional Mapping of the Human Brain; Sendai, Japan. 2002.
- Burton MW, Krebs-Noble D, Gullapalli RP, Berndt RS. Functional neuroimaging of grammatical class: ambiguous and unambiguous nouns and verbs. *Cogn Neuropsychol*. 2009; 26:148–171. [PubMed: 19105056]
- Caño A, Hernández M, Ivanova I, Juncadella M, Gascon-Bayarri J, Reñé R, Costa A. When one can write SALTO as noun but not as verb: A grammatical category-specific, modality-specific deficit. *Brain Lang*. in press.
- Cappelletti M, Fregni F, Shapiro K, Pascual-Leone A, Caramazza A. Processing nouns and verbs in the left frontal cortex: a transcranial magnetic stimulation study. *J Cogn Neurosci*. 2008; 20:707–720. [PubMed: 18052789]
- Caramazza A, Hillis A. Lexical organization of nouns and verbs in the brain. *Nature*. 1991; 349:788–790. [PubMed: 2000148]
- Carreiras M, Mechelli A, Price CJ. Effect of word and syllable frequency on activation during lexical decision and reading aloud. *Hum Brain Mapp*. 2006; 27:963–972. [PubMed: 16628608]
- Chan AH, Luke KK, Li P, Yip V, Li G, Weekes B, Tan LH. Neural correlates of nouns and verbs in early bilinguals. *Ann N Y Acad Sci*. 2008; 1145:30–40. [PubMed: 19076387]
- Crepaldi D, Berlingeri M, Paulesu E, Luzzatti C. A place for nouns and a place for verbs? A critical review of neurocognitive data on grammatical-class effects. *Brain Lang*. 2011; 116:33–49. [PubMed: 21036389]

- Crescentini C, Shallice T, Macaluso E. Item retrieval and competition in noun and verb generation: an fMRI study. *J Cogn Neurosci*. 2010; 22:1140–1157. [PubMed: 19413479]
- Croft, W. *Radical Construction Grammar: Syntactic Theory in Typological Perspective*. Oxford University Press; Oxford: 2001.
- de Diego Balaguer R, Costa A, Sebastián-Galles N, Juncadella M, Caramazza A. Regular and irregular morphology and its relationship with agrammatism: evidence from two Spanish-Catalan bilinguals. *Brain Lang*. 2004; 91:212–222. [PubMed: 15485710]
- den Ouden DB, Fix S, Parrish TB, Thompson CK. Argument structure effects in action verb naming in static and dynamic conditions. *J Neurolinguistics*. 2009; 22:196–215. [PubMed: 20160850]
- Downing PE, Wiggett AJ, Peelen MV. Functional magnetic resonance imaging investigation of overlapping lateral occipitotemporal activations using multi-voxel pattern analysis. *J Neurosci*. 2007; 27:226–233. [PubMed: 17202490]
- Ellis AW, Ferreira R, Cathles-Hagan P, Holt K, Jarvis L, Barca L. Word learning and the cerebral hemispheres: from serial to parallel processing of written words. *Philos Trans R Soc Lond B Biol Sci*. 2009; 364:3675–3696. [PubMed: 19933140]
- Evans, N. *A Grammar of Kayardild*. Berlin: Mouton de Gruyter; 1995.
- Evans, N. Word classes in the world's languages. In: Booij, G.; Lehmann, C.; Mugdan, J., editors. *An International Handbook on Inflection and Word-Formation*. Berlin: Walter de Gruyter; 2000. p. 708–732.
- Evans N, Levinson SC. The myth of language universals: Language diversity and its importance for cognitive science. *Behav Brain Sci*. 2009; 32:429–492. [PubMed: 19857320]
- Francis, WN.; Kucera, H. *Frequency Analysis of English Usage: Lexicon and Grammar*. Boston: Houghton Mifflin Company; 1982.
- Haller S, Radue EW, Erb M, Grodd W, Kircher T. Overt sentence production in event-related fMRI. *Neuropsychologia*. 2005; 43:807–814. [PubMed: 15721193]
- Haxby JV, Gobbini MI, Furey ML, Ishai A, Schouten JL, Pietrini P. Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*. 2001; 293:2425–2430. [PubMed: 11577229]
- Hernández M, Costa A, Sebastián-Gallés N, Juncadella M, Reñé R. The organisation of nouns and verbs in bilingual speakers: A case of bilingual grammatical category-specific deficit. *J Neurolinguistics*. 2007; 20:285–305.
- Hernández M, Caño A, Costa A, Sebastián-Gallés N, Juncadella M, Gascón-Bayarri J. Grammatical category-specific deficits in bilingual aphasia. *Brain Lang*. 2008; 107:68–80. [PubMed: 18294684]
- Hopper PJ, Thompson SA. The Discourse Basis for Lexical Categories in Universal Grammar. *Language*. 1984; 60:703–752.
- Indefrey P. A meta-analysis of hemodynamic studies on first and second language processing: Which suggested differences can we trust and what do they mean? *Lang Learn*. 2006; 56:279–304.
- Kable JW, Lease-Spellmeyer J, Chatterjee A. Neural substrates of action event knowledge. *J Cogn Neurosci*. 2002; 14:795–805. [PubMed: 12167263]
- Kambanaros M, van Steenbrugge W. Noun and verb processing in Greek-English bilingual individuals with anomic aphasia and the effect of instrumentality and verb-noun name relation. *Brain Lang*. 2006; 97:162–177. [PubMed: 16290262]
- Kambanaros M. The trouble with nouns and verbs in Greek fluent aphasia. *J Commun Disord*. 2008; 41:1–19. [PubMed: 17408685]
- Kemmerer D, Eggleston A. Nouns and verbs in the brain: Implications of linguistic typology for cognitive neuroscience. *Lingua*. 2010; 120:2686–2690.
- Khader PH, Jost K, Mertens M, Bien S, Rösler F. Neural correlates of generating visual nouns and motor verbs in a minimal phrase context. *Brain Res*. 2010; 1318:122–132. [PubMed: 20053347]
- Li P, Jin Z, Tan LH. Neural representations of nouns and verbs in Chinese: an fMRI study. *Neuroimage*. 2004; 21:1533–1541. [PubMed: 15050577]
- Liljeström M, Tarkiainen A, Parviainen T, Kujala J, Numminen J, Hiltunen J, Laine M, Salmelin R. Perceiving and naming actions and objects. *Neuroimage*. 2008; 41:1132–1141. [PubMed: 18456517]

