

**Neural circuits subserving the retrieval of stems and grammatical features
in regular and irregular verbs**

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Abstract

Many languages, including English and Spanish, feature regular (dance → danced) and irregular (catch → caught) inflectional systems. According to psycholinguistic theories, regular and irregular inflections are either instantiated by a single or by two specialized mechanisms. Those theories differ in their assumptions concerning the underlying information necessary for the processing of regular verbs. While single mechanism accounts have stated an increased involvement of phonological processing for regular verbs, dual accounts emphasize the prominence of grammatical information. Using event-related fMRI, we sought to delineate the brain areas involved in the generation of complex verb forms in Spanish. This language has the advantage of isolating specific differences in the regular-irregular contrasts in terms of the number of stems associated with a verb while controlling for compositionality (regular and irregular verbs apply suffixes to be inflected). The present study showed that areas related to grammatical processing are active for both types of verbs (left opercular inferior frontal gyrus). In addition, major differences between regular and irregular verbs were also observed. Several areas of the prefrontal cortex were selectively active for irregular production presumably reflecting their role in lexical retrieval (bilateral inferior frontal area and dorsolateral prefrontal cortex). On the other hand, regular verbs showed increased activation in areas related to grammatical processing (anterior superior temporal gyrus/insular cortex) and in the left hippocampus, the latter possibly related to a greater implication of the phonological loop necessary for the reutilization of the same stem shared across all forms in regular verbs.

In the complex process of language production, verbs play a central role in the organization of words into a coherent utterance. In most languages, the form of a verb will vary according to the words related to it (its subject, its complements, its tense adverb). Our cognitive system is able to generate the resulting morphologically complex forms online with amazing speed. A breakdown of this process is frequently detected in patients with language processing difficulties (Badecker and Caramazza, 1991;Caplan, 1992;Caramazza et al., 1985) but knowledge about the specific brain areas involved and the cognitive operations supporting the processing of those forms is still scarce. This mapping is particularly problematic because in fact all verbs may not be processed in the same manner. Many languages, including English and Spanish, feature regular and irregular inflectional systems. Regular verbs form their complex forms according to what appears to be a systematic grammatical rule, independent of their base form (e.g. walk/walk-ed, play/play-ed). Irregular verbs follow apparently idiosyncratic variations (e.g. sing/sang, bring/brought, go/went) and therefore seem to require a specific lexical retrieval process. Due to the differential weights on lexical and grammatical information, the regular-irregular distinction has been used as an analogy for the study of the relations between lexicon and grammar. This has led to an intense debate regarding the cognitive and – more recently – the neural instantiation of the production of regular and irregular verbs echoing more general discussions in the language sciences (see, for example, (Aslin et al., 2004;Marcus et al., 2003;Pinker, 1997;Saffran et al., 1996).

In the context of this debate, it has been claimed that regular and irregular inflections are instantiated either by a single (Joanisse and Seidenberg, 1999;McClelland and Patterson, 2002b) or by two specialized mechanisms (Clahsen, 1999;Pinker and Ullman, 2002;Ullman, 2001a), according to different psycholinguistic theories. The strongest evidence supporting

dual accounts is based on data showing neural dissociations. From this point of view dissociations are clear evidence that the underlying mechanisms differ across types of verbs. However, recent discussions suggest that such dissociations do not provide sufficient evidence when deciding between Single and Dual mechanism models (McClelland and Patterson, 2002a;McClelland and Patterson, 2002b;McClelland and Patterson, 2003;Seidenberg and Arnoldussen, 2003b), because: (i) dissociations might merely be an epiphenomenon of the differences in phonological and semantic overlap between the studied forms (Bird et al., 2003;Joanisse and Seidenberg, 1999;McClelland and Patterson, 2003;Patterson et al., 2001;Seidenberg and Arnoldussen, 2003b), and (ii) an increasing amount of data from brain-lesioned patients of different languages have shown patterns of performance counter to those expected by dual models in Spanish (De Diego Balaguer et al., 2004), in Italian (Laiacona and Caramazza, 2004), in English (Faroqi-Shah and Thompson, 2003;Shapiro and Caramazza, 2003), in Greek (Tsapkini et al., 2000) and in German (Penke et al., 1999). In addition, imaging studies have shown areas activated by both regular and irregular inflectional processing, particularly in frontal regions (Beretta et al., 2003;Jaeger et al., 1996;Rhee et al., 2001;Sahin et al., 2005;Ullman et al., 1997a).

The aim of this study is to overcome this theoretical impasse by reformulating the present research question by focusing on the kind of information needed for the computation of regular verbs. The goal is to move beyond the gross distinction between phonology and grammar and to refine the more precise distinctions between inflectional types using Spanish, a language with a richer inflectional system than English. Indeed, single and dual mechanism accounts differ with respect to the information required to compute regular verb inflections, and we can therefore make predictions about the brain areas likely to be involved. Dual models state that regular forms are generated by the application of a default rule and thus demand grammatical processing (Clahsen, 1999;Pinker and Ullman, 2002). In contrast, single

system accounts argue that the information underlying the production of regular forms is in fact the same as that needed for irregular verbs, but that phonological information weighs more heavily in these words (Bird et al., 2003;Joanisse and Seidenberg, 1999;Patterson et al., 2001). In light of these predictions, using event-related functional MRI, the present study evaluated the involvement of language-related brain regions in the processing of regular and irregular verbs. Previous imaging work suggests that the brain regions sustaining grammatical and phonological processing can be segregated (Burton et al., 2000;Fiebach et al., 2001;Friederici et al., 2003;Heim et al., 2003a;Heim et al., 2003b;Jacquemot et al., 2003;Liebenthal et al., 2003;Poldrack et al., 1999;Stromswold et al., 1996) (see Gernsbacher and Kaschak, 2003 for a review). **Nevertheless, these studies have not compared directly grammatical and phonological processing. Actually, it is an issue of debate whether it is really possible to isolate the two and whether some studies on grammatical processing are actually tapping non-linguistic variables.** Thus, the differential involvement of regions when producing regular and irregular verbs should serve as an aid in deciding between single vs. dual mechanism accounts **and teasing apart more clearly the brain regions in charge with phonological and grammatical processing.**

A number of neuroimaging studies have been published **on the issue of regularity** (Beretta et al., 2003;Jaeger et al., 1996;Rhee et al., 2001;Sach et al., 2004;Sahin et al., 2005), some of which have met with methodological criticisms (Beretta et al., 2003;Seidenberg and Arnoldussen, 2003a). The current study tries to avoid those previously identified problems in several ways: (i) event-related fMRI was used with a fast presentation rate, (ii) a verb repetition task was used as a baseline condition in order to isolate as much as possible the activations due to inflection and lexical retrieval exclusively in the comparisons, and (iii) behavioural responses were also recorded online to ensure that the subjects did indeed inflect the verbs. Furthermore, in addition to a whole-brain fMRI analysis, the time-course of the

hemodynamic response was studied in critical regions of interest. Finally, a morphologically rich Romance language (Spanish, see appendix A for a brief account of its morphological features) was selected in order to complement previous data collected exclusively in Germanic languages.

The Spanish language is particularly suited to an investigation of the contrast between regular and irregular verbs, as it allows a more sensitive contrast than the broad one provided by the extreme differences between regular and irregular verbs in English. In English, two aspects of the regularity status of the verb are confounded. First, the existence of a common stem shared by all regular forms of a verb versus the existence of different associated forms that will vary in irregular verbs (**e.g. English; regular: play, play-ed; irregular: go, went**). Second, the combinatorial process of stems and their corresponding suffixes present for regular verbs versus the full form storage of irregular forms (**e.g., English; regular: play-ed, walk-ed, sav-ed; irregular: went, ate, spoke**). Thus, differences observed in English can be due to either or both of these confounds, and the sharp contrast between regular and irregular forms may well cause differences in processing complexity, an issue that has been a matter of some debate (Seidenberg and Arnoldussen, 2003b). The use of Spanish, will, by contrast, enable us to have a more precise idea about information that differs and information that is common to both regular and irregular verbs. It permits the perfect control of the suffixation process since it is required in both regular (*cant-ar* [to sing], *yo cant-o* [I sing]) and irregular verbs (*sent-ir* [to feel], *sient-o* [I feel]). This concerns the retrieval of the grammatical features associated with a verb that are necessary in sentence building. For example, the subject of the verb form and the tense are essential for the retrieval of the appropriate suffix (in Spanish, *yo habl-o, él habl-a/ yo habl-é, él habl-ó* : I talk, he talk-s/ I talk-ed, he talk-ed). As suffixes must be applied in both regular and irregular verbs, grammatical features should always be retrieved. In contrast, regular and irregular verbs in Spanish differ in terms of the number of stems

associated to a given verb: while regular verbs have a single stem associated to all suffixes (e.g. *viv-ir*, “to live” in 1st person singular: *viv-o* (present tense), *viv-í* (simple past)), irregular verbs vary their stem, according to the tense and the person to be specified (e.g. *ven-ir*, “to come” in 1st person singular: *veng-o* (present tense), *fui* (simple past)).

This fact is thus crucial when considering the predictions of the present study. Based on the previous literature, overlapping and distinct regions should appear related to regular and irregular processing. Overlapping areas in this study should correspond to the retrieval of grammatical features and suffixation as they are both used for all verbs. Areas of distinct activation should either correspond to increased phonological processing, if regular verbs rely more heavily on this information, **as suggested by single system accounts**, or differences in the number of stems characterizing the regular/irregular status of the verb in Spanish, **as sustained by dual models**.

