Previous behavioral and electrophysiological studies have shown dissociation between consonants and vowels. We used functional magnetic resonance imaging to investigate whether vowel and consonant processing differences are expressed in the neuronal activation pattern and whether they are modulated by task. The experimental design involved reading aloud and lexical decision on visually presented pseudowords created by transposing or replacing consonants or vowels in words. During reading aloud, changing vowels relative to consonants increased activation in a right middle temporal area previously associated with prosodic processing of speech input. In contrast, during lexical decision, changing consonants relative to vowels increased activation in a right middle frontal area associated with inhibiting go-responses. The task-sensitive nature of these effects demonstrates that consonants and vowels differ at a processing, rather than stimulus, level. We argue that prosodic processing of vowel changes arise during self-monitoring of speech output, whereas greater inhibition of go-responses to consonant changes follows insufficient lexico-semantic processing when nonwords looking particularly like words must be rejected. Our results are consistent with claims that vowels and consonants place differential demands on prosodic and lexico-semantic processing, respectively. They also highlight the different types of information that can be drawn from functional imaging and neuropsychological studies.

**Keywords:** consonants and vowels, fMRI, lexico-semantic processing, prosodic processing, transposed letters, visual word recognition

**Introduction**

Recent neuropsychological evidence suggests that consonants and vowels, the building blocks of words, are functionally distinct and engage different neuronal systems such that the representation of one can be damaged while the other remains intact (Cubelli 1991; Caramazza et al. 2000; Cotelli et al. 2003; Miceli et al. 2004; Tainturier and Rapp 2004). The proposal of Caramazza et al. (2000) is based on the performance of 2 aphasic patients, who were asked to repeat a large number of words and showed contrasting patterns of errors when producing vowels and consonants: 1 patient made 3 times as many errors in vowels than in consonants, whereas the other patient made 5 times as many errors in consonants than in vowels. Curiously, this double dissociation was found again recently in the spelling abilities of 2 other patients. Cotelli et al. (2003) reported a dyssynergic patient who made significantly more errors on vowels (errors on 13.5% of all vowels) than consonants (errors on 2% of all consonants). See also Ferreres et al. (2003) for a selective impairment for vowels in reading. In contrast, Miceli et al. (2004) reported another dysgraphic individual with a selective impairment for consonants (98.8% of incorrectly spelled letters are consonants).

Behavioral evidence has also shown processing differences between vowels and consonants. Recent research suggests that differences arise at the level of visual-word perception (Berent and Perfetti 1995; Lee et al. 2001, 2002; Carreiras et al. 2007) as well as auditory speech perception (Boatman et al. 1997; Bonatti et al. 2004). Interestingly, consonant information constrains lexical selection more strongly than vowel information. van Ooijen (1996) demonstrated that when English-speaking subjects are instructed to change 1 phoneme, for example, in a nonword to make it a word, they are more likely to alter a vowel than a consonant (zebra becomes zebra, rather than cobra). This phenomenon is independent of the specific phonemic repertoire of a language (Cutler et al. 2000). For example, it occurs in speakers of Spanish, which has very few vowels and thus an unbalanced consonant to vowel ratio, and in speakers of Dutch, where the consonant to vowel ratio is quite balanced because of the large number of vowels.

Other studies have demonstrated that the “transposed-letter confusability effect,” is different for consonants and vowels. There is substantial empirical evidence, obtained from different paradigms, that shows that transposed-letter nonwords tend to be misperceived as their corresponding base words (CHOLOCA TE being read as CHOCOLATE) (Perea and Lupker 2004; Perea and Carreiras 2006a, 2006b; Duñabeitia et al. 2007). For instance, when the relationship between the transposed-letter nonwords and their corresponding base words is tested via a masked priming procedure (e.g., retosuración-REvolución), there is a facilitative transposed-letter priming effect relative to an orthographic control in which the 2 letters that are transposed in the experimental condition are replaced in the control condition (e.g., retosuración-REVOLUCIÓN). Interestingly, Perea and Lupker (2004) found significant masked priming effects for consonant transpositions (retosuración-REvolución vs. retosuración-REvolución), but not for vowel transpositions (revulación-REVOLUCIÓN vs. revulación-REVOLUCIÓN). Differences between consonants and vowels were also found with a single-presentation lexical decision task in which subjects are presented with words and pseudowords created by either transposing or replacing 2 internal letters (Perea and Lupker 2004; Perea and Carreiras 2006a). Transposed-pseudowords created by transposing 2 nonadjacent consonants activate their base words to a considerable degree (45% vs. 5% of errors of misclassifying words the transposed-letter condition and its replaced letters control, respectively), whereas effects for transposing 2 nonadjacent vowels relative to the appropriate orthographic replaced letters control are smaller (25% vs. 5% of errors for the transposed-letter condition and its replaced letters control, respectively).
condition and its control, respectively). The increased latencies and false positives for transposed-consonant pseudowords arise because these stimuli are even more ‘word-like’ than transposed-vowel pseudowords. Thus, transposed-consonant pseudowords result in more lexical competition than transposed vowels.

