



ELSEVIER

NeuroImage

www.elsevier.com/locate/ynimg
NeuroImage xx (2007) xxx–xxx

Age of acquisition modulates neural activity for both regular and irregular syntactic functions

Arturo E. Hernandez,^{a,*} Juliane Hofmann,^b and Sonja A. Kotz^c

^aUniversity of Houston, Houston, TX, USA

^bSaarland University, Saarbrücken, Germany

^cMax Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

Received 5 January 2007; revised 18 February 2007; accepted 25 February 2007

Studies have found that neural activity is greater for irregular grammatical items than regular items. Findings with monolingual Spanish speakers have revealed a similar effect when making gender decisions for visually presented nouns. The current study extended previous studies by looking at the role of regularity in modulating differences in groups that differ in the age of acquisition of a language. Early and late learners of Spanish matched on measures of language proficiency were asked to make gender decisions to regular (-o for masculine and -a for feminine) and irregular items (which can end in e, l, n, r, s, t and z). Results revealed increased activity in left BA 44 for irregular compared to regular items in separate comparisons for both early and late learners. In addition, within-group comparisons revealed that neural activity for irregulars extended into left BA 47 for late learners and into left BA 6 for early learners. Direct comparisons between groups revealed increased activity in left BA 44/45 for irregular items indicating the need for more extensive syntactic processing in late learners. The results revealed that processing of irregular grammatical gender leads to increased activity in left BA 44 and adjacent areas in the left IFG regardless of when a language is learned. Furthermore, these findings suggest differential recruitment of brain areas associated with grammatical processing in late learners. The results are discussed with regard to a model which considers L2 learning as emerging from the competitive interplay between two languages.

© 2007 Elsevier Inc. All rights reserved.

Introduction

Is second language (L2) processing fundamentally similar or different from first language (L1) processing? Work investigating language processing in bilingual aphasics (Fabbro, 1999; Fabbro et al., 2000; Junque et al., 1995; Paradis, 1987; Paradis, 1995a;

Paradis, 1995b) and healthy normals using fMRI (Abutalebi et al., 2001; Chee et al., 2001; Dehaene et al., 1997; Hernandez et al., 2001; Hernandez et al., 2000; Illes et al., 1999; Perani et al., 1998; Rodriguez-Fornells et al., 2002; Wartenburger et al., 2003) has reported evidence that both languages are most likely processed by similar neural circuits. Despite the fact that brain activity is mediated by mostly overlapping neural circuits, recent work in the neuroimaging literature suggests that both age of second language acquisition (AoA) and language proficiency modulate the magnitude of such activity (Chee et al., 2001; Perani et al., 1998; Wartenburger et al., 2003). Furthermore, results from a recent fMRI study suggest a dissociation between syntax and semantics (Wartenburger et al., 2003). In this study, comparisons were made between groups that differed on 2nd language (L2) age of acquisition (AoA) but were matched on proficiency. In a second comparison, groups that differed on proficiency but were matched on L2 AoA were compared. Results revealed that syntax was more strongly modulated by 2nd language (L2) age of acquisition (AoA) whereas semantic processing was more strongly modulated by language proficiency. Finally, studies have found that L2 learners show increased neural activity for irregular items relative to regular items (Tatsuno and Sakai, 2005). The current study sought to extend the findings of previous studies by testing early and late Spanish learners matched on language proficiency using a grammatical gender decision task. Both regular and irregular gender marked items were used. These results should help to elucidate whether differences in AoA modulate neural activity differentially for regular and irregular gender marked items.

Neural correlates of syntactic processing in a second language

As noted above, earlier studies have not found a clear relationship between second language AoA and recovery of function in bilingual aphasics or in the location or amount of neural activity. However, two studies suggest that age of acquisition plays a more critical role than proficiency in determining the neural activity associated with grammatical processing (Wartenburger et al., 2003; Weber-Fox and Neville,

* Corresponding author. 126 Heyne Bldg., Department of Psychology, University of Houston, Houston, TX 77204-5022, USA. Fax: +1 713 743 8354, +1 713 743 8588.

E-mail address: aehernandez@uh.edu (A.E. Hernandez).

Available online on ScienceDirect (www.sciencedirect.com).

1996). In a seminal study, Weber-Fox and Neville (1996) presented a group of early and late L2 learners sentences that contained semantic or syntactic anomalies while observing neural activity with Event Related Potentials (ERPs). Results across both error types revealed differences in the neural signatures of these effects when L2 was learned later in life. Differences were observed when comparing the data obtained for L2 learners with that which had been collected in other studies with native speakers. For syntactic anomalies, second language speakers' data were found to diverge from that seen in native speakers even when the former began L2 acquisition between 1 and 3 years of life. For semantic processing, however, differences between monolinguals and L2 speakers were observed only in individuals who learned L2 after the age of 11. That is, the neural signatures associated with syntactic anomalies are influenced to a greater extent by the age of L2 acquisition than those associated with semantic anomalies.

More recently, Wartenburger et al. (2003) asked participants to detect syntactic anomalies (violations of case, gender or number) or semantic anomalies in a set of visually presented sentences. Like Weber-Fox and Neville (1996), the investigators were interested in understanding the influence of language proficiency and AoA on the neural signatures associated with semantic and syntactic processing. In order to investigate these differences, Wartenburger et al. included one early high-proficiency group, one late high-proficiency group and one late low-proficiency group. Differences in neural activity due to AoA were detected via comparisons between early and late high-proficiency subjects. Differences in neural activity due to proficiency were estimated by comparing late high and low proficiency subjects. The results from their study were in line with those observed by Weber-Fox and Neville (1996). For semantic judgments, there were differences between high and low proficiency late bilinguals, but no differences between early and late high-proficiency subjects. For syntactic anomalies, there were significant differences between the two high-proficiency groups, which differed on AoA, and very subtle differences between the two late AoA groups that differed on proficiency.

Taken together, the two studies by Weber-Fox and Neville and Wartenburger et al. suggest that second language AoA may have an important influence on the nature of neural activity during grammatical processing. However, some of these effects could be due to methodological limitations of the previous studies. First, many of the conclusions attributed to AoA by Weber-Fox and Neville (1996) are based on comparisons between the data collected in their study on L2 learners with other studies in monolinguals. This leaves open the possibility that differences attributed to maturational changes may be due in part to differences in methodologies, procedures and data analytic methods across studies. Follow-up studies should compare native and nonnative speakers directly. Second, both studies do not address the issue of whether these effects appear for all syntactic functions. In this respect, a recent study by Rossi et al. (in press) has found that differences between native speakers and high-proficiency L2 learners may not appear for all types of syntactic violations. Subsequent studies should consider carefully under what conditions L2 AoA effects appear. In this respect, Wartenburger et al. (2003) did not consider differences in regularity of a syntactic function as a factor that may influence AoA effects.

It is precisely the issue of regularity and how it is modulated in bilingual speakers that was addressed by two seminal studies (Sakai et al., 2004; Tatsuno and Sakai, 2005). In the first study, Sakai et al. (2004) tested pairs of twins that were trained on the

past tense conjugations of verbs in English over a 2 month period. Participants were then asked to perform a verb matching task or a past tense identification task. The results revealed increased activity in left dorsal Inferior Frontal Gyrus (IFG) as accuracy improved. This appeared in both a comparison between post- and pre-training periods as well as in the individual performance of each subject. In a second study, Tatsuno and Sakai (2005) used the same task to test a group of Japanese native speakers who had learned English as a second language. Comparable to Sakai et al. (2004), the results revealed increased neural activity in the superior and anterior portion of left BA 45 with decreased proficiency in English. The results revealed increased activity in the lower portion of left IFG (BA 45/47) during processing of irregular (but not regular) past tense items compared to processing of similar items in a verb matching task. These two studies indicate the importance of inferior portions of left IFG in the processing of past tense verbs in late learners of a second language. Furthermore, these results suggest that a more superior and anterior portion of left BA 45 may be more sensitive to proficiency in a language as measured by improved accuracy in the task.