Method

Participants

Twelve native Spanish volunteers gave written informed consent to participate (mean age 23 years; 8 women). All subjects were strongly right-handed (Oldfield, 1971). The protocol was approved by the **Ethics Committee of the University of Magdeburg**.

Task and stimulus materials

A total of 120 regular and 120 irregular verbs were selected for the *inflection* conditions and matched for surface, lemma frequency and length in syllables using the LEXESP database (Sebastian-Gallés et al., 2000). In addition, for the *repetition* conditions, two additional sets of 120 verbs each were selected to match regular and irregular inflection conditions in frequency

and length (see table 1). Different sets of verbs were used in the repetition and inflection conditions in order to avoid repetition effects. Nonce verbs were created by changing one letter of existing regular (n=120) and irregular (n=120) verbs. Half of these were used for inflection and half for repetition. The materials used are available on request. Each subject was presented with six runs of stimulation. Within one run, 20 words from each condition together with 20 fixation trials were presented in a pseudorandom order.

Each run started with a fixation asterisk lasting for 9 seconds to allow time for T1 equilibration effects. Each trial began with the presentation of a fixation cross lasting 200 ms, which was replaced by the infinitive form of a verb / nonce verb for 600 ms. This was followed by either a red square or a blue circle that remained on the screen for 2200 milliseconds. These cue stimuli indicated whether the subject had to covertly produce the present tense form of the verb/nonce verb (Inflection condition) or to repeat the verb/nonce verb in the given infinitive form (Repetition condition). The meaning of the two cues was counterbalanced across participants. Stimulus presentation was synchronized with MRI data acquisition with an accuracy of 1 ms. The trial length was designed to fit two TR of 1.5 seconds. **This design was chosen to have a better signal to noise ratio. The fact that the SOA (3s) was an integer multiple of the TR (1.5s), may lead to a systematic bias in parameter estimation. However, at this short TR the effect described should be negligible.**

To ensure task performance, a secondary monitoring task was introduced which required subjects to indicate the location of the stress in the word that they had covertly produced¹. The location of the stress in Spanish is different in the repetition and the inflection responses, allowing control for the correct execution of the task. Words contained between one and four syllables in all conditions and were matched for stress variability across conditions in order to

¹ In Spanish, stress is a cue in lexical access (Dupoux et al., 1997; Soto-Faraco et al., 2001), thus native speakers of Spanish are sensitive to stress location in words.

control for motor and executive aspects and avoid strategic effects. Subjects indicated the location of the stress by means of four response key buttons. First and second syllable stress location corresponded to responses with the middle and index finger of the left hand and third and fourth syllable to the index finger and middle finger of the right hand, respectively. The verb “CANTAR”, for example, resulted in “cán-to” (stress on the first syllable; left middle finger) in the inflection condition and “can-tár” (stress on the second syllable; right index finger).

Prior to the recording session and outside of the scanner, participants were instructed about the procedure and were presented with a short version with 10 training items that were not included in the experimental set. The training items were repeated until the subject understood the dual task situation and performed it correctly. Scanning began with a 10 min structural scan acquisition which was followed by a repetition of the training items and six experimental runs of 120 trials, each of which lasted ~7 min. A short rest was given between runs. The stimuli were projected on to a mirror in direct view of the reclining volunteer.

While the stress-monitoring task provided a measure of performance accuracy in the real word conditions, the inflection performance for the novel verbs was verified by a questionnaire given immediately after the scanning session. The questionnaire comprised the 120 nonce verbs (60 derived from regular, 60 from irregular verbs) and subjects were instructed to produce the inflected form as fast as possible, trying to give the same response as in the scanner. Subjects were debriefed about the nature of the experiment at the end of the session.

MRI scanning methods

Imaging was performed with a GE Medical Systems 1.5 Tesla Signa Neurovascular MR scanner with standard quadrature head coil. Visual images were back-projected onto a screen

by a LED-projector and participants viewed the images through a mirror on the head coil. Two magnet-compatible response boxes (one in each hand) were used, containing two response keys each (middle finger and forefinger). Response times as well as responses were recorded for subsequent analyses. Conventional high-resolution structural images (rf-spoiled GRASS sequence, 60 slice sagittal, 2.8 mm thickness) were followed by functional images sensitive to blood oxygenation level-dependent contrast (echo planar T_2^* -weighted gradient echo sequence, TR/TE/flip angle =1500 ms/40 ms/90°). Each functional run consisted of 295 sequential whole-brain volumes comprising 16 axial slices aligned to the plane intersecting the anterior and posterior commissures, 3.125 mm in-plane resolution, 7 mm thickness, 1 mm gap between slices, positioned to cover the entire brain. Volumes were acquired continuously and the four first volumes were discarded due to T1 equilibration effects. To allow precise coregistration of functional data a separate T1-weighted 2D spin echo-image was acquired in the same slice orientation as the functional scans covering the whole volume.

Preprocessing

Different preprocessing steps were implemented using statistical parametric mapping (SPM99, (Friston et al., 1995; Friston et al., 1998). First, for each volunteer, functional volumes were phase shifted in time with reference to the first slice to minimize purely acquisition-dependent signal-variations across slices. Second, head-movement artifacts were corrected based on an affined rigid body transformation with reference to the first image of the first run. Third, structural and functional data were spatially normalized to an EPI template based on the Montreal Neurological Institute (MNI) reference brain (Cocosco et al., 1997), an approximation of canonical space (Talairach and Tournoux, 1988), using a 12-parameter affined transformation along with a nonlinear transformation using cosine basis functions. Functional EPI volumes were resampled into 4 mm cubic voxels and then spatially

smoothed with an 8 mm full-width half-maximum isotropic Gaussian Kernel to accommodate residual anatomical differences across volunteers.

Data analysis

For the statistical model, an event-related design matrix including all conditions of interest was specified using the canonical hemodynamic response function for all event types (Friston et al., 1998). The data was high-pass filtered, smoothed temporally with a 4 s full-width half-maximum Gaussian kernel and rescaled to the global mean. Scans corresponding to trials where the subjects committed errors were not included in the analyses. Significant differences in hemodynamic responses were validated using the linear model approach as implemented in SPM99. A random effects, event-related statistical analysis was performed: at a first level, a separate general linear model was specified for each subject. The BOLD responses to six event types (Repetition Regular, Inflection Regular, Repetition Irregular, Inflection Irregular, Repetition nonce verb and Inflection nonce verbs) for each run were modeled with a basis function consisting of a synthetic hemodynamic response function and its temporal derivative. Contrast images were calculated for each subject. The individual contrast images were entered into a second-level analysis using a one-sample t test. Unless mentioned otherwise, contrasts are thresholded at $p < 0.001$, and only **clusters of a minimal extent of 20 voxels** with a significant $p < 0.001$ corrected for multiple comparisons are reported (Worsley and Friston, 1995). The maxima of suprathreshold regions were localized by rendering them onto the volunteers' normalized T1 structural images on the MNI reference brain (Cocosco et al., 1997). Maxima and all coordinates are reported in MNI coordinates, as used by SPM99 and labeled following the probability mapping for the pars opercularis (Tomaiuolo et al., 1999).

Regions of interests (ROI) definition and signal extraction were performed using the ROI toolbox (<http://spm-toolbox.sourceforge.net/toolboxes.html>). Selective averaging was computed upon a finite impulse response (FIR) model. **ROIs were functionally defined and**

their extent was set at 8 mm radius. The activation pattern derived from the contrast between irregular inflection minus repetition was used to define two ROIs: left inferior frontal gyrus (BA 44, coordinates $-52, 16, 6$) and left middle frontal gyrus (BA 46, coordinates $-48, 48, 4$)(see Figure 3). Two additional ROIs were selected from the regular minus irregular inflection contrast. Left BA 44 was chosen, as it is the area most likely related to grammatical processing in the literature that appeared to be active for both regular and irregular inflection. Left BA 46 and the left anterior superior temporal gyrus/insular ROIs (coordinates $-44, 8, -4$) were further explored as they appeared in the main analyses as the principal regions differing across regular and irregular verb inflection. The BOLD responses in each contrast were averaged separately for each subject in each of the six runs in the same voxel cluster and for a 16 second epoch. These formed the basis for repeated measures analyses of variance (ANOVA) with the Huynh-Feldt correction for non-sphericity. Time course hemodynamic responses were baseline corrected for each subject using the mean value between -4.5 and 0 s before the appearance of the stimuli. The corrected baseline values were used for the statistical analysis and the corresponding figures.

Scans near the peak of the bold signal were selected for the ANOVA. (t_1 : the average between 1.5 s to the peak, and t_2 : the average between 1.5 s to 3 s after the peak). For real verbs separate ANOVAs were performed for each ROI with Task (repetition vs. inflection), Verb-type (regular vs. irregular) and Time (t_1 vs. t_2) as within subject factors. For the non-verbs only Task and Time were used.

Results

Behavioral performance

Mean reaction times (RTs, relative to the onset of cue presentation) and percentage of errors are given in table 2. RTs above and below three standard deviations from the mean (**2.6% of**

data) and error trials were discarded. RTs and percentage of errors were subjected to a two-way repeated measure ANOVA with factors type of verb (regular, irregular and nonce verb) and task (repetition and inflection).