To explain differences in vowel and consonant processing, Nespor et al. (2003) proposed that although the main role of consonants concerns the lexicon, the main role of vowels is that of allowing the identification of the rhythmic class of a particular language as well as of specific properties of its syntactic structure. This was based on evidence that vowel alternation concerns duration, pitch, and intensity, which are in different degrees responsible for prosody, whereas consonant alternation concerns different manners and places of articulation that are crucial to the detection of words in continuous speech. Indeed, Bonatti et al. (2004; see also Peña et al. 2002; Nespor et al. 2003) demonstrated that participants appear unable to use transitional probabilities between successive vowels to find words in an artificial stream of continuous speech, even though they have no difficulty doing so using transitional probabilities between successive consonants. In contrast, both the rhythm and the melody of an utterance largely rest on vowels. Languages can therefore be classified into different rhythmic groups based on the percentage of vowels in the speech stream and the regularity with which vocalic intervals occur (Ramus et al. 1999). Moreover, the perception of these different rhythmic classes enables 3- or 4-day-old infants to discriminate speech in 2 different languages (Mehler et al. 1996; Ramus et al. 1999). Interestingly, Semitic languages attest to the role of consonants in making lexical distinctions. In these languages, lexical roots are formed exclusively by consonants, whereas vowels are inserted to indicate morphological patterns (McCarthy 1985). For instance, in Hebrew, most words can be decomposed into 2 abstract morphemes: a tri-consonantal root, which represents the core meaning of the word, and a word-pattern, which can be a sequence of vowels and/or consonants and represents morpho-syntactic information.

With respect to the anatomical location of consonant-vowel dissociation, there have been very few studies. The neuro-psychological reports only offer vague descriptions of lesions in left temporal, parietal and fronto-parietal regions or bilateral parietal cortex (Caramazza et al. 2000). However, there is no clear dissociation between the lesions associated with vowel or consonant differences. Electrophysiological evidence suggests anterior-posterior dissociation for consonants and vowels, respectively. Specifically, Carreiras et al. (2007) demonstrated that correct no responses to pseudowords during lexical decision evoked N400 effects in anterior and middle regions when consonants are transposed but in middle and posterior regions when vowels are transposed. However, there was no clear lateralization associated with these effects. To our knowledge, there is only 1 functional imaging study that compared vowel and consonant processing (Sharp et al. 2005). Here, participants were asked to generate real words from heard pseudowords created by the substitution of either a vowel or consonant. When consonants needed to be substituted, word generation was more difficult and left inferior frontal activation was higher. Critically, however, there was no increase of activation for vowels relative to consonants.

The apparent absence of vowel-specific processing in the study by Sharp et al. (2005) may relate to the speech production task. In functional imaging studies of speech perception, there is some evidence to suggest that vowel processing shares neural resources with prosodic processing. For instance, the right temporal cortex has been associated with vowel relative to nonspeech processing (Obleser et al. 2006; Uppenkamp et al. 2006), changes in spectral envelope that are crucial for vowel identification (Warren et al. 2005), prosodic processing (Hesling et al. 2005), and sentence level suprasegmental information, namely speech melody, accentuation, and boundary marking (Meyer et al. 2002). Additionally, several recent neuropsychological models have suggested a bilateral cerebral implementation of speech perception (Hickok and Poeppel 2000; Friederici 2002) with the right hemisphere playing a prominent role in processing intonation (Dologil et al. 2002; Poeppel 2003; Friederici and Alter 2004) and suprasegmental sentence level processing (e.g., Gandour et al. 2000, 2004; Meyer et al. 2002; Zatorre et al. 2002).

In summary, neuropsychological and electrophysiological evidence indicates a double dissociation in the processing requirements for consonants and vowels, and behavioral evidence shows differences between consonant and vowel processing as well, but the neuronal systems underlying these effects are not known. Structure-function relationships are notoriously difficult to establish from neuropsychological investigations. Likewise, the available electrophysiological evidence suggesting anterior-posterior dissociation in consonant and vowel processing (Carreiras et al. 2007) has poor spatial resolution. Our anatomical predictions are therefore derived indirectly on the basis of cognitive theory. Specifically, the work of Nespor et al. (2003) predicts that vowel alternation will impact upon neuronal systems involved in processing prosody, whereas consonant alternation will impact upon neuronal systems involved in lexical processing. Prosodic processing is typically associated with right hemisphere activation (see above) and lexical processing is typically associated with the left hemisphere activation. Critically, however, we predict that a double dissociation in activation associated with consonant and vowel processing will only be apparent in tasks that tap into the relevant processes.