On the regular/irregular distinction

The cognitive and neural mechanism underlying the computation of inflectional morphology is a point of debate. In the cognitive literature, researchers are divided on whether regular and irregular inflectional morphology is handled by separate systems or by a single system. A prominent variant of the separate system theory is the "Words and Rules" theory, developed by Pinker (Pinker, 1991; Pinker and Ullman, 2002). In this theory, the regular past tense is generated by a combinatorial grammatical system which applies a rule without reference to the phonology or semantics of the stem. Irregular past tense forms, on the other hand, are stored in the lexicon and retrieved via an associative memory mechanism. More recently, Ullman and colleagues (Ullman, 2001a; Ullman, 2004) have extended this account by proposing that regular and irregular grammatical forms are handled by distinct neural systems. Because it is a subsystem of declarative memory, lexical memory should be modulated by the medial temporal and temporo-parietal regions which are considered to be responsible for the consolidation and long-term retention of declarative memories. Consequently, regular inflection, which is more dependent on grammatical processing and more reliant on the procedural system, should involve the basal ganglia, Broca's area and neighboring anterior regions. Results from a series of studies have lent support to this view (Patterson et al., 2001; Tyler et al., 2002; Ullman et al., 1997). Ullman and colleagues have termed this framework the Declarative Procedural (DP) model due to the involvement of different memory systems during language processing.

Dissociations between regular and irregular processing can also be explained using an interactive/activation account (Rumelhart and McClelland, 1986). Although the interactive/activation (IA) model has a single system for all past tense forms, retrieval of regular and irregular forms depends on differential contributions of phonological and semantic components. In this view, irregular inflection may be more vulnerable to disruption from a semantic deficit whereas regular past tense forms place a greater demand on the phonological system (Bird et al., 2003; Burzio, 2002; Lambon Ralph et al., 2005). Unlike the irregular past tense, however, the transformation into the regular past tense in English should be more vulnerable after phonological impairments because of the

addition of the ending “ed” after regular forms. This theory has received support from connectionist simulations (Joanisse and Seidenberg, 1999), work with language impaired populations (Bird et al., 2003; Joanisse, 2004), as well as newer work with neuroimaging methodologies (Desai et al., 2006; Joanisse, 2004).

A number of studies have found increased activity for irregular relative to regular past tense items in English (Desai et al., 2006; Jaeger et al., 1996; Sahin et al., 2006). Desai et al. (2006) found that processing of the irregular relative to the regular past tense involves increased activity in left IFG in BA 45/47 (Desai et al., 2006). This region has been associated with semantic processing (Bookheimer, 2002; Dapretto et al., 1999; Devlin et al., 2003; Hagoort et al., 2006; Hagoort et al., 2004; Poldrack et al., 1999). Hence, these results are supportive of the IA claim that generation of the irregular past tense involves greater semantic processing than that of the regular past tense.

Desai et al. also found increased activity in another locus of the IFG near the anterior insula. This increased activity is in the right homologue of the area traditionally associated with motor planning and/or articulatory processing (Bates et al., 2003b; Dronkers, 1996; Wise et al., 1999). One potential interpretation of this finding is that right insula and IFG activity involve recruitment of right hemisphere homologues during more difficult processing. Sahin et al. (2006), however, have found that processing of the irregular past tense involves increased activity in the medial portion of the supplementary motor area and the anterior cingulate gyrus, suggesting that processing of irregular items may involve more motor and attentional control. Taken together these results suggest that processing of the irregular past tense may also involve additional articulatory processing, motor planning and execution as well as attentional control.

An important question that arises with regard to the DP model is whether fMRI studies as currently designed are a valid test of this model. To date most studies have employed an overt past tense generation task in which participants are asked to take a present tense form and generate the past tense. This task clearly asks participants to make a conscious explicit judgment in generating the past tense. Hence, it is unclear if the past tense generation task can adequately test the DP model.

Finally, one key aspect of the DP and the IA models of past tense hinges on whether they are able to generalize beyond the English past tense to irregular/regular distinctions in other domains or languages. Of particular interest to the current study is the adaptation of either of these models for the processing of grammatical gender. We will return to models of gender processing after introducing the concept of grammatical gender.

On grammatical gender

Theoretical approaches

Grammatical gender is a pervasive phenomenon in many of the world's languages. However, this gender is not based on biological gender. Across languages, translation equivalents of the same lexical item may have completely different grammatical gender. Furthermore, gender marked nouns have to agree with determiners and adjectives. Hence, gender plays a role at the syntactic level.

Like the English past tense, there are two basic models for grammatical gender. Some models posit that grammatical gender involves a separate node or abstract representation (Caramazza and Miozzo, 1997; Levelt et al., 1999). However, others suggest that grammatical gender involves a combination of semantic and

phonological information (Corbett, 1991; Zubin and Koepcke, 1981). For example, Corbett (1991) suggests that grammatical gender in most languages utilizes a semantic core by employing a range of morphological information to build up separate gender classes. More recently, Mirkovic et al. (2005) simulated the acquisition of gender using connectionist models in which gender was represented explicitly or as a combination of semantic and phonological information. Both models were able to learn gender accurately and within the same number of learning cycles. In addition, both models were able to generalize accurately to a set of items which were outside the training set. These results suggest that a network which represents gender explicitly or via a combination of phonological and semantic rules can show equivalent performance. This conceptualization is compatible with previous neuroimaging work in our laboratory which has found that processing of irregular items may rely on areas that are both more closely associated with syntactic processing and which have been less directly linked to these processes (Hernandez et al., 2004). More specifically these results suggest that grammatical gender may be represented as both a syntactic rule and as a combination of phonological and semantic information.

Behavioral studies

Like other gender marked languages, Spanish has both phonologically regular items (-o for masculine, -a for feminine) and irregular items (with items forming smaller neighborhoods of items ending in e, l, n, r, s, t and z). Phonologically regular endings mark both biological gender (son, *hijo*, daughter, *hija*) as well as non-biological gender (moon, *luna*, river, *rio*). However, irregular endings are not associated with any particular biological gender. Previous studies have found that grammatical gender of nouns is learned easily by children (Devescovi et al., 1998; MacWhinney et al., 1989; Pizzuto and Caselli, 1992), can be detected by adults (Bates et al., 1995; Brooks et al., 1993; Cole and Segui, 1994; Radeau et al., 1989) and can be primed by gender marked adjectives (Akhtina et al., 1999; Bates et al., 1996, 2001; Cole and Segui, 1994; Deutsch et al., 1999; Friederici and Jacobsen, 1999; Gurjanov et al., 1985; Hagoort and Brown, 1999; Jescheniak and Schriefers, 1999). Furthermore, gender decisions are slower for irregularly marked nouns than for regularly marked nouns (Bates et al., 1995). Hence, retrieval of irregular gender is more effortful and may require more complex lexical processing (Bates et al., 1995). The effect of regularity on grammatical gender provides an interesting parallel to the effects that have been observed for past tense processing in English.

Neuroimaging studies

To date, only two published studies have considered the neural bases of grammatical gender processing. In a seminal study, Miceli et al. (2002) asked Spanish monolinguals to make gender (with regular and irregular items combined), semantic or phonological judgments about a series of visually presented words. Results revealed that processing of grammatical gender relative to semantic processing leads to increased activity in mid left BA 44/45. In an extension of this work, Hernandez et al. (2004) asked a group of Spanish speakers to monitor the gender of irregular and regular gender marked items. Like Miceli et al. (2002), results revealed increased activity in left BA 44/45. Increased activity was also observed in left superior BA 44 and left BA 45/47 when comparing gender decisions for irregular items to those of regular items (Hernandez et al., 2004). Hence, processing of both regular and

irregular gender marked items relative to a semantic task leads to increased activity in left BA 44/45 (Miceli et al., 2002). Furthermore, comparisons between irregular items and regularly marked items reveal increased activity in additional areas both superior and inferior to the activity observed in left BA 44/45, an area which has been posited to be important for syntactic processing.

The presence of neural activity in left hemisphere including superior BA 44, BA 44/45, BA 45/47 and the insula sheds light on the differences in the manner in which processing of regular and irregular grammatical gender occurs. Left superior BA 44 has been observed across a wide range of studies which involve articulation and is thought to be involved in phonological encoding and retrieval (Wise et al., 1999; Zatorre et al., 1996). This area also shows increased activity when comparing generation of a determiner to picture naming (Heim et al., 2002) suggesting that the retrieval of a gender marked noun's determiner may involve more complex phonological encoding and retrieval. The region of activity in left BA 44/45 is within a region that is known to be involved in a number of language processes including grammatical processing (Bookheimer, 2002; Dapretto et al., 1999; Friederici, 2002; Friederici et al., 2006; Miceli et al., 2002) as well as semantic processing (Vigliocco et al., 2006). Finally, a number of studies have linked neural activity in the left anterior insula with articulation. Using a lesion overlap method in two separate patient studies, Bates et al. (2003b) and Dronkers (1996) found speech difficulties to be associated with brain lesions in the left anterior insula. Furthermore, Ackermann and Riecker (2004) found increased activity in the left anterior insula during overt pronunciation of memorized syllables. This suggests that the left anterior insula can be directly linked to the coordination of muscle movements needed for articulation. In summary, fMRI results suggest that when processing irregularly marked gender items in Spanish, native speakers engage areas in left IFG associated with language related processes including phonological retrieval, syntactic processing and articulation.