For RT a main effect of task ($F(1,11) = 25.7, p < .0001$) was found, with repetition faster than inflection and a main effect of type of verb ($F(2,22) = 29.3, p < .001$). A task by type of verb ($F(2,22) = 9.6, p < .001$) interaction reflected the fact that the task effect was less prominent in the regular than in the other two conditions, as illustrated in figure 1. The analyses of the errors showed no significant main effects ($F_s < 1$) and the type of verb by task interaction was not significant ($F(1,11) = 3.67; p < .082$).

In the post-scan questionnaire, the subjects showed a regular pattern in 97% of nonce verbs derived from regular verbs and 82% of those derived from irregular verbs. Phonological changes, analog to those occurring in real irregular verbs, were used in 2%/17% of the stimuli derived from regular/irregular verbs. For both kinds of nonce verbs 1% of idiosyncratic responses were found. As the overwhelming majority of the responses were regularizations, the activations in the nonce verb inflection condition should reflect the regular inflectional pattern of Spanish.

Event-related fMRI

In an attempt to isolate the brain regions related to inflection, the activations in the repetition task were subtracted from the inflection task separately for each verb type (see table 3 and figure 2a). The contrast between regular inflection and regular repetition led to differences in activation in the right parahippocampal gyrus and right sensorimotor cortex. In the left hemisphere, differences appeared in the inferior frontal gyrus (BA 44) and the cerebellum.

The analogous comparison for irregular verbs showed activation in the cerebellum, the left inferior frontal gyrus (BA 44/45) extending to the DLPFC / middle frontal gyrus (BA 46) and the right sensorimotor cortex.

Finally, in the nonce verbs, activations were found in the right sensorimotor cortex, the left inferior frontal gyrus (BA 44) and the left cerebellum. Contrasts between nonce inflection and real verbs inflection (regular and irregular) are depicted in table 4.

For the critical comparison, irregular versus regular inflection (Figure 2b, Table 4), increased activity for irregular inflection was found in the left inferior frontal area (BA 44/45 and BA 45) and the left DLPFC (BA 46). With a more liberal threshold, the right DLPFC and the right inferior frontal gyrus (BA 44/45) were also activated (see figure 2b). In the reverse contrast, one differential cluster of activation was observed in the left hippocampus and in the insular cortex at the edge with the anterior superior temporal gyrus (BA 22/52).

We also compared activation maps for nonce inflection and verb inflection (regular and irregular, see figure 2c and Table 4). This contrast should isolate activity related to lexical-**semantic** processing. Both the regular versus nonce inflection contrast, and the irregular versus nonce inflection contrast showed significant activations in the precuneus, right middle temporal gyrus, bilateral superior temporal gyrus, and cingulate cortex (anterior and posterior). In addition, regular versus nonce inflection showed activation in the parahippocampal gyrus, while the irregular versus nonce inflection showed activation in the right cerebellum.

ROI hemodynamic time courses

We also analysed the ROIs of the areas reported in the critical contrasts in order to further explore the possible time course differences appearing in those areas, as related to the type of verb and the task performed.

Left inferior frontal gyrus (BA 44, figure 3, top). Inflection was associated with a greater BOLD response than repetition (main effect of Task: $F(1,11) = 25$, $P < 0.001$). Neither the interaction between verb Type and Task ($F(1,11) = 1.08$, $P > 0.3$) nor the main effects of Time ($F(1,11) = 1.4$, $P > 0.2$) and Verb Type ($F < 1$) were significant. For the nonce verbs, a main effect was found only for the Task factor ($F(1,11) = 21.8$, $P < 0.001$), reflecting the greater BOLD response in the inflection condition. Neither the main effect of Time ($F < 1$) nor the interaction between Time and Task ($F(1,11) = 1.9$, $P > 0.19$) were significant.

Left middle frontal gyrus (DLPFC; BA 46, figure 3, middle). The most striking feature of the BOLD responses of the real verbs in this ROI was the long-lasting response in the irregular inflection condition, which was reflected by a Task x Time x Verb type interaction ($F(1,11) = 6.8$, $P < .024$). A main effect of verb type was found ($F(1,11) = 6.94$, $P < .023$) but the main effects of Time ($F(1,11) = 3.58$, $P > 0.085$) and Task ($F(1,11) = 1.24$, $P > 0.3$) were not significant. Nevertheless, the interaction between Verb and Task was marginally significant ($F(1,11) = 3.9$, $P < 0.074$). No other significant interactions were observed. For the nonce verbs, the inflection condition also showed a larger amplitude in the BOLD response (Task, $F(1,11) = 14.4$, $P < 0.003$). Time and the interaction between Time and Task were not significant ($F < 1$).

Left Insular cortex/anterior superior temporal gyrus (figure 3, bottom). By contrast to the results in BA 46, a clear long-lasting response was observed for regular inflection in this ROI. This was reflected in a significant Time x Verb x Task interaction ($F(1,11) = 7.36$, $P < 0.02$). Regular verbs showed a more pronounced BOLD response, thus displaying a main effect of Verb type ($F(1,11) = 8.64$, $P < 0.013$) and a Verb x Task interaction ($F(1,11) = 9.95$, $P < .009$) in this ROI. The Task effect was marginally significant ($F(1,11) = 4.26$, $P < 0.063$) and the remaining effects were not significant. Nonce verbs showed no significant effects or interactions at this ROI.

As it is evident in Fig. 3, the LIFG was particularly sensitive to inflection regardless of the type of verb, while differential patterns appeared for the DLPFC and the aSTG/insular cortex. Irregular inflection showed a greater and more sustained activation than the rest of conditions in DLPFC. The STG/insular cortex was the only ROI that showed a selective activation for regular inflection, while the other conditions showed no significant increased from baseline. These results are in agreement with those obtained in the inclusive masking analysis for regular and irregular inflection compared to repetition (thresholded at $p < 0.01$). The common map involved the activation of Broca's area, peaking at BA 44 (coordinates -52, 12, 8; $T = 3.89$, $p < 0.0001$), the right parahippocampal gyrus (peak coordinates 32, -60, 4; $T = 4.74$, $p < 0.002$) and motor related areas [right sensorimotor cortex (32, -36, 56; $T = 5.27$, $p < 0.0001$) and left cerebellum (-16 -52 -36; $T = 7.77$, $p < 0.0001$)]. Note that the aSTG/insular region and the DLPFC were not present in this inclusive map.

Discussion

The current investigation aimed to delineate the brain areas responsible for the generation of regular and irregular verb forms and to detect possible differences in their hemodynamic response. A complex pattern of activations emerged in the different contrasts. In the following discussion, we attempt an interpretation of this pattern according to three strategies: (a) we will examine the hypothesis that the activation differences between regular and irregular words simply reflect the fact that the latter are "harder" to process (Seidenberg and Arnoldussen, 2003b), (b) we will compare the present findings with the predictions derived from single and dual mechanism models, and (c) by using information about the functions of

the different brain areas derived from other imaging studies, we will attempt a brain-inspired novel interpretation of the distinctions between regular and irregular verbs.

a) The brain makes a distinction between easy and hard stimuli

One of the major criticisms of the neuroimaging studies previously published on the topic (Jaeger et al., 1996) is that the differences observed across types of verbs generally involves areas of overlap and a general increase of activation for irregular compared to regular inflection. Indeed, this pattern of results can easily be explained by the greater attentional demands imposed by irregular verbs, and the fact that they are more difficult to process. Because irregular production is harder, such stimuli produce “greater activation across a broader range of brain areas” (Seidenberg and Arnoldussen, 2003b, pg. 527). This is clearly not the case in the present data set. **As stated in the introduction, the similar characteristics of regular and irregular verbs in Spanish make this possibility more difficult to sustain in our study. This is in agreement with the absence of accuracy differences between the conditions in the stress-monitoring task. Moreover, the greater activations for irregular verbs in DLPFC might be related to the greater difference in the reaction times between repetition and inflection for irregular than for regular verbs. However, more importantly, regular inflection involved regions that did not appear in irregular inflection.** While irregular verbs showed a more dorsolateral prefrontal pattern, regular verbs were characterized by a more inferior (anterior STG/insular) and hippocampal pattern of activations. This complementary pattern of activation is at odds with the difficulty argument.

b) Predictions derived from single and dual mechanism models

While the dual model states that regular forms are generated by the application of a default rule and demand grammatical (rule-based) processing, single system accounts posit that the

same types of information are used in the production of regular and irregular forms but that phonological information features more prominently in the production of regular words (Joanisse and Seidenberg, 1999). In the following section, we will discuss the suggestion of Seidenberg and Arnoldussen (2003b) who proposed that the different claims of dual and single mechanism accounts might be distinguished by determining what other stimuli activate the observed brain areas. We will thus inspect the areas activated for regular and irregular inflection and check whether they correspond to the known areas related to grammatical versus phonological processing as described in the literature.