- Loftus GR, Masson MEJ. Using confidence intervals in within-subject design. *Psychon Bull Rev*. 1994; 1:476–490.
- Longe O, Randall B, Stamatakis EA, Tyler LK. Grammatical categories in the brain: the role of morphological structure. *Cereb Cortex*. 2007; 17:1812–1820. [PubMed: 17060365]
- Meillet, A. *Linguistique historique et linguistique generale*. Paris: Honore Champion; 1926.
- Mestres-Misse A, Rodriguez-Fornells A, Munte TF. Neural differences in the mapping of verb and noun concepts onto novel words. *Neuroimage*. 2009; 49:2826–2835. [PubMed: 19837174]
- Miceli G, Silveri MC, Villa G, Caramazza A. On the basis for the agrammatic's difficulty in producing main verbs. *Cortex*. 1984; 20:207–220. [PubMed: 6204813]
- Nachev P, Kennard C, Husain M. Functional role of the supplementary and pre-supplementary motor areas. *Nat Rev Neurosci*. 2008; 9:856–869. [PubMed: 18843271]
- O'Grady, W. *Syntactic Development*. University of Chicago Press; 1997.
- Palti D, Ben Shachar M, Hendler T, Hadar U. Neural correlates of semantic and morphological processing of Hebrew nouns and verbs. *Hum Brain Mapp*. 2007; 28:303–314. [PubMed: 16977624]
- Paradis, M. Neuolinguistic aspects of implicit and explicit memory: Implications for bilingualism and SLA. In: Ellis, N., editor. *Implicit and Explicit Learning of Lanugages*. London: Academic Press; 1994. p. 393–419.
- Peelen MV, Wiggett AJ, Downing PE. Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron*. 2006; 49:815–822. [PubMed: 16543130]
- Perani D, Cappa SF, Schnur T, Tettamanti M, Collina S, Rosa MM, Fazio F. The neural correlates of verb and noun processing. A PET study. *Brain*. 1999; 122 (Pt 12):2337–2344. [PubMed: 10581226]
- Perani D, Abutalebi J. The neural basis of first and second language processing. *Curr Opin Neurobiol*. 2005; 15:202–206. [PubMed: 15831403]
- Pinker, S. *Language Learnability and Language Development*. Cambridge: Harvard University Press; 1984.
- Postle N, McMahon KL, Ashton R, Matthew M, de Zubicaray GI. Action word meaning representations in cytoarchitectonically defined primary and premotor cortices. *Neuroimage*. 2008; 43:634–644. [PubMed: 18786644]
- Robins RH. Noun and Verb in Universal Grammar. *Language*. 1952; 28:289–298.
- Sahin NT, Pinker S, Halgren E. Abstract grammatical processing of nouns and verbs in Broca's area: evidence from fMRI. *Cortex*. 2006; 42:540–562. [PubMed: 16881266]
- Sapir, E. *Language: An introduction to the study of speech*. New York: Harcourt, Brace and Company; 1921.
- Sebastián-Gallés, N.; Cueto, F.; Martí, MA.; Carreiras, M. *LEXESP: Lexico informatizado del espanol*. Barcelona: Edicions de la Universitat de Barcelona; 2000.
- Shapiro KA, Pascual-Leone A, Mottaghy FM, Gangitano M, Caramazza A. Grammatical Distinctions in the Left Frontal Cortex. *J Cogn Neurosci*. 2001; 13:713–720. [PubMed: 11564316]
- Shapiro KA, Mottaghy FM, Schiller NO, Poeppel TD, Flüß MO, Müller HW, Caramazza A, Krause BJ. Dissociating neural correlates for nouns and verbs. *Neuroimage*. 2005; 24:1058–1067. [PubMed: 15670683]
- Shapiro KA, Moo LR, Caramazza A. Cortical signatures of noun and verb production. *Proc Natl Acad Sci USA*. 2006; 103:1644–1649. [PubMed: 16432232]
- Shapiro, KA.; Caramazza, A. Morphological processes in language production. In: Gazzaniga, M., editor. *The Cognitive Neurosciences*. 4. Cambridge, MA: MIT Press; 2009. p. 777–788.
- Shetreet E, Friedmann N, Hadar U. The neural correlates of linguistic distinctions: unaccusative and unergative verbs. *J Cogn Neurosci*. 2010; 22:2306–2315. [PubMed: 19925202]
- Tranel D, Adolphs R, Damasio H, Damasio AR. A neural basis for the retrieval of words for actions. *Cogn Neuropsychol*. 2001; 18:655–647. [PubMed: 20945232]
- Tremblay P, Gracco VL. On the selection of words and oral motor responses: evidence of a response-independent fronto-parietal network. *Cortex*. 2010; 46:15–28. [PubMed: 19362298]