Of particular interest to the current study is the increase in neural activity observed in left BA 45/47 for irregular items in Hernandez et al.'s study. This particular area is proximal to that observed for processing of the irregular past tense items in monolingual English speakers (Desai et al., 2006) and late learners of L2 (Sakai et al., 2004). The results from Hernandez et al. (2004) suggest that increased activity in left BA 45/47 for irregular items generalizes beyond the irregular past tense to other languages and processing of other types of grammatical functions. As noted earlier, this area has been linked to semantic processing. As such, it suggests that processing of irregular items may involve deeper semantic processing. It remains to be seen if this activity in this area differentiates between native and non-native speakers of a language.

The current study employed a unique approach in order to elucidate the difference between first and second language acquisition. Unlike previous studies which compared early and late learners of an L2 (Wartenburger et al., 2003; Weber-Fox and Neville, 1996), the present study compared two groups of Spanish speakers that differ in AoA but were matched in proficiency. Early Spanish–English bilinguals were chosen such that they learned Spanish first and were exposed to English by the age of 5. Late English–Spanish bilinguals were chosen such that they learned Spanish after the age of 12. Both groups were matched for proficiency on measures of word reading, vocabulary and basic grammar. To our knowledge, it is the first published study that has

attempted to directly compare native and non-native speakers who are being scanned with fMRI while processing regular and irregular gender marked items.

In line with the literature reviewed so far, we expect to find the following: (1) speakers of Spanish as their first or second language will differ in neural activity during syntactic processing even when the former group learns L2 very early in life; (2) regular and irregular marked items differ in the amount of grammatical processing and may also differ in the co-activation of semantic and phonological information; (3) processing of irregular grammatical functions will lead to increased activity in left BA 45/47, which is thought to be due to the increased need for semantic retrieval when processing these items.

The main aim of the current study is to distinguish processing of an early learned L1 from a late learned L2. There is evidence that late learners have particular difficulty learning irregularly marked items (Birdsong and Flege, 2001; Flege et al., 1999). Hence, there should be larger cross-group differences for irregular items than for regular items. As noted above, processing of irregular items leads to increased activity in left BA 45/47 across at least two different grammatically irregular forms in two different languages. It will be of particular interest to observe whether activity in left BA 45/47 differentiates early and late learners. Furthermore, activity in additional areas recruited by non-native speakers involves other portions of left IFG devoted to language related processes. The presence of differences between these groups should elucidate how AoA influences the processing of regular and irregular morphology.

Experimental procedure

Subjects

Early Spanish learners

This group was composed of twelve subjects (7 female and 5 male) with a mean age of 22.3 (SD=1.35, range 20 to 25) who learned Spanish as a native language but were dominant in English, their second language. None had any past medical history or had used medication. All were right handed as assessed by our internal handedness questionnaire and reported no left-handed members in their immediate family.

Late Spanish learners

This group was composed of twelve subjects (7 female and 5 male) with a mean age of 24.5 (SD=1.41, range 20 to 28) who learned English as their native language and had learned Spanish as a second language after the age of 12. This group was also dominant in English. None had any past medical history or had used medication. All were right handed as assessed by our internal handedness questionnaire and reported no left-handed members in their immediate family.

All participants were given informed consent in a protocol approved by both the UCLA and UCSB Human Subjects Committees. Participants in both groups were given a set of language proficiency measures in order to insure adequate proficiency in Spanish (see Table 1). This included the following measures:

Word Reading. Participants' were asked to read words in Spanish aloud (Sparks et al., 1997). The test was comprised of a list of 46 common Spanish words (e.g., lapiz, zanahoria). Each

Table 1
Proficiency and behavioral data for early and late Spanish Learners

Measure	Early Spanish learners		Late Spanish learners		Between-group difference	
	Mean	Sdev	Mean	Sdev	F	p
<i>Language history</i>						
AGE 1ST exposure to English	4.33	1.16	0.00	0.00	169*	0.001*
Years of study English	15.58	1.96	16.33	1.92	0.89	0.36
AGE 1ST exposure to Spanish	0.25	0.45	15.83	2.95	327.369*	0.001*
Years of study Spanish	3.42	2.49	6.83	3.01	9.168*	0.006*
<i>Language use</i>						
% of English spoken per day	0.73	0.08	0.74	0.09	0.06	0.81
% of Spanish spoken per day	0.23	0.07	0.18	0.09	2.30	0.14
<i>Self-assessed subjective language fluency</i>						
English speaking	6.67	0.65	7.00	0.00	3.14	0.09
English listening	6.92	0.29	7.00	0.00	1.00	0.33
English reading	6.75	0.45	7.00	0.00	3.67	0.07
English writing	6.58	0.90	7.00	0.00	2.57	0.12
Spanish speaking	5.67	0.99	5.17	1.40	1.02	0.32
Spanish listening	6.17	0.84	5.50	1.24	2.38	0.14
Spanish reading	4.75	1.22	5.17	1.12	0.77	0.39
Spanish writing	4.42	0.90	4.92	1.24	1.28	0.27
<i>Objective language fluency</i>						
English vocabulary	50.83	4.59	53.25	3.14	2.27	0.15
Spanish vocabulary	45.42	3.42	46.25	3.28	0.37	0.55
Spanish questionnaire	17.00	1.65	17.67	1.44	1.11	0.30
Spanish reading	45.42	3.43	46.25	3.28	0.37	0.55
<i>Behavioral performance in experiment</i>						
Response time to regulars	1006.89	162.23	966.82	118.34	0.48	0.50
Response time to irregulars	1029.39	178.78	971.91	99.32	0.95	0.34
Accuracy for regulars	0.96	0.03	0.97	0.02	0.18	0.68
Accuracy for irregulars	0.97	0.02	0.97	0.02	0.23	0.64

*=statistically significant, ns=not statistically significant, Sdev=standard deviation.

word was presented in the middle of a computer screen, one at a time, for a total of 4 s. Participants' responses were tape recorded and reviewed by a native Spanish-speaking research assistant for accuracy.

Vocabulary. Participants' vocabulary in Spanish was measured using the Spanish version of the Boston Naming Test (Kaplan et al., 1983), a standardized test of expressive vocabulary. Participants were presented with a total of 60 line drawings, one at a time, and were asked to name each out loud. The items ranged from least difficult (e.g., bed, tree) to most difficult (e.g., yoke, stilts, abacus). Participants were given as much time as they needed to name each picture. When the participant experienced a tip-of-the-tongue state, experimenters followed up with one or both of the following two questions: "What is the first letter of the word?" and "What does the word sound like?" The total number of pictures named correctly served as participants' Spanish-language vocabulary knowledge.

Spanish Competency. Participants' second language competency was measured using the Spanish Questionnaire (SQ), a paper-and-pencil task comprised of 20 multiple-choice items measuring Spanish grammar, vocabulary, and reading comprehension ability. The verbal and grammar items were intermixed, and the reading comprehension passage and follow-up questions appeared at the end of the test. The questionnaire items were

obtained from various old versions of Spanish placement tests, and the questionnaire was constructed with the help of an Introductory Spanish coordinator at UCSB.

Scores from all three tests as well as statistical tests between the groups can be seen in Table 1. The groups were very well matched on all three language measures. This was confirmed with 3 one-way ANOVAS which revealed no significant difference between the groups for Spanish vocabulary, $F(1,11)=0.37$, $p=0.55$; Spanish Proficiency, $F(1,11)=1.11$, $p=0.30$; and Spanish reading $F(1,11)=0.31$, $p=0.62$.

Apparatus and procedure. Functional MRI (fMRI) data were acquired with a General Electric 3.0 T magnetic imager equipped with echo-planar imaging (EPI) from Advanced NMR. Using an EPI gradient echo sequence (TR=3000 ms; TE=25 ms; a 64×64 scan matrix with a 24 cm FOV), 108 images were obtained for each subject over 19 slices (4 mm thick/1 mm gap). According to the atlas of the Montreal Neurological Institute, the most inferior and superior slices approximately corresponded to $z=-24$ and $z=+56$, respectively. A set of 19 coplanar high-resolution EPI structural images (TR=4000 ms; TE=65 ms; matrix size 128 X 128; FOV=20 cm) which were in the same plane as the functional images were also collected at the same time to later allow for spatial normalization of each subject's data into a standard coordinate system.