b.1 Areas related to grammatical processing

Grammatical processing has traditionally been linked to the left inferior frontal gyrus, as patients with lesions in Broca's area and the underlying white matter are characterized by agrammatic speech. Broca's area, in the posterior part of the left inferior frontal gyrus, exhibits two general anatomical subdivisions referred to as pars triangularis (BA 45) and pars opercularis (BA 44) (Tomaiuolo et al., 1999). These areas can be differentiated cytoarchitectonically and functionally: brain imaging studies of grammatical processing have shown that BA 44 is sensitive to the grammatical complexity of sentences (Caplan et al., 1998; Fiebach et al., 2001; Stromswold et al., 1996). Also, intracranial stimulation has located grammatical errors in this region (Ojemann, 1983). Finally, the posterior-inferior portion of BA 44 on the border to the ventral premotor cortex has been related to syntactic structure building processes (Friederici et al., 2003) and morphological processing (Heim et al., 2003a). As predicted by dual models, in our study, regular verbs activated the left pars opercularis region (BA 44) but contrary to their prediction the same region was also activated by irregular verbs. This pattern has also been reported by previous neuroimaging studies addressing morphological processing and, in fact, it is the only one replicated systematically (Jaeger et al., 1996; Rhee et al., 2001; Ullman et al., 1997a). This overlapping activation is consistent

with single system accounts, which posit that both regular and irregular verbs entail grammatical processing (McClelland and Patterson, 2003). This notion is especially straightforward for Spanish: in this language a verb cannot be produced before the subject of the verb has been identified, because suffixes vary depending on the grammatical feature *person* (i.e. “Yo com-o” [I eat], “tu com-es” [you eat], “él com-e [he eats]”). However, the need for grammatical processing in both regular and irregular inflection is also consistent with results from other languages. Recent studies have shown that left frontal lesions encompassing BA 44 lead to problems with irregular as well as regular verbs (De Diego Balaguer et al., 2004;Faroqi-Shah and Thompson, 2003;Shapiro and Caramazza, 2003;Tsapkini et al., 2000);(Penke et al., 1999). The current data, as well as previous neuroimaging and patient studies, thus show an involvement of left BA 44 – and hence the processing of grammatical features – with no major difference for regular and irregular words at this site. **This idea is strengthened by the BOLD time-course reconstruction in this area showing no differential t1/t2 effect between verb types for inflection at this site. This implies by no means that BA 44 is solely involved in grammatical processing, as other linguistic and non-linguistic functions have been related to BA 44 (Burton et al., 2000;Burton et al., 2005;Habeck et al., 2005). For example, several studies on phonological processing have observed activation of the superior part of the inferior frontal gyrus (at the border with the middle frontal gyrus) (Burton et al., 2000;Demonet et al., 1992;Heim et al., 2003b;Poldrack et al., 1999;Zatorre et al., 1996). However, the activations observed in our study in the left posterior inferior frontal gyrus and in previous studies on grammatical processing are located inferiorly to this region.**

Nevertheless, it is important to note that another region related to grammatical processing, the anterior superior temporal gyrus (aSTG) (Friederici and Kotz, 2003;Kaan and Swaab, 2002;Kotz et al., 2003), appears to characterize the inflection of regular verbs compared to irregular inflection in our study. This activation extended to the anterior insular

cortex. We will further comment on the implications of this adjacent area in section b.2. The specificity of this insular/anterior STG to regular inflection was confirmed by the BOLD time-course reconstruction of this ROI **showing that while regular inflection showed an increased activation at this site, the other conditions did not differ from baseline**. As stated in the introduction, areas of differential activation could only be due to the fact that regular verbs have always the same stem while irregular verbs vary their stem when they have to be inflected in the tense demanded in our task (present tense). Thus, the greater involvement of the aSTG in regular inflection could be related to the **use** of the just presented stem embedded in the probe infinitive form when producing the inflected form required by the task (e.g. “to live” *viv-ir*, “I live” *viv-o*). In contrast, irregular verbs cannot benefit from the previously presented stem and they should retrieve a different adequate stem for the present tense (e.g. “to come” *ven-ir*, “I come” *ven-g-o*). The areas related to lexical retrieval associated to irregular inflection (that we will comment on later) are consistent with this idea.

Thus, in terms of grammatical processing, our overall results show partly similar and partly distinct regions involved in the processing of regular and irregular verbs. This pattern could be assimilated into the proposal of Friederici and Kotz (2003) of a functional differentiation between the roles of the inferior portion of BA 44 and the anterior STG. Adopting their model at the morphological level, the online syntactic structure-building process would correspond to the retrieval of grammatical features (inferior portion of BA 44) common to both regular and irregular verbs. This process would correspond to the retrieval of all the grammatical information associated with the verb that is crucial in sentence building. In contrast, the anterior STG might be involved in the automatic stem reactivation engaged by regular verbs when the same verb has to be used more than once in a given sentence or throughout a discourse.

b.2 Areas related to phonological processing

According to the simulation results of Joanisse and Seidenberg (Joanisse and Seidenberg, 1999), a single system account expects regular verbs to engage brain systems involved in phonological processing to a greater extent than irregular verbs. Areas that have previously been found in relation to phonological processing include the planum temporale (Liebenthal et al., 2003), Wernicke's area and the supramarginal gyrus (Demonet et al., 1994; Jacquemot et al., 2003; Petersen et al., 1988; Zatorre et al., 1996) and the superior posterior region of the inferior frontal gyrus (BA44/6; (Burton et al., 2000; Demonet et al., 1992; Heim et al., 2003b; Poldrack et al., 1999; Zatorre et al., 1996). In addition, the anterior inferior frontal region, in the vicinity of BA 45/46 has also been associated to maintenance of phonological information in working memory (Awh et al., 1996; Barde and Thompson-Schill, 2002; Paulesu et al., 1993; Zurovski et al., 2002). Therefore, these regions seem to be the most likely candidates for the processing of regular verbs (c.f., (Joanisse and Seidenberg, 1999) according to single system accounts.

In the present study, none of the mentioned areas appeared in the critical contrasts, speaking against an interpretation in terms of a more prominent involvement of phonological processing in regular inflection. However, it could be argued that the activations in the insular and hippocampal regions in regular compared to irregular inflection could actually be interpreted as related to phonological processing although via a rehearsal component. While the insular region has been related to several different functions ranging from lexical/semantic processing (Friederici et al., 2003; Nestor et al., 2003) to speech motor planning (Dronkers, 1996), it is also true that a number of studies have related this region to the phonological loop needed for rehearsal (Chee et al., 2004; Vallar et al., 1997). The hippocampal activation is also consistent with this interpretation. This region has been related to the reactivation of just presented object representations in studies of human amnesia, animal models of memory

impairment, as well as neurophysiological and neuroimaging experiments (Cabeza et al., 2001; Cabeza et al., 2002; Meyer et al., 2005; Ranganath et al., 2004; Squire et al., 2004) for a revision. As previously stated, regular verbs likely automatically reactivate the previously presented stem. This interpretation is consistent with Opitz et al study (Opitz and Friederici, 2003) showing a frontal hippocampal loop related to the learning of language-like rules probably leading to an automatization of the task. The engagement of the insula in the automatization of verbal tasks has previously been proposed by Raichle and colleagues (Raichle et al., 1994). This study showed that as task performance became more automatic due to practice in a verb generation task the activity in the insular cortex increased, whereas activity in other cortical areas (e.g. inferior frontal cortex) decreased (see also (Petersen et al., 1998; van Turennout et al., 2000)).

In sum, the fact that the left pars opercularis region (BA 44) was engaged in the production of both regular and irregular verbs supports the idea that the production of morphologically complex forms of all verbs requires the retrieval of grammatical features in both types of verbs. While this particular notion is more compatible with a single system approach, the assumption that regular verbs engage phonological processing to a greater extent than irregular verbs, put forward by proponents of a single system account (Joanisse and Seidenberg, 1999) was only partially supported by the rehearsal component needed for regular inflection (insular and hippocampal activations). This rehearsal process is also closely related to the greater engagement of grammatical processing in regular inflection, in terms of maintenance and reactivation of the just presented stem of the probe infinitive form, as suggested by the greater involvement of the anterior superior temporal gyrus. Regarding the activations in more posterior areas, it should be noted that the repetition condition was used as a baseline to reveal areas related to morphological processing. Using this baseline should

eliminate all activations related to recognition, maintenance, phonological translation and the requirements of the secondary monitoring task. This cancelled out the activations in temporal regions related to those processes and to semantic processing in the comparisons across conditions. However, as expected, an activation in the superior and middle temporal gyrus is seen when real verb inflection conditions (regular as well as irregular) are compared to the nonce verb inflection condition, which is most probably related to the semantic and lexical processing engaged by the real verbs (Demonet et al., 1994; Vandenberghe et al., 1996). These results contradict the predictions of the declarative/procedural model stating that the lexical/semantic system for irregular verb inflection is rooted in the temporo-parietal cortex. They are however in agreement with the available evidence showing that verb representations and processing rely on frontal regions, while nouns seem to rely on temporal regions (Caramazza and Hillis, 1991; Damasio and Tranel, 1993; Hillis et al., 2003; Rapp and Caramazza, 1997; Shapiro and Caramazza, 2003). Studies taking into account regularity status and grammatical category indicate that the regularity effect is independent of the grammatical category (Shapiro and Caramazza, 2003; Tsapkini et al., 2000). In fact, the anterior superior part of the inferior frontal gyrus (BA 44/45) appeared to be active in the inflection of irregular but not regular forms compared to repetition. This difference between inflection types in the IFG was also evident in the direct contrast of regular and irregular inflections (figure 2b). Although the interpretation of this activation pattern is difficult because this area appears to have multiple functions, it has been suggested that it supports lexical-semantic processing (Chee et al., 1999; Friederici et al., 2000). Thus, these results might reflect a greater reliance on lexical/semantic processes during the processing of irregular verbs (Marslen-Wilson and Tyler, 1998).

c) Interpretation derived from other brain imaging data

In a commentary (Munte et al., 1999) two of us have argued that brain imaging should not only be used to test predictions derived from psycholinguistic models but that patterns of activations might be used to derive brain-inspired hypotheses about processing differences between regular and irregular words, for example. In the following section, we try to apply this approach to the current data set.