- Tsapkini K, Jarema G, Kehayia E. A morphological processing deficit in verbs but not in nouns: a case study in a highly inflected language. *J Neurolinguistics*. 2002; 15:265–288.
- Turkeltaub PE, Eden GF, Jones KM, Zeffiro TA. Meta-analysis of the functional neuroanatomy of single-word reading: method and validation. *Neuroimage*. 2002; 16:765–780. [PubMed: 12169260]
- Tyler LK, Randall B, Stamatakis EA. Cortical differentiation for nouns and verbs depends on grammatical markers. *J Cogn Neurosci*. 2008; 20:1381–1389. [PubMed: 18303983]
- Ullman M. The neural basis of lexicon and grammar in first and second language: The declarative/procedural model. *Biling-Lang Cogn*. 2001; 4:105–122.
- Vigliocco G, Vinson DP, Druks J, Barber H, Cappa SF. Nouns and verbs in the brain: A review of behavioral, electrophysiological, neuropsychological, and imaging studies. *Neurosci Biobehav Rev*. 2011; 35:407–426. [PubMed: 20451552]
- Yokoyama S, Miyamoto T, Riera J, Kim J, Akitsuki Y, Iwata K, Yoshimoto K, Horie K, Sato S, Kawashima R. Cortical mechanisms involved in the processing of verbs: an fMRI study. *J Cogn Neurosci*. 2006; 18:1304–1313. [PubMed: 16859416]

Figure 1.