Each scanning session consisted of two runs, each comprised of four activation blocks of 48 s, which alternated with five rest blocks of 24 s each. Before each block, participants were shown the cue “M o F” (Masculine or Feminine) to indicate that they would be making a gender judgment during the experimental portion of the run. They were also told that there would be rest blocks in which no stimulus was presented. They were instructed to simply stare at the blank screen during these rest blocks. In each activation block, 24 words were presented visually through a set of goggles composed of non-magnetic materials. Stimuli were presented for a full second with one second between each stimulus. Behavioral data were acquired via a response box for each subject during the fMRI sessions. Participants were allowed to make responses up to 1800 ms after the presentation of the stimulus. Male/Female gender judgments were indicated via button press with the middle or index finger of the right hand. Data on reaction time and percent correct were collected during the scanning session. Finally, the finger press associated with each judgment was counterbalanced across subjects.

Design and materials

A set of 192 nouns were used in the present experiment. Half of these items were regular (where gender was marked with an -a or an -o ending), and half the items were irregular (where gender is not marked and words end in e, l, n, r, s, t and z). These were further subdivided into four sets (two irregular and two regular) which were presented in four separate blocks (see below). Across all four sets, items were matched on length, frequency, imageability and age of acquisition which are known to influence visual word recognition. Word frequency was determined for items by using Corpus del Español (<http://www.corpusdelespanol.org/>) which is a 100 million word corpus from Spanish texts. Imageability and age of acquisition were determined by using norms gathered as part of the International Picture Naming project (Bates et al., 2003a; Szekely et al., 2003).

Data analysis

The functional images for each subject were preprocessed and analyzed using SPM2 (Friston, 1995) which includes realignment, spatial transformation and smoothing using a 9 mm FWHM isotropic Gaussian kernel to increase the signal-to-noise ratio.

Statistical random effects analyses were also conducted using SPM2 (Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK). For these analyses, a set of regions of interest were determined from previously published studies. The MNI coordinates of the peak activity of these regions were selected and a spherical volume of 15 mm was chosen that surrounded the peak. Activity was corrected using the Small Volume Correction (SVC) module in SPM2. Statistically significant areas were superimposed on individual brain anatomy in MNI space using SPM routines. Direct comparisons were also exclusively masked by activation vs. rest contrasts which were thresholded at $p < 0.001$. The masking procedure was employed in order to eliminate any voxels in which the condition of interest would be less active than the rest condition. A similar procedure was used for calculating interaction effects between groups. Each interaction effect was exclusively masked by the activation vs. rest mask of a particular group. The list of direct contrasts, interaction effects and activation vs. rest masks used can be found in Table 2.

Table 2

Direct contrasts and corresponding activation vs. rest masks

Contrasts	Activation vs. rest mask
<i>Simple main effects</i>	
Irregular–Rest	
Regular–Rest	
<i>Direct contrasts</i>	
Irregular–Regular	Irregular–Rest
Regular–Irregular	Regular–Rest
<i>Interaction effects</i>	
Early Spanish speakers > Late Spanish speakers	
(Irregular–Regular)	(Irregular–Rest) _{ESS}
$_{ESS} - (Irregular - Regular)_{LSS}$	
(Regular–Irregular) _{ESS} –	(Regular–Rest) _{ESS}
(Regular–Irregular) _{LSS}	
Late Spanish speakers > Early Spanish speakers	
(Irregular–Regular) _{LSS} –	(Irregular–Rest) _{LSS}
(Irregular–Regular) _{ESS}	
(Regular–Irregular) _{LSS} –	(Regular–Rest) _{LSS}
(Regular–Irregular) _{ESS}	

ESS=Early Spanish Speakers, LSS=Late Spanish Speakers.

In order to establish the particular loci of activity of interest, a set of studies were identified which addressed questions of importance to the current study. This included addressing the difference between processing of regular and irregular items as well as the nature of visual and orthographic processing. A list of these ROIs and their sources can be found in Table 3. The first study by Tatsuno and Sakai (2005) compared novice and more experienced English second language learners during processing of the past tense (both regular and irregular). The second compared processing of irregular and regular gender marked items by native Spanish speakers (Hernandez et al., 2004). The third was a meta-analysis by Price and Devlin (2003) of studies that have investigated visual form and word form processing. The fourth, by Meschyan and Hernandez (2006), compared reading of English and Spanish words in English dominant bilinguals. Increased activity for English relative to Spanish was posited to be due to deeper orthographic processing in English. These two areas were included in our study to test the hypothesis that brain areas involved in visual processing during reading would be more likely to be recruited during the processing of gender. These ROIs allowed a more systematic approach to uncovering differences in both direct contrasts and group \times condition interactions in areas that have been found to be involved in the past tense, in visual form analysis, and in orthographic processing.

Behavioral results

Results from mean error rates and RTs were placed into a 2 (group) \times 2 (irregular vs. regular) mixed ANOVA with group as a between-subjects factor and gender regularity as a within-subjects factor. Within each group, there was no effect of regularity for reaction time or for errors. There was no statistically significant difference in the reaction times or errors across groups. There was no interaction between group and regularity. Results from the behavioral portion of the experiment can be seen in Table 1. Finally, both groups reported generating the determiner and noun in order to make the correct gender

Table 3
Regions of interest used in the current study

Study	Condition	Group	Location	x	y	z
Tatsuno and Sakai (2005)	English past tense vs. rest	19 vs. 13 year old English language Learners	F3t/BA 46	−39	21	12
Hernandez et al. (2004)	Spanish gender irregular vs. regular	Native Spanish speakers	BA 44/45 BA 44/6 Ant insula	−51 −44 26	18 2 20	14 33 3
Price and Devlin (2003)	Visual form processing	Meta analysis	VisWordFA	−42	−57	−10
Meschyan and Hernandez (2006)	Reading English vs. Spanish	Late Spanish learners	Precuneus Inf Par Lob	−24 42	−70 −58	22 40

decision. They reported using this strategy to a greater extent for irregularly marked items.

fMRI results

Within-group comparisons

Irregular vs. regular comparisons. Irregular vs. regular comparisons yielded two distinct patterns of activity in each group (see Fig. 1 and Table 4). In the early Spanish group, there was increased activity in left superior BA 44 which extended into superior BA 6, left IFG corresponding to BA 45, and the left inferior occipitotemporal cortex. For the late Spanish group, increased activity appeared in the middle portion of left IFG (BA 44/45) which extended down into inferior portions of IFG as well as the left anterior insula. There were no significant increases in neural activity when comparing regular items to irregular items for either group.

Between-group interaction effects

Group interaction effect yielded increased activity in left BA 44/45 for late Spanish learners (see Fig. 2 and Table 5) for irregular items relative to regular items. No interaction effects were observed

for regular items relative to irregular items. These results revealed that when comparing irregulars to regulars, late learners relative to early learners, show increased activity in left mid BA 44/45, an area that has been implicated in grammatical processing. These differences in age of acquisition of a language clearly modulate differences to a greater extent for irregular items than for regular items. The implications of the particular areas recruited will be taken up in the discussion.

Discussion

Results from the current experiment extend findings from previous studies by revealing the role that regularity and AoA play in modulating neural activity during grammatical processing. To our knowledge, this is the first study which has shown that regularity can modulate differences in early and late learners matched in language proficiency.

Regularity and gender in early and late Spanish learners

fMRI findings

Within-group comparisons. The first question the current study sought to address was whether items which had irregular gender markings would elicit increased activity in regions of the left IFG that have been associated with specific aspects of language processing, such as phonological retrieval, syntactic processing, semantic processing or articulation. Increased activity associated with irregular items revealed a different pattern of activity in each group. For early learners, there was increased activity of left BA 45, left superior BA 44/BA 6 and the left inferotemporal region. Late Spanish learners revealed increased activity in left IFG extending from mid BA 44/45 up to superior precentral gyrus (BA 44/6) as well as the left anterior insula.