A key area showing differential activation for regular and irregular inflection is the left DLPFC (BA 46). This area was activated in the irregular minus repetition contrast (Figure 2a), in line with previous findings for irregular transformations in German (Beretta et al., 2003). In addition, a bilateral activation of the DLPFC was found in the contrast between irregular and regular inflection. This region has been related to the selection of appropriate responses based on internal representations in a number of neuroimaging studies (Duzel et al., 1999; Rugg et al., 1997).

Together with the inferior frontal gyrus (BA 45), these areas have been shown to support the maintenance of items in memory for manipulation and the selection of a response based on internal and external cue information. A summary can be found in the hierarchical model proposed by (Christoff et al., 2001) and other researchers (Petrides, 2000; Wagner et al., 2001). A similar idea has been proposed by (Curtis and D'Esposito, 2003), who have suggested that during the maintenance of verbal material, top-down signals from the DLPFC select the relevant verbal representations in the inferior portion of the parietal cortex and Broca's area, thus enhancing those representations. **As opposed to the ROI analyses in the LIFG, the DLPFC showed a differential time effect for the inflection of irregular verbs compared to the other conditions. This sustained activation matching the reaction time results, is also in agreement with this interpretation.**

In the context of morphological processing of irregular forms, the role of the DLPFC might be the selection of the correct response from information supplied by the brain regions where

lexical representations are stored. The inflection of irregular forms in Spanish involves phonological changes in the stem. If this stem allomorphy is lexically represented, then different stems exist in the lexicon related to the same verb. For example, for the irregular verb “medir” (to measure), a regular lexical entry (e.g., “med-i-mos”) and an irregular entry (e.g., “mid-o”) should exist. In our experiment, in a first step, the presentation of the cue asking for inflection would, in regular verbs, reactivate the just presented stem form leading to the activation of hippocampal and insular structures together with the anterior STG. In the case of irregular verbs, the presentation of the cue would activate two alternative stems in parallel that would compete for lexical selection. The inhibition of one of the recruited lexical entries is convergent with the involvement of the right middle frontal gyrus when comparing irregular versus regular inflections which has been systematically related to the inhibition of responses (Bunge et al., 2002; Garavan et al., 1999; Konishi et al., 1999). In a second step, the retrieval of the grammatical information (tense and person) would disambiguate the stem competition and at the same time select the correct suffix to be appended. This retrieval of grammatical information and the suffixation process that is needed in this second step is applied in both regular and irregular verbs, hence the implication of the posterior inferior region of BA 44 for both types of verbs. For example, the first-person singular of the present tense will always attach as an inflectional suffix “-o” (e.g., “mid-o”, “I measure”; “cant-o”, “I sing”) irrespective of whether or not a change in the stem is produced. A very similar proposal has recently been made by (Tyler et al., 2004) for the inflection of verbs in English. The authors considered that the larger activation in BA 44 found in regular verbs when compared to inflected nouns reflects the process of attaching one of the different possible inflections available when a verb stem is processed (in English, *-ing*, *-ed*, *-s*). For the inflection of the nonce verbs, which also showed strong bilateral BA 46 activation compared to regular forms but not to irregular inflection, a similar explanation would apply. The first *stem selection* step is consistent with the dual system proposal (Pinker, 1999; Ullman, 2001b) as it varies across

types of verbs and would occur in the same way in languages such as English or German. As some languages such as Spanish use suffixation in both regular and irregular verbs while others (e.g. English) do not, the second step may vary across languages. While the retrieval of grammatical features may happen in any case, languages such as English would not engage the suffixation process. The dissociation in the recruitment of the brain areas for these two steps is consistent with Clahsen's proposal of stem formation and suffixation (Clahsen, 1999) and it is in agreement with recent data from morphological acquisition of Spanish (Clahsen et al., 2002b).

Naturally, a data driven brain-inspired interpretation of our data, as attempted in this section, has certain limitations, as we sought to explain the exact pattern of results of the current experiment. A fuller and more adequate picture will emerge, if this approach will be applied to a set of studies addressing morphological processing with varying paradigms. We believe that this approach will prove extremely fruitful in the future, as is attested by the recent emergence of brain-inspired models of language functions (Hagoort, 2005).

CONCLUSION

The inflection of regular and irregular verbs in Spanish leads to activation of partially overlapping and partially distinct neural systems: more inferior frontal regions were activated by the inflection of regular verbs, while irregulars show a more anterior dorsal pattern. Predictions derived from single (e.g. Joanisse and Seidenberg, 1999) and dual (e.g. Ullman et al., 1997b) mechanism accounts were only partially supported by the present data set. As predicted by single system accounts, functionally, both types of verbs seem to engage the retrieval of grammatical features and suffixation related to the IFG (BA 44). In addition, regular verbs differed in the implication of a phonological rehearsal loop (hippocampus and insula) for the maintenance of a just presented stem. However, this later result is more

consistent with dual models supporting a greater grammatical processing for regular verbs. Irregular verbs were characterized by a system of regions comprising bilateral inferior frontal (BA 45) and middle frontal regions (BA 46). In line with earlier studies, we propose that this system supports memory (lexical) retrieval, manipulation of information and the selection of correct response based on internal and external representations (Christoff et al., 2001; Curtis and D'Esposito, 2003; Petrides, 2000; Wagner et al., 2001). In light of these results, we support the idea of a functional differentiation within the neural basis of the different components of grammatical processing, similar the one promoted by Friederici and Hahne (Friederici et al., 2003) and Clahsen (Clahsen et al., 2002a) at the morphological level: a *stem selection* component involving lexical selection of the correct stem in irregular verbs and a *suffixation* component that includes also the retrieval of grammatical information in all verbs.

This neurofunctional interpretation, motivated by the known processes supported by the involved brain regions, could be viewed as a further instance of a dual process account. It is different from previous proposals, however, as it is data driven (Munte et al., 1999). Earlier dual mechanism proposals have contrasted a frontostriatal procedural system as the basis for regular verb processing and a temporal system as the basis for retrieval processes required by irregular verbs. By contrast, and in line with previous data (Beretta et al., 2003; Rhee et al., 2001), the present study has shown that it is the activation of different areas within the prefrontal cortex that reflects the major difference between the production of regular and irregular verbs.

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References

- Aslin RN, Saffran JR, Newport EL (2004) Computation of conditional probability statistics by human infants. *Psychol Sci* 9: 321-324.
- Awh E, Jonides J, Smith EE, Schumacher EH, Koeppel RA, Katz S (1996) Dissociation of storage and rehearsal in verbal working memory: evidence from PET. *Psychol Sci* 7: 25-31.
- Badecker W, Caramazza A (1991) Morphological composition in the lexical output system. *Cogn Neuropsychol* 8: 335-367.
- Barde LH, Thompson-Schill SL (2002) Models of functional organization of the lateral prefrontal cortex in verbal working memory: evidence in favor of the process model. *J Cogn Neurosci* 14: 1054-1063.
- Beretta A, Campbell C, Carr TH, Huang J, Schmitt LM, Christianson K, Cao Y (2003) An ER-fMRI investigation of morphological inflection in German reveals that the brain makes a distinction between regular and irregular forms. *Brain Lang* 85: 67-92.
- Bird H, Lambon Ralph MA, Seidenberg MS, McClelland JL, Patterson K (2003) Deficits in phonology and past tense morphology. *J Mem Lang* 48: 502-526.
- Bunge SA, Dudukovic NM, Thomason ME, Vaidya CJ, Gabrieli JD (2002) Immature frontal lobe contributions to cognitive control in children: evidence from fMRI. *Neuron* 33: 301-311.
- Burton MW, LoCasto PC, Krebs-Noble D, Gullapalli RP (2005) A systematic investigation of the functional neuroanatomy of auditory and visual phonological processing. *Neuroimage* 26: 647-661.
- Burton MW, Small SL, Blumstein SE (2000) The role of segmentation in phonological processing: an fMRI investigation. *J Cogn Neurosci* 12: 679-690.
- Cabeza R, Dolcos F, Graham R, Nyberg L (2002) Similarities and differences in the neural correlates of episodic memory retrieval and working memory. *Neuroimage* 16: 317-330.
- Cabeza R, Rao SM, Wagner AD, Mayer AR, Schacter DL (2001) Can medial temporal lobe regions distinguish true from false? An event-related functional MRI study of veridical and illusory recognition memory. *Proc Natl Acad Sci U S A* 98: 4805-4810.
- Caplan D. 1992. *Language: Structure, Processing and Disorders*. Cambridge, MA: MIT Press.
- Caplan D, Alpert N, Waters G (1998) Effects of Syntactic Structure and Propositional Number on Patterns of Regional Cerebral Blood Flow. *J Cogn Neurosci* 10: 541-552.
- Caramazza A, Hillis AE (1991) Lexical Organization of Nouns and Verbs in the Brain. *Nature* 349: 788-790.
- Caramazza A, Miceli G, Silveri MC, Laudanna A (1985) Reading mechanisms and the organisation of the lexicon: Evidence from acquired dyslexia. *Cogn Neuropsychol* 2: 81-114.
- Chee MW, O'Craven KM, Bergida R, Rosen BR, Savoy RL (1999) Auditory and visual word processing studied with fMRI. *Hum Brain Mapp* 7: 15-28.