Experimental Design: Each trial consisted of a stimulus phrase followed by a cue word. The task was to complete the second phrase by saying one word. Given “*one window, two*”, participants said “*windows*”. Likewise, “*una ventana, dos*” was completed with “*ventanas*”, “*he delivers, they*” with “*deliver*”, and “*tú mandas, él*” with “*manda*”. In both languages, half the trials involved either the removal or addition of an “-s” suffix; half involved no change (i.e., “*two windows, two*”).

Figure 2.

Whole-brain Verb > Noun contrast across all trials in Spanish and English ($p < 0.01$, FDR-corrected, cluster threshold = 40). Four regions of interest were defined based on this contrast: (A) left posterior middle temporal gyrus (LMTG, BA 22); (B) left posterior middle frontal gyrus (LMFG, BA 9, 46, and 6); (C) pre-supplementary motor area (pre-SMA, BA 6 and 8); (D) right middle occipital gyrus (RMOG, BA 18). The reverse contrast (Noun > Verb) showed no suprathreshold voxels.

Figure 3.

Language-invariance in the Verb > Noun regions; low overlap even with less stringent thresholds suggests that the Verb > Noun effect is not driven by just one language. Fewer than 0.03% of the voxels (7 voxels) overlap between the Language $\times$ Grammatical Class interaction (blue, $p < 0.05$, uncorrected, 24,768 voxels) and the Verb > Noun regions (yellow, $p < 0.01$, FDR-corrected, 2,174 voxels). The overlap (red) is at the anterior edge of LMTG (6 voxels) and in RMOG (1 voxel).

Figure 4.

Univariate region of interest (ROI) analyses show that the higher activity for verbs than for nouns is driven by both languages in all ROIs. Raw noun and verb activation levels were extracted for each subject from all four ROIs in both languages. The y-axis represents a simple subtraction of noun activity from verb activity. Points represent individual subjects. In LMTG, the effect of Grammatical Class was stronger in English (Language $\times$ Grammatical Class interaction, $F(1,1) = 5.6$, $p < 0.031$), but remained significant in each language individually. Other ROIs presented no interactions.

Figure 5.

Results of multi-voxel pattern analysis. There was no main effect of Language Comparison (within language vs. across language) in any of the ROIs, indicating that Spanish and English stimuli produced statistically indistinguishable multi-voxel activity patterns. LMTG and LMFG carried significant information about grammatical class, with higher correlations between activity patterns of the same class versus different class. Grammatical class information was not influenced by Language Comparison in LMTG, pre-SMA and rMOG, and was, if anything, stronger across language than within language in LMFG. Shown here, for each ROI, are the average Fisher-transformed correlations of multi-voxel patterns in four different comparisons: within-language, within-class (e.g., EN_EN); within-language, across-class (e.g., EN_EV); across-language, within-class (e.g., EN_SN), and across-language, across-class (e.g., EN_SV). Error bars represent within-subject standard error of the mean (Loftus and Masson 1994).

Table 1
Regions more active for verbs than nouns in a whole brain analysis across English and Spanish.

Brain Region	BA	Cluster Size	Cluster p	Voxel Z	MNI Coordinates		
					x	y	z
L. Middle / Superior Temporal Gyrus	22/39	470	0.000026	5.78	-50	-42	4
L. Superior Frontal Gyrus	6	325	0.00028	5.33	-2	14	64
	8			4.82	-2	20	56
L. Middle Frontal Gyrus	9	1308	5.9e-010	5.25	-46	6	42
	46			5.02	-48	20	26
	6			4.44	-34	6	58
R. Middle Occipital Gyrus	18	71	0.063	4.21	34	-86	0

Threshold: $p < 0.01$, FDR-corrected, cluster extent threshold = 40. Sub-regions denote local maxima greater than 8mm apart. No voxels were active in the contrasts Nouns > Verbs, Spanish > English, or English > Spanish. (BA = Brodmann area; Cluster p = cluster-level corrected p -value; Voxel Z = peak voxel Z -score).