Each of these patterns of activity suggests that these groups may be processing irregular items differently. Late Spanish learners showed two loci of increased activity in left IFG for irregular items, one in left BA 44/45 and the second was more superior encompassing the left IFG and extending into portions of the precentral gyrus (BA 44/6). Interestingly, this area of activity has been associated with both semantic processing and syntactic processing. The more inferior portion of this cluster which is posited by others to be in BA 47 has been associated with semantic processing (for a review see Bookheimer, 2002; Dapretto et al., 1999) but also with the processing of the irregular past tense in first (Desai et al., 2006) and second language learners (Tatsuno and Sakai, 2005). The more superior portion has been associated with

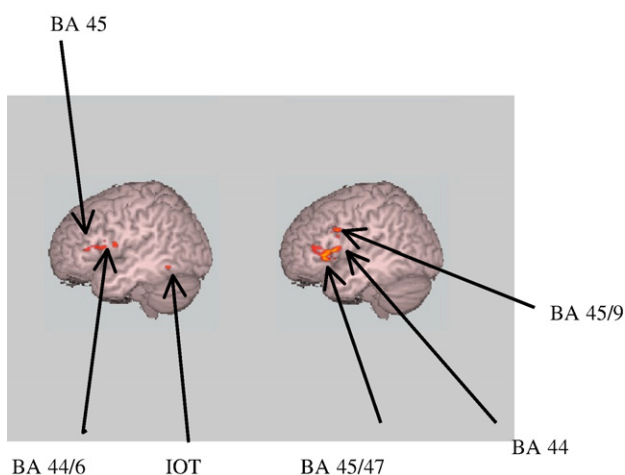


Fig. 1. Results from direct comparisons between irregular and regular gender marked items in early and late Spanish learners. Statistical parametric maps of the *t* statistics during gender decisions for direct comparison between irregular and regular items for early (left) and late (right) Spanish learners. Comparisons were computed using the Small Volume Correction within SPM2 for areas of interest. BA=Broadmann Area, IOT=Inferior Occipital Temporal juncture.

Table 4
Within-group comparisons

Region	Side	BA	Regular vs. rest					Irregular vs. rest					Irregular vs. regular				
			Voxels	x	y	z	Z	Voxels	x	y	z	Z	Voxels	x	y	z	Z
<i>Early Spanish learners</i>																	
IFG (p. trian)	L	45	-	-	-	-	-	126	-46	36	14	4.7					
IFG (p. trian)	L	-	-	-	-	-	-		-46	32	8	4.7	12	-42	32	10	4
IFG (p. trian)	L	45	-	-	-	-	-		-50	26	10	4.2		44	28	10	3.6
														-46	32	10	3.5
IFG (p. oper)	L	44	-	-	-	-	-	281	-56	6	14	4.7					
IFG (p. oper)	L	44	-	-	-	-	-		-50	4	12	4.2					
Roland. Oper.	L	44	-	-	-	-	-		-56	10	12	4.6	90	-56	10	14	5.1
IFG (p. trian)	L	44/45	-	-	-	-	-							-44	20	12	3.9
														-50	14	10	3.7
PCG	L	44/6	15	-48	6	36	3.3	410	-52	8	32	4.65					
				-50	2	36	3.2		-56	0	26	4.3					
									-46	-2	28	4.1					
Ant insula			19	-22	24	0	3.6	65	-28	20	6	4.3		-	-	-	-
IOT	L	-	-	-	-	-	-	23	-42	-56	-10	3.6	12	-46	-58	-10	4.3
<i>Late Spanish learners</i>																	
IFG (p. oper)	L	-	-	-	-	-	-	190	-46	10	10	4.2	104	-54	10	8	5.2
IFG (p. trian)	L	44	-	-	-	-	-		-54	16	6	4.6		-46	14	8	4.9
IFG (p. trian)	L	45	-	-	-	-	-		-52	32	6	4.5		-50	24	4	4.8
IFG (p. trian)	L	44	-	-	-	-	-	346	-44	12	26	3.7	16	-58	12	24	4.3
IFG (p. trian)	L	44/45	-	-	-	-	-		-50	16	30	4.6		-54	10	24	3.9
PCG	L	44/6	-	-	-	-	-		-52	10	36	4.2	29	-48	10	30	4.2
PCG	L	44/6	11	-42	2	30	3.3							-56	8	30	3.5
Ant insula			19	-22	24	0	3.6	108	-36	22	4	3.8	48	-32	22	4	4.2
									-34	26	8	3.7		-32	24	-2	3.3

Ant insula=anterior insula, IFG=inferior frontal gyrus, IOT=inferior occipital temporal lobe, MFG=middle frontal gyrus, SMA=supplementary motor area, PCG=postcentral gyrus, p. oper=pars opercularis, p. trian=pars triangularis, Roland. Oper.=rolandic operculum.

syntactic processing (Dapretto et al., 1999) and with the processing of irregular gender marked items (Hernandez et al., 2004; Miceli et al., 2002). As noted earlier, increased activity in the left anterior insula has been associated with articulatory processing.

Early learners revealed increased activity in left superior BA 44, left BA 45 (called BA 45/47 by others in the literature) as well as the left inferotemporal cortex. As noted earlier, activity in left

superior BA 44 has been associated with phonological processing (Wise et al., 1999; Zatorre et al., 1996) and is known to be active when participants generate the gender marked article for a picture (Heim et al., 2002). Furthermore, left inferior BA 45 (called 45/47 by others in the literature) has been associated with semantic processing (Bookheimer, 2002; Dapretto et al., 1999; Devlin et al., 2003; Hagoort et al., 2006; Hagoort et al., 2004; Poldrack et al., 1999) and with processing of irregular forms (Desai et al., 2006; Hernandez et al., 2004; Sahin et al., 2006). Finally, increased activity in the left inferotemporal region was proximal to areas involved in visual form processing for both lexical and non-lexical items (Price and Devlin, 2003). Taken together these results suggest that early learners engage areas that have been associated with phonological and visual word form processing during gender decisions for irregularly marked items.

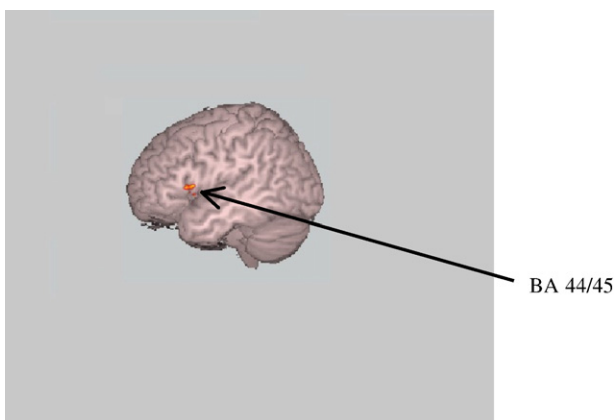


Fig. 2. Areas of increased activity for the interaction effect between regularity and group (early vs. late learner of Spanish). Statistical parametric maps of the *t* statistics for late learners relative to early learners for direct comparison between irregular and regular items. Comparisons were computed using the Small Volume Correction within SPM2 for areas of interest. BA=Brodmann Area.

Table 5
Cross-group interaction effects

Region	Side	BA	Regular vs. irregular					Irregular vs. regular				
			Voxels	x	y	z	Z	Voxels	x	y	z	Z
<i>Early Spanish learners</i>												
-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Late Spanish learners</i>												
IFG	L	44/45	-	-	-	-	27	-46	10	8	3.8	
								-48	14	8	3.8	
								-40	16	8	3.5	

IFG=inferior frontal gyrus.

The results of irregular/regular comparisons suggest that processing of irregular gender in late and early learners leads to increased activity in slightly different areas within the IFG as well as other regions of the brain. However, these distinctions are based on observations of differences observed when performing the irregular/regular comparison in each group. In order to establish these differences in a more statistically valid manner, it would be important to observe which differences appear in interaction effects.

Between-group interaction effects. The finding of slightly different loci in the left IFG for irregular/regular comparison for early and late learners of Spanish, leaves open the question of whether activity in this brain area differs interacts across groups. In fact, results revealed increased activity in late learners for irregular items in BA 44/45. As noted above, activity in BA 44/45 has been associated with syntactic processing (Bookheimer, 2002; Dapretto et al., 1999; Friederici, 2002; Friederici et al., 2006; Miceli et al., 2002) and processing of gender marked items (Hernandez et al., 2004; Miceli et al., 2002). The fact that this area shows increased activity in late learners suggests that processing irregular marked items when a second language is acquired later in life involves additional syntactic processing. Interestingly, this is consistent with theoretical frameworks which view second language learning as involving the formation of stronger within-language links in order to establish resonance (Hernandez et al., 2005), a point we will return to later. Finally, activity in left BA 44/45 in our study was somewhat posterior and inferior to the area of activity observed by Sakai et al. (2004), an area which has been associated with semantic processing in monolinguals (Vigliocco et al., 2006). Because of its proximity to areas that have been observed in grammatical processing, it seems more likely that it reflects processing of syntax rather than indicating more general proficiency differences. However, future studies are needed to more directly investigate the difference between areas involved in grammatical processing and those modulated by language proficiency.