The present fMRI study examined consonant and vowel dissociations during 2 different visual word processing tasks: reading aloud and lexical decision. This allowed us to investigate whether differences between consonant and vowel processing depend on whether speech production is required or not. In line with previous experiments, we also compared whether the effect of vowel versus consonant processing was influenced by the type of letter manipulation. To this end, pseudowords were created by transposing or replacing 2 nonadjacent letters. For example (PRIVAMERA) from the word PRIMAVERA “SPRING” and their replaced consonant controls (PRISALERA) as well as transposed letter-vowel pseudowords (PRIMEVARA) and their replaced consonant controls (PRIMOVURA). On the basis of the previous findings discussed above, we predicted that vowel and consonant changes would produce dissociation in brain activation, which should be greater in more anterior and/or left hemisphere regions for consonants and greater in more posterior and/or right hemisphere regions for vowels. In addition, we predicted that effects would be stronger for the transposed versus replaced conditions, irrespective of task.

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Method

Participants

A total of 20 right-handed volunteers (13 females), native speakers of Spanish, aged between 22 and 46 years participated in the study. All subjects had normal or corrected vision with no history of neurological disorders or reading impairments. This project has been approved by the "National Hospital for Neurology and Neurosurgery and the Institute of Neurology Joint Ethics Committee," Ethics code 00/N032. Informed consent was obtained from each participant.

Design and Task

The 2 x 2 x 2 factorial design included 4 different pseudoword stimuli by combining 2 factors: the type of letters changed (consonants vs. vowels) and the type of change (transposition vs. replacement of 2 nonadjacent letters). The 4 types of pseudowords were: 1) nonadjacent transposed consonant (TLC), and 2) its corresponding control (RLC) of replaced consonants—for example, PRIVAMER and PRISARERA, 3) nonadjacent transposed vowel (TLv), and 4) its corresponding control (RLv) of replaced vowels—for example, PRIMEVARA and PRIMOVURA, all from the base word PRIMAVERA (SPRING). The 3rd factor was the task: lexical decision versus reading aloud. For the lexical decision task they were instructed to make 1 finger press response to indicate that the letter string was a real word and another finger press response to indicate that the letter string was not a word. In the reading aloud task, participants were instructed to read each stimulus, whispering their sounds into a microphone. They wore headphones to reduce auditory input from scanner noise and from hearing their own voice.

In addition to the pseudoword conditions, the design included an equal number of words and task-specific baseline conditions that involved viewing strings of false fonts, consonants, or vowels. Only the baseline involving strings of false fonts will be considered in this paper. For the reading aloud baseline, participants were instructed to whisper the Spanish word FALSO "false" and accuracy was recorded. In the decision-making baseline, participants were instructed to make a yes/no response to indicate that the stimulus was not a word. Accuracy and response time were recorded. These baselines were included to control for sensorimotor processing and to determine whether differences between conditions are due to increases or decreases in activation. That is, to determine whether the experimental conditions produced increases or decreases of the blood oxygen level-dependent (BOLD) signal with respect to the baseline conditions.

Data were acquired in 4 different runs using a mixed block and event-related design. Blocking stimuli maximizes sensitivity and minimizes task-switching costs (Friston et al. 1999). Randomizing stimuli minimizes strategic effects. In total, there were 32 blocks within a run and 128 blocks (32 x 4) across runs. In half the blocks, 7 pseudowords of the same type were randomly intermixed with 7 words, with 1 stimulus (in Arial 80) presented every 1.8 s. These blocks of words and pseudowords alternated with an equal number of baseline blocks. Within each baseline block, 7 strings of false fonts, 7 strings of consonants, or 7 strings of vowels were presented, 1 string at a time every 1.8 s (as in the pseudoword/word blocks). The baseline blocks were therefore half the length of the pseudoword blocks. One task (lexical decision or reading aloud) was performed during the 1st and the last 8 blocks of the run (2 blocks for each of the 4 conditions in counterbalanced order), whereas the other task was performed during the other 16 blocks in the middle of the run (2 blocks for each of the 4 conditions in counterbalanced order). In the 1st 2 runs, all conditions were fully counterbalanced within and between subjects. In the 3rd and the 4th runs, the same stimuli were presented again, but with a different task and in a different order.