- Chee MWL, Soon CS, Lee HL, Pallier C (2004) Left insula activation: A marker for language attainment in bilinguals. *Proc Natl Acad Sci U S A* 101: 15265-15270.
- Christoff K, Prabhakaran V, Dorfman J, Zhao Z, Kroger JK, Holyoak KJ, Gabrieli JD (2001) Rostrolateral prefrontal cortex involvement in relational integration during reasoning. *Neuroimage* 14: 1136-1149.
- Clahsen H (1999) Lexical entries and rules of language: A multidisciplinary study of German inflection. *Behav Brain Sci* 22: 991-1014.
- Clahsen H, Avelado F, Roca I (2002a) The development of regular and irregular verb inflection in Spanish Child language. *J Child Lang* 29: 591-622.
- Clahsen H, Avelado F, Roca I (2002b) The development of regular and irregular verb inflection in Spanish child language. *J Child Lang* 29: 591-622.
- Cocosco CA, Kollokian V, Kwan RKS, Evans AC (1997) BrainWeb: online interface to a 3D MRI simulated brain database. *Neuroimage* 5: S425.
- Curtis CE, D'Esposito M (2003) Persistent activity in the prefrontal cortex during working memory. *Trends Cogn Sci* 7: 415-423.
- Damasio AR, Tranel D (1993) Nouns and Verbs Are Retrieved with Differently Distributed Neural Systems. *Proceedings of the National Academy of Sciences of the United States of America* 90: 4957-4960.
- De Diego Balaguer R, Costa A, Sebastián-Gallés N, Juncadella M, Caramazza A (2004) Regular and Irregular morphology and its relationship with agrammatism: Evidence from two Spanish/Catalan bilinguals. *Brain Lang* 91: 212-222.
- Demonet JF, Chollet F, Ramsay S, Cardebat D, Nespoulous JL, Wise R, Rascol A, Frackowiak R (1992) The anatomy of phonological and semantic processing in normal subjects. *Brain* 115 (Pt 6): 1753-1768.
- Demonet JF, Price C, Wise R, Frackowiak RS (1994) Differential activation of right and left posterior sylvian regions by semantic and phonological tasks: a positron-emission tomography study in normal human subjects. *Neurosci Lett* 182: 25-28.
- Dronkers NF (1996) A new brain region for coordinating speech articulation. *Nature* 384: 159-161.
- Dupoux E, Christophe P, Sebastian-Gallés N, Mehler J (1997) A distressing deafness in French. *J Mem Lang* 36: 406-421.
- Duzel E, Cabeza R, Picton TW, Yonelinas AP, Scheich H, Heinze HJ, Tulving E (1999) Task-related and item-related brain processes of memory retrieval. *Proc Natl Acad Sci U S A* 96: 1794-1799.
- Faroqi-Shah Y, Thompson CK (2003) Effect of lexical cues on the production of active and passive sentences in Broca's and Wernicke's aphasia. *Brain Lang* 85: 409-426.
- Fiebach CJ, Schlesewsky M, Friederici AD (2001) Syntactic working memory and the establishment of filler-gap dependencies: insights from ERPs and fMRI. *J Psycholinguist Res* 30: 321-338.
- Friederici AD, Kotz SA (2003) The brain basis of syntactic processes: functional imaging and lesion studies. *Neuroimage* 20: S8-S17.
- Friederici AD, Opitz B, von Cramon DY (2000) Segregating semantic and syntactic aspects of processing in the human brain: an fMRI investigation of different word types. *Cereb Cortex* 10: 698-705.

- Friederici AD, Ruschemeyer SA, Hahne A, Fiebach CJ (2003) The role of left inferior frontal and superior temporal cortex in sentence comprehension: localizing syntactic and semantic processes. *Cereb Cortex* 13: 170-177.
- Friston KJ, Holmes AP, Worsley KJ, Poline JP, Frith CD, Frackowiak R (1995) Statistical Parametric Maps in Functional Imaging: A General Linear Approach. *Hum Brain Mapp* 2: 189-210.
- Friston KJ, Josephs O, Rees G, Turner R (1998) Nonlinear event-related responses in fMRI. *Magn Reson Med* 39: 41-52.
- Garavan H, Ross TJ, Stein EA (1999) Right hemispheric dominance of inhibitory control: an event-related functional MRI study. *Proc Natl Acad Sci U S A* 96: 8301-8306.
- Gernsbacher MA, Kaschak MP (2003) Neuroimaging studies of language production and comprehension. *Annu Rev Psychol* 54: 91-114.
- Habeck C, Rakitin BC, Moeller J, Scarmeas N, Zarahn E, Brown T, Stern Y (2005) An event-related fMRI study of the neural networks underlying the encoding, maintenance, and retrieval phase in a delayed-match-to-sample task. *Brain Res Cogn Brain Res* 23: 207-220.
- Hagoort P (2005) On Broca, brain, and binding: a new framework. *Trends in Cognitive Sciences* 9: 416-423.
- Heim S, Opitz B, Friederici AD (2003a) Distributed cortical networks for syntax processing: Broca's area as the common denominator. *Brain Lang* 85: 402-408.
- Heim S, Opitz B, Muller K, Friederici AD (2003b) Phonological processing during language production: fMRI evidence for a shared production-comprehension network. *Brain Res Cogn Brain Res* 16: 285-296.
- Hillis AE, Wityk RJ, Barker PB, Caramazza A (2003) Neural regions essential for writing verbs. *Nature Neuroscience* 6: 19-20.
- Jacquemot C, Pallier C, LeBihan D, Dehaene S, Dupoux E (2003) Phonological grammar shapes the auditory cortex: a functional magnetic resonance imaging study. *J Neurosci* 23: 9541-9546.
- Jaeger JJ, Lockwood AH, Kemmerer DL, VanValin RD, Murphy BW, Khalak HG (1996) A Positron Emission Tomography Study of Regular and Irregular Verb Morphology in English. *Language* 72: 451-497.
- Joanisse MF, Seidenberg MS (1999) Impairments in verb morphology after brain injury: a connectionist model. *Proc Natl Acad Sci U S A* 96: 7592-7597.
- Kaan E, Swaab TY (2002) The brain circuitry of syntactic comprehension. *Trends in Cognitive Sciences* 6: 350-356.
- Konishi S, Kawazu M, Uchida I, Kikyo H, Asakura I, Miyashita Y (1999) Contribution of working memory to transient activation in human inferior prefrontal cortex during performance of the Wisconsin Card Sorting Test. *Cereb Cortex* 9: 745-753.
- Kotz SA, von Cramon DY, Friederici AD (2003) Differentiation of syntactic processes in the left and right anterior temporal lobe: Event-related brain potential evidence from lesion patients. *Brain and Language* 87: 135-136.
- Laiacoma M, Caramazza A (2004) The noun/verb dissociation in language production: Varieties of causes. *Cognitive Neuropsychology* 21: 103-123.
- Liebenthal E, Binder JR, Piorkowski RL, Remez RE (2003) Short-term reorganization of auditory analysis induced by phonetic experience. *J Cogn Neurosci* 15: 549-558.

- Marcus GF, Vouloumanos A, Sag IA (2003) Does Broca's play by the rules? *Nat Neurosci* 6: 651-652.
- Marslen-Wilson WD, Tyler LK (1998) Rules, representations and the English past tense. *Trends Cogn Sci* 2: 428-436.
- McClelland JL, Patterson K (2002a) 'Words or Rules' cannot exploit the regularity in exceptions. *Trends Cogn Sci* 6: 464-465.
- McClelland JL, Patterson K (2002b) Rules or connections in past-tense inflections: what does the evidence rule out? *Trends Cogn Sci* 6: 465-472.
- McClelland JL, Patterson K (2003) Differentiation and integration in human language. Reply to Marslen-Wilson and Tyler. *Trends Cogn Sci* 7: 63-64.
- Meyer P, Mecklinger A, Grunwald T, Fell J, Elger CE, Friederici AD (2005) Language processing within the human medial temporal lobe. *Hippocampus* 15: 451-459.
- Munte TF, Rodriguez-Fornells A, Kutas M (1999) One, two or many mechanisms? The brain's processing of complex words. *Behav Brain Sci* 22: 1031-1032.
- Nestor PJ, Graham NL, Fryer TD, Williams GB, Patterson K, Hodges JR (2003) Progressive non-fluent aphasia is associated with hypometabolism centred on the left anterior insula. *Brain* 126: 2406-2418.
- Ojemann GA (1983) Brain organization for language from the perspective of electrical stimulation mapping. *Behav Brain Sci* 2: 189-230.
- Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9: 97-113.
- Opitz B, Friederici AD (2003) Interactions of the hippocampal system and the prefrontal cortex in learning language-like rules. *Neuroimage* 19: 1730-1737.
- Patterson K, Lambon Ralph MA, Hodges JR, McClelland JL (2001) Deficits in irregular past-tense verb morphology associated with degraded semantic knowledge. *Neuropsychologia* 39: 709-724.
- Paulesu E, Frith CD, Frackowiak RS (1993) The neural correlates of the verbal component of working memory. *Nature* 362: 342-345.
- Penke M, Janssen U, Krause M (1999) The representation of inflectional morphology: evidence from Broca's aphasia. *Brain Lang* 68: 225-232.
- Petersen SE, Fox PT, Posner MI, Mintun M, Raichle ME (1988) Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature* 331: 585-589.
- Petersen SE, Van Mier H, Fiez JA, Raichle ME (1998) The effects of practice on the functional anatomy of task performance. *Proc Natl Acad Sci U S A* 95: 853-8.
- Petrides M (2000) The role of the mid-dorsolateral prefrontal cortex in working memory. *Exp Brain Res* 133: 44-54.
- Pinker S (1997) Words and rules in the human brain. *Nature* 387: 547-548.
- Pinker S (1999) *Words and Rules: the Ingredients of Language*. Cambridge, MA: MIT Press.
- Pinker S, Ullman MT (2002) The past and future of the past tense. *Trends in Cognitive Sciences* 6: 456-463.
- Poldrack RA, Wagner AD, Prull MW, Desmond JE, Glover GH, Gabrieli JD (1999) Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage* 10: 15-35.