Limitations of the current study

Although it is a novel experimental design, comparisons of native and non-native speakers does come with a number of limitations. The use of groups with different native languages has two potential problems. First, matching groups' language proficiency across all dimensions is potentially more difficult. The current study employed a small language proficiency test as well as a vocabulary test in order to match both groups. The proficiency test relied mostly on comprehension with a few grammar questions. It is entirely possible that these tests lack the sensitivity or specificity to detect differences between these groups. Although normed tests of language proficiency such as the Woodcock Muñoz Language Survey (WMLS) are more extensive than the test used in the current study, they do not necessarily include large grammar batteries. Rather, they define proficiency in a more operational manner relying for the most part on comprehension and production. Hence, it is possible that subjects showed small differences in grammatical processing ability that were not detected by the screening measures utilized in the current study. Although it is entirely possible that there are subtle differences between these groups, every step was taken to match native and non-native speakers as closely as possible. Finally, groups were matched on

behavioral performance in the grammatical decision task used. Whereas this does not preclude the possibility that some dimension of grammatical ability differs between the groups, it does suggest that the differences may indeed be subtle. In order to uncover these possible differences, future studies should employ tests such as the WMLS in order to establish more complete proficiency profiles. This might allow future studies to uncover more subtle differences that underlie these group differences.

A second limitation that arises from using native and non-native speakers of a language might involve differences in proficiency of subjects in English, the language that was not tested. Slightly higher English vocabulary scores were observed in late Spanish learners. In addition, these subjects showed marginally significant differences in their self-ratings of reading and speaking in English. Although these results did not reach significance, they may be indicative of subtle differences in English proficiency between these two groups. It seems unlikely that English proficiency accounts for the entire difference observed in the current study. However, future studies should seek to explore the influence of English proficiency on the processing of Spanish grammar in both native and non-native speakers.

Theoretical implications

Earlier, two models of regularity were discussed, the DP model of Ullman and colleagues (Pinker and Ullman, 2002; Ullman, 2001a; Ullman et al., 1997; Ullman, 2001b; Ullman, 2004) and the IA model of Seidenberg, McClelland, Patterson and colleagues (Bird et al., 2003; Joanisse and Seidenberg, 1999; McClelland and Patterson, 2002; Mirkovic et al., 2005; Patterson et al., 2001; Seidenberg and Hoeffner, 1998). The DP model predicts that irregular items should be more reliant on declarative memory whereas regular items should be more reliant on procedural memory. The IA Model suggests that irregular items are more reliant on semantic processing and regular items are reliant on phonological processing. Interestingly, connectionist models, which code grammatical gender explicitly or as a combination of semantic and phonological features, are able to learn the gender of words equally well. Our results, at least on the surface, do not entirely confirm the predictions of either model. One particular complication with regard to the DP model is the use of tasks which explicitly ask participants to generate the gender of a noun. Using an explicit task like the one used in the current study may in fact reduce the likelihood of being able to look at differences in declarative and procedural memory. Clearly, further systematic research is needed to more clearly delineate how the brain handles the regular/irregular distinction across various linguistic functions and across many different languages. Furthermore, future research should employ more implicit tasks in order to uncover conditions in which declarative memory plays a role for irregular items but not for regular items.

More recent studies investigating the nature of regular and irregular inflection have indeed found similar findings which do not support either the IA or the DP model (Balaguer et al., 2004; Desai et al., 2006). Of particular interest to the current study are cross-linguistic differences that appear because of the linguistic characteristics of the language. Recently, De Diego Balaguer et al. (2004) have suggested that differences between regular and irregular inflectional morphology can be traced to differences in the linguistic similarity of two languages. De Diego Balaguer et al. (2004) found that two Catalan-Spanish bilinguals with agrammatism had

similar deficits of regular morphology. In the current study, comparisons were made between late learners and early learners of Spanish. However, late learners of Spanish did not encounter the gender system until much later in life. If De Diego Balaguer et al. (2004) are correct in their assertion that language similarity plays a role in the nature of neural activity then this effect should be reduced between languages that are similar (for further discussion see Hernandez et al., 2005). Future studies should actively manipulate the similarity of languages in order to further understand how this factor modulates neural activity.

Implications for models of L2 learning

A second prediction of the DP model arises because of the fact that procedural memory is more sensitive to maturational constraints than declarative memory. According to the DP model, AoA effects for grammatical processing have to do with the maturational nature of procedural memory. In this view, learning a language later in life involves more use of declarative memory (Paradis, 1994) leading to increased activity in the declarative system (e.g. left BA 47) since grammatical transformations are memorized rather than computed. The locus of increased activity for late learners, when directly compared to early learners, centered around BA 44/45, an area which might be implicated in procedural learning. However, the DP model offers no account for the role of the precuneus and cuneus in processing of irregular items by early learners. Hence, the predictions made by the DP model with regard to second language learning were also not borne out. The current study finds little support for the notion that late learners rely to a greater extent on neural structures involved in declarative memory, or that limitations on the latter impact late learners more than early learners. Finally, the use of explicit tasks also makes it difficult to ascertain whether L2 learners use declarative memory whereas L1 learners use procedural memory. Future studies should use more implicit tasks in order to tease this apart.

The differences between first and second language learning are also not handled well by connectionist models of regularity. Whereas these models predict that learning of regular and irregular items can be conceived of as involving a combination of semantic and phonological information, they do not make explicit predictions about how first and second language learning differ. More recently, Hernandez et al. (2005) have proposed a model of L2 learning which is compatible with connectionist views of learning. Specifically, Hernandez et al. propose that L2 learning involves a competitive interplay between a bilingual's two languages in which speakers must overcome interference from L1. In this view, as L1 becomes more solidified and entrenched learning L2 becomes more difficult. As the L2 learner becomes more proficient, structures in the second language begin to resonate with each other. Finally, early stages of learning will result in L2 being heavily reliant (e.g. parasitic) on L1. Although L1 parasitism will diminish over time, L2 will always be partially parasitic on L1. Finally, entrenchment and parasitism will dictate which particular functions are easier or harder to learn in L2. Specifically, forms or functions that overlap across languages should be easier to learn than those which do not, a notion which has been confirmed by De Diego Balaguer et al. (2004).

Grammatical gender, a function that does not overlap across languages, should differ between native and L2 speakers because

of the need to create a grammatical representation with no equivalent in L1. In our study, L2 learners were able to successfully learn grammatical gender and show interesting similarities with native speakers. Specifically, activity in left BA 44/45 was present in both groups, suggesting that processing of irregular syntactic structures in early and late learners of a language involves more effortful grammatical processing. The presence of additional areas of activity in non-native speakers is compatible with the notion that non-language areas must be recruited in order to overcome entrenchment from L1. The regularity distinction is most likely related to resonance. In this view, resonance is more easily established for regular items in L2. However, once again this framework does not necessarily address the issue of modality of acquisition that is necessary to predict differential activity in visual areas of the cortex (for further discussion of sensorimotor differences in AoA see Hernandez and Li, in press).

In conclusion, the results from the current study revealed that the processing of both early and late learners' irregular grammatical gender involves the recruitment of areas which are differentially involved in grammatical processing. Comparisons between groups did reveal a slight increase in neural activity in BA 44/45, suggesting that late learners may use more explicit grammatical rules when processing irregular items. These findings do not fit in well with either DP or IA models (to be fair, IA never attempts to account for the case of L2). Whereas the competitive framework developed by Hernandez, Li and MacWhinney promises hope, future theoretical work is needed to expand this model to more adequately account for the neural correlates of L2 learning.

Acknowledgments

This material is based upon work supported by the National Science Foundation Grants "fMRI studies of language and task switching" (BCS0092043) and "Neural correlates of grammatical gender processing" (INT0202686) as well as a grant from the National Institute of Child Health and Development (1 R03HD050313-01).