Each trial started with the fixation point—a cross in the middle of the screen—that lasted for 1500 ms and then the corresponding stimuli for 500 ms. Immediately before each block a brief instruction—the Spanish words LEE "read" for the reading aloud task or ¿PALABRA? "word?" for the lexical decision task—was displayed for 2500 ms. To remind the participants of the task for each particular block. In addition, for each participant these brief instructions together with the corresponding stimuli of the block were presented in red for 1 task, whereas in black for the other task. The assignment of the colors to the 2 tasks was counterbalanced across participants.

Stimuli

A list of 224 words selected from a Spanish standard corpus (Sebastián-Gallés et al. 2000) was used as the base words for the 4 pseudoword conditions: TL-consonant pseudoword and its corresponding control—for example, PRIVAMER and PRISARERA, TL-vowel pseudoword and its corresponding control—for example, PRIMEVARA and PRIMOVURA, all from the base word PRIMAVERA (SPRING). The pseudowords had, on average, very few neighbors (range 0–1) and of low frequency. In all cases, the 1st syllable of the base word remained unchanged. Four lists of materials were constructed so that if the TL-consonant pseudoword PRIVAMER appeared in one list, its orthographic control (PRISARERA) would appear in another list, the TL-vowel pseudoword (PRIMEVARA) in another list, and its orthographic control (PRIMOVURA) in another list. Different groups of participants were used for each list. An additional set of 224 words 7–11 letters long (mean frequency per million words: 69, range: 16–841), which were different from the base words for the 4 pseudoword conditions were also included.

Data Acquisition

A Siemens 1.5-T scanner was used to acquire $T_2^*$-weighted echo planar images with BOLD contrast. Each echo planar image comprised 35 axial slices of 2-mm thickness with 1-mm slice interval and 3 x 3-mm in-plane resolution. Volumes were acquired with an effective repetition time of 3.15 s/volume and the first 6 (dummy) volumes of each run were discarded to allow for $T_1$ equilibration effects. A total of 864 volume images were taken in 4 separate runs. After the 4 functional runs, a $T_1$-weighted anatomical volume image was acquired from all participants.

Data Analysis

Data were analyzed with statistical parametric mapping (SPM2: Wellcome Department of Imaging Neuroscience, London, UK; http://www.fil.ion.ucl.ac.uk), running under Matlab 6.5.1 (Mathworks, Sherborn, MA). All volumes from each participant were realigned and unwarped (Jesper et al. 2001), adjusting for residual motion-related signal changes. The functional images were spatially normalized (Friston, Ashburner, et al. 1995) to a standard MNI-305 template using nonlinear basis functions. Functional data were spatially smoothed with a 6-mm full width half maximum isotropic Gaussian kernel, to compensate for residual variability after spatial normalization and to permit application of Gaussian random-field theory for corrected statistical inference (Friston, Holmes, et al. 1995). At the 1st level, data were analyzed in a participant-specific fashion, with each pseudoword type, each baseline condition and words modeled separately and convolved with a canonical hemodynamic response function. The data were high-pass filtered using a set of discrete cosine basis functions with a cut-off period of 128 s.

Statistical Analysis

The contrasts of interest were each of the 8 pseudoword conditions (2 tasks: lexical decision and reading aloud) x 2 types of letter change: [consonants vs. vowels] x 2 types of change: [transposed-replaced]) relative to the false fonts specific baseline. The other baseline conditions will not be discussed here. These contrast images were then entered into a 2nd level analysis of variance (ANOVA) to permit inferences about condition effects across participants (i.e., a random-effects analysis; Holmes and Friston 1998).

From this 2nd level analysis, we focus on the effects of consonants versus vowels, 1) over task and for each task separately and 2) over letter change type (transposed versus replaced) and each letter change type separately. Details of the relevant interactions are reported in the tables. Activation over and above the baseline conditions is illustrated in the figures.
Results

Behavioral Data
The focus of this paper is entirely on the effect of processing different types of pseudowords. Before reporting these effects, we note that word stimuli were fully controlled across the different pseudoword conditions and there were no significant differences in the behavioral responses to words presented with different types of pseudowords. Turning now to the pseudoword effects, we note that the pattern of behavioral effects reported below is consistent with that reported in previous studies that randomized rather than blocked the different types of pseudowords. The mean response times and error percentages for pseudowords during lexical decision and the error percentages for pseudowords during reading aloud are presented in Table 1. ANOVAs on mean response latencies and error rates to pseudoword targets for lexical decision and for error rates only in the reading aloud task were conducted based on the 2 (type of letter: consonants vs. vowels) by 2 (type of change: transposed vs. replaced) design.

Lexical Decision
Incorrect responses (9.6%) were excluded from the latency analysis. In addition, in order to avoid the influence of outliers, reaction times more than 2.0 standard deviations above or below the mean for that participant in each condition were excluded.