Raichle ME, Fiez JA, Videen TO, MacLeod AM, Pardo JV, Fox PT, Petersen SE (1994) Practice-related changes in human brain functional anatomy during nonmotor learning. *Cereb Cortex* 4: 8-26.

Ranganath C, Cohen MX, Dam C, D'Esposito M (2004) Inferior temporal, prefrontal, and hippocampal contributions to visual working memory maintenance and associative memory retrieval. *Journal of Neuroscience* 24: 3917-3925.

Rapp B, Caramazza A (1997) The modality-specific organization of grammatical categories: Evidence from impaired spoken and written sentence production. *Brain and Language* 56: 248-286.

Rhee J, Clark D, Casasanto D, Ullman MT, Wagner AD, Pinker S (2001) Neural substrates of English past tense generation. *J Cogn Neurosci* 13: S 131.

Rugg MD, Fletcher PC, Frith CD, Frackowiak RS, Dolan RJ (1997) Brain regions supporting intentional and incidental memory: a PET study. *Neuroreport* 8: 1283-1287.

Sach M, Seitz RJ, Indefrey P (2004) Unified inflectional processing of regular and irregular verbs: a PET study. *Neuroreport* 15: 533-537.

Saffran JR, Aslin RN, Newport EL (1996) Statistical learning by 8-month-old infants. *Science* 274: 1926-1928.

Sahin, N., Pinker, S., and Halgren, E. (in press) Abstract Grammatical Processing of Nouns and Verbs in Broca's Area: Evidence from fMRI. *Cortex*.

Ref Type: Generic

Sebastian-Gallés N, Martí MA, Carreiras M, Cuetos F. 2000. LEXESP: Léxico informatizado del Español. Barcelona: Edicions Universitat de Barcelona.

Seidenberg MS, Arnoldussen A (2003a) The brain makes a distinction between hard and easy stimuli: Comments on Beretta et al. *Brain Lang* 85: 527-530.

Seidenberg MS, Arnoldussen A (2003b) The brain makes a distinction between hard and easy stimuli: comments on Beretta et al. *Brain Lang* 85: 527-530.

Shapiro K, Caramazza A (2003) Grammatical processing of nouns and verbs in left frontal cortex? *Neuropsychologia* 41: 1189-1198.

Soto-Faraco S, Sebastian-Gallés N, Cutler A (2001) Segmental and supra-segmental cues for lexical access in Spanish. *J Mem Lang* 45: 412-432.

Squire LR, Stark CEL, Clark RE (2004) The medial temporal lobe. *Annual Review of Neuroscience* 27: 279-306.

Stromswold K, Caplan D, Alpert N, Rauch S (1996) Localization of syntactic comprehension by positron emission tomography. *Brain Lang* 52: 452-473.

Talairach J, Tournoux P (1988) Co-Planar Stereotaxic Atlas of the Human Brain. New York: Thieme Medical Publishers.

Tomaiuolo F, MacDonald JD, Caramanos Z, Posner G, Chiavaras M, Evans AC, Petrides M (1999) Morphology, morphometry and probability mapping of the pars opercularis of the inferior frontal gyrus: an in vivo MRI analysis. *Eur J Neurosci* 11: 3033-3046.

Tsapkini K, Jarema G, Kehayia E (2000) Manifestations of morphological impairments in Greek aphasia: A case study. *J Neurolinguistics* 14: 197-212.

Tyler LK, Bright P, Fletcher P, Stamatakis EA (2004) Neural processing of nouns and verbs: the role of inflectional morphology. *Neuropsychologia* 42: 512-523.

- Ullman MT (2001a) A neurocognitive perspective on language: The declarative/procedural model. *Nat Rev Neurosci* 2: 717-726.
- Ullman MT (2001b) A neurocognitive perspective on language: the declarative/procedural model. *Nat Rev Neurosci* 2: 717-726.
- Ullman MT, Bergida R, O'Craven KM (1997a) Distinct fMRI activation patterns for regular and irregular past tense. *Neuroimage* 5: S549.
- Ullman MT, Corkin S, Coppola M, Hickok G, Growdon JH, Koroshetz WJ, Pinker S (1997b) A Neural Dissociation within Language: Evidence that the Mental Dictionary Is Part of Declarative Memory, and that Grammatical Rules Are Processed by the Procedural System. *J Cogn Neurosci* 9: 289-299.
- Vallar G, DeBetta AM, Silveri MC (1997) The phonological short-term store rehearsal system: Patterns of impairment and neural correlates. *Neuropsychologia* 35: 795-812.
- van Turennout M, Ellmore T, Martí MA (2000) Long-lasting cortical plasticity in the object naming system. *Nat Neurosci* 3: 1329-1334.
- Vandenberghe R, Price C, Wise R, Josephs O, Frackowiak RS (1996) Functional anatomy of a common semantic system for words and pictures. *Nature* 383: 254-256.
- Wagner AD, Maril A, Bjork RA, Schacter DL (2001) Prefrontal contributions to executive control: fMRI evidence for functional distinctions within lateral Prefrontal cortex. *Neuroimage* 14: 1337-1347.
- Worsley KJ, Friston KJ (1995) Analysis of fMRI time-series revisited--again. *Neuroimage* 2: 173-181.
- Zatorre RJ, Meyer E, Gjedde A, Evans AC (1996) PET studies of phonetic processing of speech: review, replication, and reanalysis. *Cereb Cortex* 6: 21-30.
- Zurowski B, Gostomzyk J, Gron G, Weller R, Schirmer H, Neumeier B, Spitzer M, Reske SN, Walter H (2002) Dissociating a common working memory network from different neural substrates of phonological and spatial stimulus processing. *Neuroimage* 15: 45-57.

Table 1: Mean frequency (per million) and length (in syllables) of the verb stimuli

	Inflection		Repetition		<i>p</i> value	
	Frequency**	Length	Frequency	Length	Frequency	Length
Regular	9.97	2.52	19.38	2.44	.46	.30
Irregular	15.53	2.55	16.65	2.68	.84	.06
<i>p</i> value	.22	.63	.83	.001*		

* The number of syllables was matched to the best degree. Stimuli were also matched for number of phonemes (6.25 for repetition regular, 6.35 for repetition irregular, $p < .5$)

** Regular and irregular verbs were also matched for the frequency of their infinitive forms (regular: 22.75, irregular: 30.49).

Table 2. Mean reaction times (RT) in ms and % of errors for the two tasks (standard deviations in parentheses).

	Repetition		Inflection	
	<u>RT</u>	<u>Errors</u>	<u>RT</u>	<u>Errors</u>
Regular verbs	1102 (178)	2.75 (2.38)	1157 (165)	2.83 (1.9)
Irregular verbs	1110 (178)	2.58 (2.19)	1261 (218)	3.75 (3.11)
Nonce verbs	1153 (166)	4 (4.28)	1291 (208)	3.5 (3.58)

Table 3. Activated brain regions for each condition comparing inflection and repetition. MNI coordinates and T value for the peak location in a particular identified anatomical cluster ($P < 0.001$; 20 voxels spatial extent) for the statistically significant differences of the corresponding activated regions. ^b $P < 0.005$; 20 voxels. BA = approximate Brodmann's area; L = Left hemisphere, R = Right hemisphere, IFG = inferior frontal gyrus; MFG = middle frontal gyrus; IPL = inferior parietal lobe; STG = superior temporal gyrus.

Brain region	Stereotactic coordinates				T peak	P corrected
	~BA	x	y	z		
<u>Regular Inflection > Regular Repetition</u>						
R Parahippocampal gyrus	19	32	-48	0	5.34	0.000
R Sensorimotor cortex	4	36	-24	60	4.98	0.000
L IFG opercular/L Ant STG	44/22	-48	8	0	6.14	0.098 ^b
L Cerebellum		-16	-52	-36	7.77	0.000
<u>Irregular Inflection > Irregular Repetition</u>						
L MFG	46	-48	36	12	13.53	0.000
L IFG	44/45	-36	20	16	5.08	
L Cerebellum		-24	-56	-44	5.87	0.003
R Sensorimotor cortex	4	20	-24	68	8.85	0.000
<u>Nonce Inflection > Nonce Repetition</u>						
L IFG opercular	44	-48	16	12	5.19	0.042
L Cerebellum		-12	-52	-32	8.16	0.000
R Sensorimotor cortex	4	28	-24	56	7.30	0.000

Table 4. Activated brain regions for the contrast of irregular compared to regular inflection, and real verbs compared to nonce inflection. MNI coordinates and T value for the peak location in a particular identified anatomical cluster ($P < 0.001$; 20 voxels spatial extent) for the statistically significant differences of the corresponding activated regions. ^a $P < 0.01$; 20 voxels. BA = approximate Brodmann's area; L = Left hemisphere, R = Right hemisphere, IFG = inferior frontal gyrus; MFG = middle frontal gyrus; IPL = inferior parietal lobe; SPL = superior parietal lobe; STG = superior temporal gyrus; MTG = middle temporal gyrus; SPL = superior parietal lobe.