References

- Abutalebi, J., Cappa, S.F., Perani, D., 2001. The bilingual brain as revealed by functional neuroimaging. *Bilingualism: Lang. Cogn.* 4, 179–190.
- Ackermann, H., Riecker, A., 2004. The contribution of the insula to motor aspects of speech production: a review and a hypothesis. *Brain Lang.* 89, 320–328.
- Akhutina, T., Kurgansky, A., Polinsky, M., Bates, E., 1999. Processing of grammatical gender in a three-gender system: experimental evidence from Russian. *J. Psycholinguist. Res.* 28, 695–713.
- Balaguer, R.d.D., Costa, A., Sebastián-Galles, 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.
- Bates, E., Devescovi, A., Pizzamiglio, L., D'Amico, S., Hernandez, A.E., 1995. Gender and lexical access in Italian. *Percept. Psychophys.* 57, 847–862.
- Bates, E., Devescovi, A., Hernandez, A., Pizzamiglio, L., 1996. Gender priming in Italian. *Percept. Psychophys.* 58, 992–1004.
- Bates, E., Marangolo, P., Pizzimiglio, L., Dick, F., 2001. Linguistic and nonlinguistic priming in aphasia. *Brain Lang.* 76, 62–69.
- Bates, E., D'Amico, S., Jacobsen, T., Szekeley, A., Andonova, E., Devescovi, A., Herron, D., Lu, C.C., Pechmann, T., Pleh, C., et al., 2003a. Timed picture naming in seven languages. *Psychon. Bull. Rev.* 10, 344–380.

- Bates, E., Wilson, S.M., Saygin, A.P., Dick, F., Sereno, M.I., Knight, R.T., Dronkers, N.F., 2003b. Voxel-based lesion-symptom mapping. *Nat. Neurosci.* 6, 448–450.
- Bird, H., Ralph, M.A.L., Seidenberg, M.S., McClelland, J.L., Patterson, K., 2003. Deficits in phonology and past-tense morphology: what's the connection? *J. Mem. Lang.* 48, 502–526.
- Birdsong, D., Flege, J.E., 2001. Regular–irregular dissociations in the acquisition of English as a second language. Paper presented at: BUCLD 25: Proceedings of the 25th Annual Boston University Conference on Language Development. Cascadilla Press, Boston, MA.
- Bookheimer, S., 2002. Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. *Annu. Rev. Neurosci.* 25, 151–188.
- Brooks, P.J., Braine, M.D., Catalano, L., Brody, R.E., et al., 1993. Acquisition of gender-like noun subclasses in an artificial language: the contribution of phonological markers to learning. *J. Mem. Lang.* 32, 76–95.
- Burzio, L., 2002. Missing players: Phonology and the past-tense debate. *Lingua* 112, 157–199.
- Caramazza, A., Miozzo, M., 1997. The relation between syntactic and phonological knowledge in lexical access: evidence from the “tip-of-the-tongue” phenomenon. *Cognition* 64, 309–343.
- Chee, M.W., Hon, N., Lee, H.L., Soon, C.S., 2001. Relative language proficiency modulates BOLD signal change when bilinguals perform semantic judgments. Blood oxygen level dependent. *NeuroImage* 13, 1155–1163.
- Cole, P., Segui, J., 1994. Grammatical incongruity and vocabulary types. *Mem. Cogn.* 22, 387–394.
- Corbett, G.G., 1991. *Gender*. Cambridge Univ. Press, Cambridge, UK.
- Dapretto, M., Bookheimer, S., Mazziotta, J., 1999. Form and content: dissociating syntax and semantics in sentence comprehension. *Neuron* 24, 427–432.
- Dehaene, S., Dupoux, E., Mehler, J., Cohen, L., Paulesu, E., Perani, D., van de Moortele, P.F., Lehericy, S., Le Bihan, D., 1997. Anatomical variability in the cortical representation of first and second language. *NeuroReport* 8, 3809–3815.
- Desai, R., Conant, L.L., Waldron, E., Binder, J.R., 2006. fMRI of past tense processing: the effects of phonological complexity and task difficulty. *J. Cogn. Neurosci.* 18, 278–297.
- Deutsch, A., Bentin, S., Katz, L., 1999. Semantic influence on processing gender agreement: evidence from Hebrew. *J. Psycholinguist. Res.* 28, 515–535.
- Devescovi, A., D'Amico, S., Smith, S., Mimica, I., Bates, E., 1998. The development of sentence comprehension in Italian and Serbo-Croatian: local versus distributed cues. In: Hillert, D. (Ed.), *Sentence Processing: A Cross-Linguistic Perspective*. Academic Press, San Diego, pp. 345–377.
- Devlin, J.T., Matthews, P.M., Rushworth, M.F., 2003. Semantic processing in the left inferior prefrontal cortex: a combined functional magnetic resonance imaging and transcranial magnetic stimulation study. *J. Cogn. Neurosci.* 15, 71–84.
- Dronkers, N.F., 1996. A new brain region for coordinating speech articulation. *Nature* 384, 159–161.
- Fabbro, F., 1999. *The Neurolinguistics of Bilingualism: An Introduction*. Hove, England UK.
- Fabbro, F., Skrap, M., Aglioti, S., 2000. Pathological switching between languages after frontal lesions in a bilingual patient. *J. Neurol. Neurosurg. Psychiatry* 68, 650–652.
- Flege, J.E., Yeni-Komshian, G.H., Liu, S., 1999. Age constraints on second language acquisition. *J. Mem. Lang.* 41, 78–104.
- Friederici, A.D., 2002. Towards a neural basis of auditory sentence processing. *Trends Cogn. Sci.* 6, 78–84.
- Friederici, A.D., Jacobsen, T., 1999. Processing grammatical gender during language comprehension. *J. Psycholinguist. Res.* 28.
- Friederici, A.D., Fiebach, C.J., Schlesewsky, M., Bornkessel, I.D., von Cramon, D.Y., 2006. Processing linguistic complexity and grammaticality in the left frontal cortex. *Cereb. Cortex* 1709–1717.
- Friston, K.J., 1995. Commentary and opinion: II. Statistical parametric mapping: ontology and current issues. *J. Cereb. Blood Flow Metab.* 15, 361–370.
- Gurjanov, M., Lukatela, G., Lukatela, K., Savic, M., Turvey, M.T., 1985. Grammatical priming of inflected nouns by the gender of possessive adjectives. *J. Exper. Psychol., Learn., Mem., Cogn.* 11, 692–701.
- Hagoort, P., Brown, C.M., 1999. Gender electrified: ERP evidence on the syntactic nature of gender processing. *J. Psycholinguist. Res.* 28, 715–728.
- Hagoort, P., Hald, L., Bastiaansen, M., Petersson, K.M., 2004. Integration of word meaning and world knowledge in language comprehension. *Science* 304, 438–441.
- Hagoort, P., Grodzinsky, Y., Amunts, K., 2006. On Broca, brain, and binding. *Broca's Region*. Oxford Univ. Press, pp. 242–253.
- Heim, S., Opitz, B., Friederici, A.D., 2002. Broca's area in the human brain is involved in the selection of grammatical gender for language production: evidence from event-related functional magnetic resonance imaging. *Neurosci. Lett.* 328, 101–104.
- Hernandez, A.E., Li, P., in press. Age of acquisition: its neural and computational mechanisms. *Psychological Bulletin*.
- Hernandez, A.E., Martinez, A., Kohnert, K., 2000. In search of the language switch: an fMRI study of picture naming in Spanish–English bilinguals. *Brain Lang.* 73, 421–431.
- Hernandez, A.E., Dapretto, M., Mazziotta, J., Bookheimer, S., 2001. Language switching and language representation in Spanish–English bilinguals: an fMRI study. *NeuroImage* 14, 510–520.
- Hernandez, A.E., Kotz, S.A., Hoffman, J., Valentin, V.V., Dapretto, M., Bookheimer, S.Y., 2004. The neural correlates of grammatical gender decisions in Spanish. *NeuroReport* 15, 863–866.
- Hernandez, A., Li, P., MacWhinney, B., 2005. The emergence of competing modules in bilingualism. *Trends Cogn. Sci.* 9, 220–225.
- Illes, J., Francis, W.S., Desmond, J.E., Gabrieli, J.D.E., Glover, G.H., Poldrack, R., Lee, C.J., Wagner, A.D., 1999. Convergent cortical representation of semantic processing in bilinguals. *Brain Lang.* 70, 347–363.
- Jaeger, J.J., Lockwood, A.H., Kemmerer, D.L., Van Valin Jr., R.D., Murphy, B.W., Khalak, H.G., 1996. A positron emission tomographic study of regular and irregular verb morphology in English. *Lang.: J. Linguist. Soc. Am.* 72, 451.
- Jescheniak, J., Schriefers, H., 1999. In search of gender recency: evidence from the production of pronouns. *J. Psycholinguist. Res.* 28, 739–745.
- Joanisse, M.F., 2004. Specific language impairments in children phonology, semantics, and the English past tense. *Curr. Dir. Psychol. Sci.* 13, 156–160.
- Joanisse, M.F., Seidenberg, M.S., 1999. Impairments in verb morphology after brain injury: a connectionist model. *Proc. Natl. Acad. Sci. U. S. A.* vol. 96, 7592–7597.
- Junque, C., Vendrell, P., Vendrell, J., 1995. Differential impairments and specific phenomena in 50 Catalan–Spanish bilingual aphasic patients. In: Paradis, M. (Ed.), *Aspects of Bilingual Aphasia*. Pergamon, Oxford.
- Kaplan, E., Goodglass, H., Weintraub, S., 1983. *Boston Naming Test*. Lee and Febiger, Philadelphia.
- Lambon Ralph, M.A., Braber, N., McClelland, J.L., Patterson, K., 2005. What underlies the neuropsychological pattern of irregular > regular past-tense verb production? *Brain and Language* 93, 106–119.
- Levelt, W.J.M., Roelofs, A., Meyer, A.S., 1999. A theory of lexical access in speech production. *Behav. Brain Sci.* 22, 1–75.
- MacWhinney, B., Leinbach, J., Taraban, R., McDonald, J., 1989. Language learning: cues or rules? *J. Mem. Lang.* 28, 255–277.
- McClelland, J.L., Patterson, K., 2002. Rules or connections in past-tense inflections: what does the evidence rule out? *Trends Cogn. Sci.* 6, 465–472.
- Meschyan, G., Hernandez, A., 2006. Impact of language proficiency and orthographic transparency on bilingual word reading: an fMRI investigation. *NeuroImage* 29, 1135–1140.