Pseudowords created by transposing/replacing 2 consonants had slower latencies than pseudowords created by transposing/replacing 2 vowels, $F_{1,19} = 6.2, P < 0.05$. Pseudoword targets created by transposing 2 nonadjacent letters were responded to 84 ms slower than pseudowords created by replacing those 2 letters, $F_{1,19} = 57.4, P < 0.0001$. Importantly, the interaction between the 2 factors was significant, $F_{1,19} = 6.3, P < 0.05$. Post hoc comparisons then confirmed that differences between consonants and vowels were found in the transposed condition ($F_{1,19} = 8.7, P < 0.01$) but not in the replaced condition ($F_1 < 1$). In addition, the difference between the transposed-letter pseudowords and the replacement-letter pseudowords was greater for the transpositions involving consonants than for the transpositions involving vowels (104 vs. 63 ms). Differences between transposed and replaced were significant both for consonants, $F_{1,19} = 45.7, P < 0.0001$, and for vowels, $F_{1,19} = 28.9, P < 0.0001$.

The data pattern for the errors was the same as for the reaction times. Thus, the ANOVA on the error data showed that there were more errors to pseudowords created by transposing/replacing 2 consonants than to pseudowords created by transposing/replacing 2 vowels, $F_{1,19} = 32.5, P < 0.0001$. There were also significantly more errors to transposed-letter pseudowords than to replaced-letter pseudowords, $F_{1,19} = 25.1, P < 0.0001$. The interaction of the 2 factors was also significant, $F_{1,19} = 25.4, P < 0.0001$. Post hoc tests confirmed significant differences between consonants and vowels in the transposed condition, $F_{1,19} = 34.8, P < 0.0001$, but not in the replaced condition, $F_1 < 1$. In addition, differences between transposed and replaced were significant both for consonants, $F_{1,19} = 27.5, P < 0.0001$, and vowels, $F_{1,19} = 17, P < 0.0001$, although the transposition-letter effect was substantially larger for consonants (22.1%) than for vowels (10.4%).

Reading Aloud
The ANOVA on the error data (including both bad pronunciations of pseudowords and lexicalizations) showed that there were more errors to pseudowords created by transposing/replacing 2 consonants than to pseudowords created by transposing/replacing 2 vowels, $F_{1,19} = 25.6, P < 0.0001$. There were also significantly more errors to transposed-letter pseudowords than to replaced-letter pseudowords, $F_{1,19} = 57.3, P < 0.0001$. The interaction of the 2 factors was also significant, $F_{1,19} = 22.7, P < 0.0001$. Post hoc tests confirmed significant differences between consonants and vowels in the transposed condition, $F_{1,19} = 27.0, P < 0.0001$, but not in the replaced condition, $F_1 < 1$. In addition, differences between transposed and replaced were significant both for consonants, $F_{1,19} = 48.9, P < 0.0001$, and vowels, $F_{1,19} = 44.7, P < 0.0001$, although the transposition-letter effect was substantially larger for consonants (26.6%) than for vowels (12%).

Consistent with the previous experiments, transposed-letter pseudowords created by transposing 2 nonadjacent consonants seem to activate their base word to a considerable degree.

fMRI Data
Vowels > Consonants
A main effect of transposed/replaced vowels relative to transposed/replaced consonants was observed in the right superior temporal sulcus (STS) and in a right sensorimotor area (see Table 2 and Fig. 1 for details). The effect in the right STS was stronger during reading aloud than lexical decision. The effect in the right sensorimotor area reflected greater deactivation for consonants rather than increased activation for vowels and was not significant when considering correct responses only. Therefore, we only discuss the effect of vowels versus consonants in the right STS where activation was observed for vowels relative to consonants and baseline.

Consonants > Vowels
The only significant effect of consonants relative to vowels was in the right middle frontal cortex for transposed stimuli during lexical decision, see Table 3 and Figure 2 for details. Within the left inferior frontal cortex, the corresponding effect did not reach significance ($-48, 28, 26, Z = 2.4, k = 36; -38, 26, 36, Z = 2.1, k = 5$).

Discussion
Vowels and consonants produced different effects on regional brain activation. Activation in the right STS was higher for

<table>
<thead>
<tr>
<th>Table 1</th>
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<tbody>
<tr>
<td>Means and standard deviations (within parentheses) of lexical decision times (in ms) and percentage of errors (in italics) of lexical decision and reading aloud for the 4 type of pseudowords</td>
</tr>
<tr>
<td>Type of change</td>
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<tr>
<td><strong>Lexical decision</strong></td>
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<td>Consonants</td>
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<tr>
<td>Vowels</td>
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<tr>
<td><strong>Reading aloud</strong></td>
</tr>
<tr>
<td>Consonants</td>
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<td>Vowels</td>
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pseudowords created by changing vowels than consonants particularly during the reading aloud task. In contrast, right middle frontal activation was higher for pseudowords created by transposing consonants than vowels, but only in the lexical decision task. Thus, we have identified vowel and consonant differences that are highly dependent on task and only significant in the right hemisphere. Below we will discuss these effects in relation to other functional neuroimaging and neuropsychological studies but 1st we consider the implications of the behavioral data.