Brain region	~BA	Stereotactic coordinates			T peak	P corrected
		x	y	z		
<u>Irregular Inflection > Regular Inflection</u>						
L IFG	44/45	-40	24	12	5.33	0.024 ^a
L IFG opercular	45	-56	24	16	4.31	
L IFG/ MFG	45/46	-44	24	20	4.69	
R IFG opercular	44/45	40	16	24	4.17	0.078 ^a
R MFG	46	48	40	16	5.93	
<u>Regular Inflection > Irregular Inflection</u>						
Left Hippocampus		-28	-12	-20	7.78	0.038 ^a
L insula/L Ant STG		-44	8	-4	5.46	
<u>Regular Inflection > Nonce Inflection</u>						
Posterior cingulate cortex	31	-4	-36	44	14.96	0.000
L STG	41	-48	-24	12	7.12	0.000
L Parahippocampal Gyrus	35	-28	-28	-28	4.44	0.000
Precuneus	31	8	-56	8	13.91	0.000
R STG	41	48	-48	12	12.46	0.000
R MTG	21	60	-48	4	8.93	0.000
Rostral anterior cingulate	32	0	44	-4	9.24	0.000
<u>Nonce Inflection > Regular Inflection</u>						
L IFG opercular	44	-48	16	24	11.19	0.000

	45	-52	36	8	6.48	
L MFG	46	-48	48	4	8.35	
L IPL	7	-28	-68	32	7.61	0.000
L Cerebellum		-28	-60	-44	9.01	0.000
R IFG opercular	44	48	16	20	7.00	0.001
R MFG	46/10	44	48	12	7.01	0.023
R IPL	40	44	-36	52	13.00	0.000

Irregular Inflection > Nonce Inflection

Posterior cingulate cortex	31	-4	-36	44	10.86	0.000
L STG	41	-40	-24	8	6.28	0.003
Precuneus	31	8	-60	12	10.99	0.000
R MTG	21	60	-48	8	6.82	0.000
R STG	41	64	32	8	5.38	0.000
R Cerebellum		28	-36	-32	6.02	0.039
Rostral anterior cingulate	32	0	60	-4	9.02	0.000

Nonce Inflection > Irregular Inflection

L IFG opercular	44	-48	12	8	7.64	0.000
	45/46	-48	48	4	6.98	0.000
L SPL	7/40	-36	-64	52	6.08	0.000
L Cerebellum		-40	-64	-40	5.50	0.000
R IFG	44	48	16	20	5.80	0.018
R IPL	7/40	40	-40	40	9.35	0.000

Figure captions:

Figure 1. Mean (\pm SEM) reaction time data.

Figure 2. A. Axial views in standard stereotactic space of the group average comparisons between the inflection task and the repetition task in each type of verb condition. B. Axial views of the crucial comparison between irregular and regular inflection conditions. Notice the differential recruitment of the middle frontal gyrus in both hemispheres. C. Axial views of the comparisons between the inflection task in the nonce verb and real verb (regular and irregular) conditions. All the views presented were superimposed on the mean anatomical image formed averaging for all 12 subjects T1 structural MRI scans mapped into normalized MNI space. Values in the color scales refer to the T values of the corresponding contrast.

Figure 3. Hemodynamic time courses and percentage of signal change of three regions of interest (ROIs): inferior frontal gyrus (BA 44/45, coordinates $-52, 16, 6$) and left middle frontal gyrus (BA 46, coordinates $-48, 48, 4$) and left anterior superior temporal gyrus (coordinates $-44, 8, -4$). ROIs views (left column) were superimposed on an anatomical T1 image mapped into normalized MNI space. On x-axis depicted the onset of 1.5 s temporal samples in relation to the presentation of the imperative task cue. In the middle column, the activation in the nonce verb conditions is compared. In the three ROIs, a main effect of Task (inflection vs. repetition) is easily noticeable near the peak activity. At the right side, time-courses of the real verb conditions are depicted. Notice the different time course of the irregular inflection condition in the middle frontal gyrus when compared to the other conditions.

Appendix A: Characteristics of the Spanish morphological system

In Spanish, as in other Romance languages, inflections are organized into three morphological classes or conjugations. Each conjugation has its characteristic thematic vowel, e.g., 1st conjugation: -a- (“estudi-a-r” [to study]), 2nd conjugation: -e- (“com-e-r” [to eat]), and 3rd conjugation: -i- (“viv-i-r” [to live]). The 1st class group is the largest and most productive one. The order of the various constituents of Spanish verbs is fixed as follows: root + thematic vowel + inflectional suffixes. The appropriate inflectional suffixes vary for each person and tense and have a different form depending on the conjugation class of the verb. The 1st person singular of the present tense is constructed by directly attaching an “-o” at the end of the verb stem. There is no theme vowel in these forms, and the inflectional ending (“-o”) is identical in all three conjugations (e.g. “estudi-a-r”/“estudi-o” [to study]; “com-e-r”/“com-o” [to eat], “viv-i-r”/“viv-o” [to live]). We chose to study this specific form to avoid the effects of different conjugation classes. Some authors have argued that in languages with conjugation classes, only the class that is most productive has default suffixes (Clahsen et al., 2002b).

Many Spanish verbs deviate from the regular pattern of verb formation due to changes in the stem or root form. The most common irregularity is a vowel-diphthong alternation affecting the stem of the verb and appearing in the present tense. In such alternations, vowels “e” and “o” unpredictably change to diphthongs “ie” and “ue”, respectively (e.g. “quer-ér”/“quiero” [to love]; “volv-ér”/“vuélv-o” [to return]). In addition, there are groups of more idiosyncratic variations affecting the stem such as “pid-o” [I ask for]-“pedir” [to ask for]. The inflectional suffixes are applied in the same manner as fully regular verbs irrespective of whether or not the stem has an irregular variation in those verbs. However, a few irregular verbs alter the suffixes they use (e.g. “est-a-r” [to be]- “est-oy”; “pon-e-r” [to put]/ “pon-go”). The irregularities appear in specific tenses and persons.

We were interested in comparing a condition where access to memorized lexical forms (irregular stems) was needed with a condition where pure decomposition and suffixation was needed. Studying this specific tense and person combination in Spanish enabled us to compare these two conditions while controlling for the influence of the presence of an inflectional ending.

Figure 1.

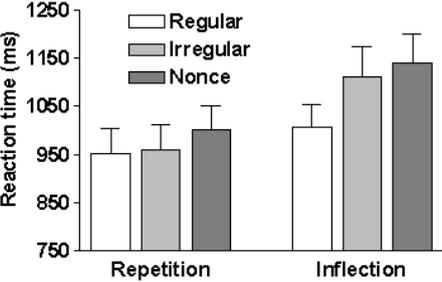


Figure 2.

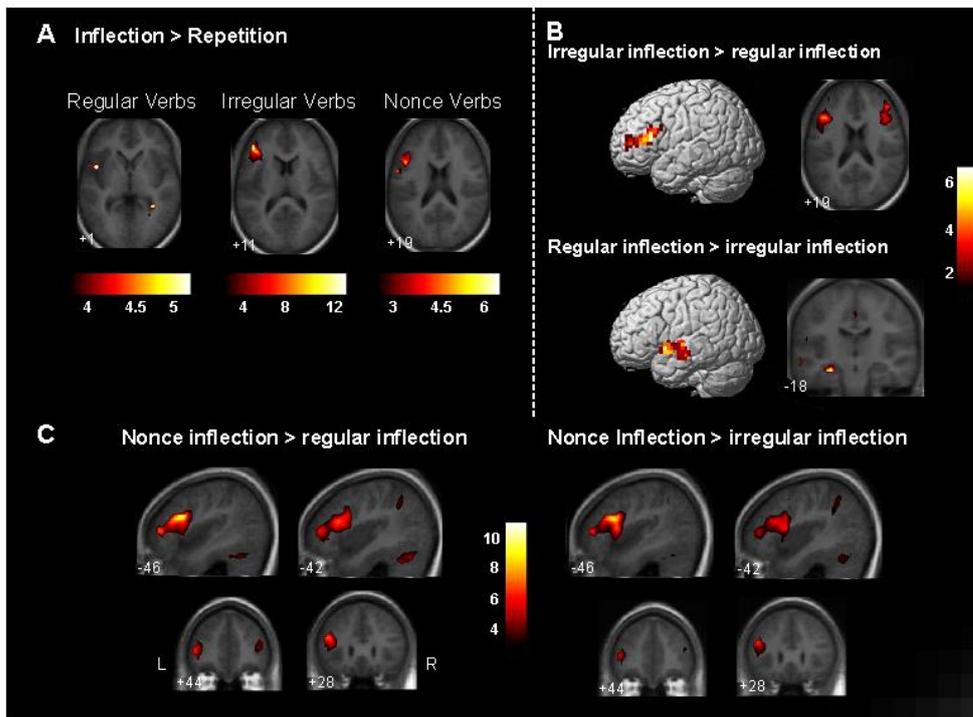


Figure 3.