- Miceli, G., Turriziani, P., Caltagirone, C., Capasso, R., Tomaiuolo, F., Caramazza, A., 2002. The neural correlates of grammatical gender: an fMRI investigation. *J. Cogn. Neurosci.* 14, 618–628.
- Mirkovic, J., MacDonald, M.C., Seidenberg, M.S., 2005. Where does gender come from? Evidence from a complex inflectional system. *Lang. Cogn. Processes* 20, 139–167.
- Paradis, M., 1987. *The Assessment of Bilingual Aphasia*. Erlbaum, Hillsdale, NJ.
- Paradis, M., 1994. Neurolinguistic aspects of implicit and explicit memory: implications for bilingualism. In: Ellis, N. (Ed.), *Implicit and Explicit Learning of Second Languages*. Academic Press, London, pp. 393–419.
- Paradis, M., 1995a. *Aspects of bilingual aphasia*, 1st ed., Pergamon, Oxford, OX, UK; Tarrytown, N.Y., U.S.A.
- Paradis, M. (Ed.), 1995b. *Bilingual Aphasia 100 Years Later: Consensus and Controversies*. Pergamon, Oxford.
- Patterson, K., Ralph, M.A.L., Hodges, J.R., McClelland, J.L., 2001. Deficits in irregular past-tense verb morphology associated with degraded semantic knowledge. *Neuropsychologia* 39, 709–724.
- Perani, D., Paulesu, E., Galles, N.S., Dupoux, E., Dehaene, S., Bettinardi, V., Cappa, S.F., Fazio, F., Mehler, J., 1998. The bilingual brain: proficiency and age of acquisition of the second language. *Brain* 121, 1841–1852.
- Pinker, S., 1991. Rules of language. *Science* 253, 530–535.
- Pinker, S., Ullman, M.T., 2002. The past and future of the past tense. *Trends Cogn. Sci.* 6, 456.
- Pizzuto, E., Caselli, M.C., 1992. The acquisition of Italian morphology: implications for models of language development. *J. Child Lang.* 19, 491–557.
- Poldrack, R.A., Wagner, A.D., Prull, M.W., Desmond, J.E., Glover, G.H., Gabrieli, J.D., 1999. Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *NeuroImage* 10, 15–35.
- Price, C.J., Devlin, J.T., 2003. The myth of the visual word form area. *NeuroImage* 19, 473–481.
- Radeau, M., Morais, J., Dewier, A., 1989. Phonological priming in spoken word recognition: task effects. *Mem. Cogn.* 17, 525–535.
- Rodríguez-Fornells, A., Rotte, M., Heinze, H.J., Nosselt, T., Munte, T.F., 2002. Brain potential and functional MRI evidence for how to handle two languages with one brain. *Nature* 415, 1026–1029.
- Rossi, S., Gugler, M.F., Friederici, A.D., Hahne, A., in press. The impact of proficiency on syntactic second language processing of German and Italian: evidence from ERPs. *Journal of Cognitive Neuroscience*.
- Rumelhart, D., McClelland, J.L., 1986. *Parallel distributed processing: explorations in the microstructure of cognition*. Foundations, vol. 1. MIT Press, Cambridge, MA.
- Sahin, N.T., Pinker, S., Halgren, E., 2006. Abstract grammatical processing of nouns and verbs in Broca's area: evidence from fMRI. *Cortex* 42, 540–562.
- Sakai, K.L., Miura, K., Narafu, N., Muraishi, Y., 2004. Correlated functional changes of the prefrontal cortex in twins induced by classroom education of second language. *Cereb Cortex* 14, 1233–1239.
- Seidenberg, M.S., Hoeffner, J.H., 1998. Evaluating behavioral and neuroimaging data on past tense processing. *Language* 74, 104–122.
- Sparks, R.L., Ganschow, L., Patton, J., Artzer, M., 1997. Prediction of foreign language proficiency. *J. Educ. Psychol.* 89, 549–561.
- Szekely, A., D'Amico, S., Devescovi, A., Federmeier, K., Herron, D., Iyer, G., Jacobsen, T., Bates, E., 2003. Timed picture naming: extended norms and validation against previous studies. *Behav. Res. Methods Instrum. Comput.* 35, 621–633.
- Tatsuno, Y., Sakai, K.L., 2005. Language-related activations in the left prefrontal regions are differentially modulated by age, proficiency, and task demands. *J. Neurosci.* 25, 1637–1644.
- Tyler, L.K., deMornay-Davies, P., Anokhina, R., Longworth, C., Randall, B., Marslen-Wilson, W.D., 2002. Dissociations in processing past tense morphology: neuropathology and behavioral studies. *J. Cogn. Neurosci.* 14, 79–94.
- Ullman, M., 2001a. A neurocognitive perspective on language: the declarative/procedural model. *Nat. Rev., Neurosci.* 2, 717–726.
- Ullman, M.T., 2001b. The neural basis of lexicon and grammar in first and second language: the declarative/procedural model. *Bilingualism: Lang. Cogn.* 4, 105–122.
- Ullman, M.T., 2004. Contributions of memory circuits to language: the declarative/procedural model. *Cognition* 92, 231–270.
- Ullman, M., Corkin, S., Coppola, M., Hickok, G., Growden, J., Koroshetz, W., 1997. 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.
- Vigliocco, G., Warren, J., Siri, S., Arciuli, J., Scott, S., Wise, R., 2006. The role of semantics and grammatical class in the neural representation of words. *Cereb. Cortex* 17, 1790–1796.
- Wartenburger, I., Heekeren, H.R., Abutalebi, J., Cappa, S.F., Villringer, A., Perani, D., 2003. Early setting of grammatical processing in the bilingual brain. *Neuron* 37, 159–170.
- Weber-Fox, C., Neville, H.J., 1996. Maturation constraints on functional specializations for language processing: ERP and behavioral evidence in bilingual speakers. *J. Cogn. Neurosci.* 8, 231–256.
- Wise, R.J., Greene, J., Buchel, C., Scott, S.K., 1999. Brain regions involved in articulation. *Lancet* 353, 1057–1061.
- Zatorre, R.J., Meyer, E., Gjedde, A., Evans, A.C., 1996. PET studies of phonetic processing of speech: review, replication, and reanalysis. *Cereb. Cortex* 6, 21–30.
- Zubin, D.A., Koepcke, K.M., 1981. Gender: a less than arbitrary grammatical category. In: Hendrick, A., Masek, C.A., Miller, M.F. (Eds.), *Papers from the Seventeenth Regional Meeting, Chicago Linguistic Society R. Chicago Linguistic Society, Chicago*, pp. 439–449.