**Behavioral Data**

As predicted, pseudoword targets created by transposing 2 nonadjacent letters resulted in slower, less accurate responses than pseudowords created by replacing 2 letters. Interestingly, the difference between the transposed-letter pseudowords and

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**Figure 1** Left part: Axial, coronal, and sagittal sections (left part) for the contrast vowels > consonants in the right STS. All contrasts depicted at $P < 0.001$ uncorrected. Right part: Graphs of contrast estimates and 90% confidence intervals. TL, transposed letters; RL, replaced letters; CO, consonants; VO, vowels.

**Table 2**

Vowels > consonants

<table>
<thead>
<tr>
<th>Region and effect</th>
<th>$x$</th>
<th>$y$</th>
<th>$z$</th>
<th>Including errors</th>
<th>Excluding errors</th>
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<tbody>
<tr>
<td></td>
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<td></td>
<td></td>
<td>LD and reading</td>
<td>Reading</td>
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<td></td>
<td>Z</td>
<td>Vols</td>
<td></td>
<td>Z</td>
<td>Z</td>
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<tr>
<td>Right STS</td>
<td>46</td>
<td>-36</td>
<td>-6</td>
<td>4.8 101 2.6</td>
<td>5.0 103 3.5</td>
</tr>
<tr>
<td>Right sensorimotor</td>
<td>58</td>
<td>-16</td>
<td>50</td>
<td>4.4 169 3.6 6</td>
<td>4.2 51</td>
</tr>
</tbody>
</table>

**Note:** Results of analysis including errors are reported in the upper part, and excluding errors in the lower part. $x,y,z$ = coordinates of local maxima. Z = Z scores. Voxels = number of voxels at $P < 0.001$ uncorrected. Z scores and cluster size are reported in **bold** if they are significant in height or extent at $P < 0.05$ after family-wise correction for multiple comparisons across the whole brain. Those in italics were reported at $P < 0.05$ uncorrected for completion. All others are significant at $P < 0.001$ uncorrected.

**Table 3**

Effects of consonants > vowels for transposed-letter pseudowords only in the lexical decision task including errors

<table>
<thead>
<tr>
<th>Region and effect</th>
<th>$x$</th>
<th>$y$</th>
<th>$z$</th>
<th>Transposed in lexical decision</th>
<th>Interaction type of letter × type of change in lexical decision</th>
<th>Interaction letter × task in Transposed</th>
<th>3-way interaction</th>
</tr>
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<tr>
<td></td>
<td>$x$</td>
<td>$y$</td>
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<td>Z Vols</td>
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<td>Including errors</td>
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<tr>
<td>Right middle frontal</td>
<td>50</td>
<td>26</td>
<td>28</td>
<td>4.4   165</td>
<td>3.3  63</td>
<td>4.5  84</td>
<td>3.2</td>
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<tr>
<td>Right middle frontal</td>
<td>38</td>
<td>32</td>
<td>36</td>
<td>4.1</td>
<td>4.4</td>
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<td>Excluding errors</td>
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</tr>
<tr>
<td>Right middle frontal</td>
<td>54</td>
<td>28</td>
<td>26</td>
<td>3.2   10</td>
<td>3.2   2</td>
<td>4.4  51</td>
<td>3.6</td>
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<tr>
<td>Right middle frontal</td>
<td>38</td>
<td>32</td>
<td>36</td>
<td>3.5   40</td>
<td>3.6  14</td>
<td>3.7  17</td>
<td>3.2</td>
</tr>
</tbody>
</table>

**Note:** $x,y,z$ = coordinates of local maxima. Z = Z scores. Voxels = number of voxels at $P < 0.001$ uncorrected. Z scores and cluster size are reported in **bold** if they are significant in height or extent at $P < 0.05$ after family-wise correction for multiple comparisons across the whole brain. Those in italics were reported at $P < 0.05$ uncorrected for completion. All others are significant at $P < 0.001$ uncorrected.
the replaced-letter pseudowords was greater for the transpositions involving consonants than for the transpositions involving vowels. It is important to note that the very high error rates for the transposed-letter pseudowords seem to reflect the high degree of similarity between the transposed-letter pseudowords and their corresponding base words. Indeed, for any skilled reader of Spanish, the transposed-letter pseudoword DEYASUNO seems to activate its base word DESAYUNO (breakfast), which makes it more difficult to suppress the articulation of DESAYUNO when naming DEYASUNO under time pressure or to reject the possibility that the DEYASUNO is a word during lexical decision. The high error rate for transposed letters replicates other experiments that used different sets of items during lexical decision task (Perea and Lupker 2004; Perea and Carreiras 2006a) or reading aloud (Perea and Estevez Forthcoming).

The reading aloud task involves overt speech production and the lexical decision task might engage some covert production mechanism. Thus, it is important to mention that the transposed-letter effects can also be accommodated in a very simple and elegant mechanism proposed to ensure the correct sequencing of word utterances. Shattuck-Hufnagel (1979) proposed a framework to guide the serial ordering of phonological segments from a short-term store of lexical candidates for the utterance, by means of a scan-copier mechanism. The proposal is based on a distinction between structure and content. When we speak, we produce an abstract frame for the upcoming word that is copied into a buffer. The frame specifies the syllabic structure of the word (in terms of onset, nucleus, and coda). A scan-copier device works through a syllabic frame in left-to-right serial order selecting phonemes to insert into each position of the frame. As a phoneme is selected, it is checked off. Thus, if the scan-copier selects an incorrect phoneme but marks off that phoneme as used, we will end up with a phoneme exchange error such that the final stimulus could be a transposed-letter pseudoword, such as those we manipulated in the present experiment. The model does not make an explicit distinction between consonants and vowels, but they may arise naturally from the distinction present in the model between onset, nucleus, and codas. For instance, word onsets form a special set of planning elements, addressed later in the serial ordering process, and can easily become mis-selected from each other.

**Increased Activation for Vowels over Consonants**

The right STS area (46–36–6) that we found to be more activated for vowel changes than consonant changes is very close to the area that Uppenkamp et al. (2006) have previously associated with vowel relative to nonspeech sounds during speech perception (48–34–6). This suggests that vowel processing during visual word processing tasks modulates activation in regions that are also engaged with vowel processing during auditory speech processing. Moreover, Hesling et al. (2005) have associated the same region (44–34–6) with prosody in auditory speech processing. The similarity in the effects of vowel and prosody processing is consistent with the proposal that vowels increase prosodic processing (see Nespor et al. 2003) that is in turn associated with right hemisphere processing (Doggel et al. 2002; Poeppel 2003; Friederici and Alter 2004). Likewise, the location of the vowel effect in the posterior STS is consistent with event-related potential (ERP) findings that vowel-specific processing is more posterior than consonant-specific processing (Carreiras et al. 2007).

Notably, we observed increased activation in the right STS for vowels relative to consonants during visual word processing tasks, with this effect being stronger during reading aloud than lexical decision. This suggests that an important part of the effect may arise at the level of perceiving the sound of vowels that have been changed or swapped from real words to create a pseudoword, either through self-monitoring speech output and/or inner speech. Vowel changes alter prosodic information more than consonant changes. What is striking is that the change or swapping of vowels as compared with consonants produced activation in the vicinity of areas that have been identified in the auditory processing of vowels, or vowel properties, such as the spectral envelope contour, or even in suprasegmental prosody, in which vowel alternation is involved according to the linguistic hypothesis of Nespor et al. (2003). Thus, our results suggest that even written vowels modulate brain activation associated with prosodic processing.

**Increased Activation for Consonants Relative to Vowels**

The effect of changing consonants relative to vowels was specific to 1 task (lexical decision) and to 1 type of letter manipulation (transposed, not replaced; see Fig. 2). Therefore, it is quite unlikely that this brain region is specifically involved in consonant representations. In contrast, the increased right middle frontal activation for transposed consonants in the lexical decision task is more likely to reflect inhibitory control processes that compensate for insufficient lexico-semantic processing. Indeed, the right frontal cortex has long been linked to cognitive inhibition that is needed to suppress “go” responses (e.g. Sasaki et al. 1989; Konishi et al. 1998; Strik et al. 1998; Aron et al. 2004; Simmonds et al. Forthcoming). In the present experiment, during lexical decision, subjects must
consider whether a letter string is a word and inhibit word responses to word-like pseudowords. Transposed-letter consonant pseudowords are more similar to words than the transposed vowel or the replaced-letter pseudowords, as the error rates and reaction times show (see also Perea and Lupker 2004; Perea and Carreiras 2006a). Thus, the rejection reaction is more difficult in the case of transposed consonants than in any other experimental condition, and right middle frontal activation is also higher. Further support for the role of right middle frontal activation in no-go responses comes from our observation that the increase in right middle frontal activation for pseudowords with transposed consonants was only present during lexical decision, not during reading aloud when pseudowords are pronounced, not rejected. This distinguishes the rejection process from inhibitory processes that are common to the lexical decision and naming tasks, for example, those that cause high errors for transposed consonants.

When trials with errors were removed from the analyses, there was still evidence for increased right middle frontal activation during lexical decision on pseudowords with transposed consonants. In this case, the correct trials are associated with successful rejection of the word that depends on suppressing a no-go response. In summary, cognitive processes for correct trials are different for reading and lexical decision with right frontal activation reflecting no-go suppression in lexical decision, particularly when pseudowords with transposed consonants look very like words. Notably, the effect of consonant relative to vowel processing was expressed in right rather than left hemisphere areas as we predicted. However, the anterior location of the effect in frontal cortex is consistent with the predictions from the ERP data (Carreiras et al. 2007).

Our results also highlight the different types of information that neuropsychological and functional imaging studies can provide. To illustrate these differences, we consider the following hypothetical position:

1. During auditory and written speech perception, lexico-semantic processing is more dependent on consonants than vowels, whereas prosodic processing is more dependent on vowels than consonants (Nespouf et al. 2003).
2. The production of consonants is more dependent on lexico-semantic mediation than the production of vowels, whereas the production of vowels is more dependent on prosodic representations than the production of consonants.
3. Lexico-semantic processing is lateralized in the left hemisphere but prosodic processing requires the integration left and right hemisphere brain areas.

Given these assumptions, the neuropsychological predictions are that

1. Damage to left hemisphere lexico-semantic regions would result in more consonant than vowel errors during production (Caramazza et al. 2000; Cotelli et al. 2003); and changes to consonants in visually or auditorily presented words would be more difficult to perceive than changes to vowels.
2. Damage to left or right hemisphere prosodic processing areas will impair the perception and production of vowels more than the perception or production of consonants.

Finally, how might vowel and consonant processing differences be reflected in functional neuroimaging experiments? Without real or virtual lesions (e.g., using transmagnetic stimulation), neurologically normal participants are likely to engage both lexico-semantic and phonological/prosodic processing during speech perception and production tasks. Therefore, differences in consonant and vowel processing are only likely to be revealed during paradigms that differentially weight 1 type of process relative to another. It is not easy to manipulate the type of errors that neurologically normal subjects will make. Therefore, in the current study, we manipulated consonants and vowels within visually presented pseudoword stimuli. According to the above theoretical position

1. Consonant changes affect lexico-semantic processing and might therefore be expressed as activation changes (increases or decreases) in left hemisphere lexico-semantic areas. Alternatively, there may be no change in the level of lexico-semantic activation but a downstream effect on behavioral responses. For example, we found transposed consonants increased the number of pseudowords that were incorrectly read aloud or accepted as words during lexical decision. This is consistent with insufficient semantic processing to distinguish word-like pseudowords from the real words they resemble. Likewise, correct nonword categorization of pseudowords with transposed consonants resulted in longer lexical decision times and increased activation in an area associated with no-go responses (see above). This suggests compensatory processes were at work during lexical decision to overcome insufficient lexico-semantic information at an earlier level of processing.
2. Vowel position changes affect prosodic processing and might therefore be expressed as activation changes in left or right hemisphere prosodic processing areas. In our study of written pseudoword processing, vowel changes increased activation in right hemisphere areas associated with auditory perception of prosodic structure. This suggests that the observed effect occurs very late in the processing stream, perhaps at the level of self-monitoring speech output/inner speech to check whether the prosodic qualities of the produced speech match the visual input. This would explain why activation for vowel compared with consonant changes was stronger during reading aloud than lexical decision.

**Conclusion**

In sum, the reported experiments have shown different activation patterns for vowels and consonants, which were task specific. Therefore, the observed dissociation for vowels and consonants appears to be process specific rather than stimulus specific. Although left hemisphere activation in our visual word processing study was not significantly affected by consonant versus vowel changes, this does not rule out the possibility that left hemisphere differences would be observed for consonants versus vowels in other types of task such as auditory word repetition (Caramazza et al. 2000) or spelling (Cotelli et al. 2003; Miceli et al. 2004). Likewise, although we show task-dependent effects of consonant versus vowel processing during visual processing tasks, this does not rule out the possibility that consonant versus vowel differences may be independent of task in the auditory domain. Importantly, the area showing increased activation for written vowel changes is very close to areas reported to be activated during the auditory...
processing of vowels and of suprasegmental prosody. Thus, our data add more empirical evidence to a functional distinction between vowels and consonants, and suggest that vowel processing may influence similar regions during auditory perception and speech production.

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