

Effect of Word and Syllable Frequency on Activation During Lexical Decision and Reading Aloud

Manuel Carreiras,^{1,2*} Andrea Mechelli,³ and Cathy J. Price⁴

¹Universidad de La Laguna, Tenerife, Spain

²Institute of Cognitive Neuroscience, University College of London, London, UK

³Institute of Psychiatry, King's College London, London, UK

⁴Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK

Abstract: This functional MRI (fMRI) study investigated the effect of lexical and syllable frequency on visual word processing during lexical decision and reading aloud. Previous research has shown a dissociation of syllable and word frequency effects in Spanish using behavioral and electrophysiological measures, suggesting that sublexical (syllabic) representations are computed and mediate the firing of lexical candidates. Here, we characterize the neuroanatomical basis of these lexical and sublexical manipulations and their dependence on task. During lexical decision, words with low vs. high lexical frequency increased activation in left frontal, anterior cingulate, supplemental motor area (SMA), and pre-SMA regions; while words with high vs. low syllable frequency increased activation in a left anterior inferior temporal region. In contrast, when the words were read aloud those with low vs. high syllable frequency increased activation in the left anterior insula, with no other significant effects. On the basis of the neuroanatomy, we propose that the contrasting effects of syllable frequency during lexical decision and reading aloud reflect two different cognitive processes in visual word processing. Specifically, words with high-frequency syllables may increase lexical competition in the inferior temporal lobe while facilitating articulatory planning in the left anterior insula. *Hum Brain Mapp* 27:963–972, 2006.

© 2006 Wiley-Liss, Inc.

Key words: visual word recognition; fMRI; syllable frequency; word frequency

INTRODUCTION

This study investigated the neural basis of lexical and sublexical processing during reading. Previous studies have

addressed this issue by comparing hemodynamic responses to words and pseudowords. According to traditional cognitive models, reading pseudowords (e.g., ROULD) depends on sublexical processing, whereas reading words with irregular spellings (e.g., CHOIR) depends on lexical processing [e.g., Coltheart et al., 1993; Marshall and Newcombe, 1973; Paap and Noel, 1991; Patterson and Morton, 1985]. By contrast, according to PDP models [e.g., Seidenberg and McClelland, 1989] both lexical and sublexical mappings are achieved with the same form of mechanism, i.e., parallel, nonlinear interactions among simple processing units. In this case, lexical and sublexical processing would not be expected to dissociate at the neural level. Instead, the expectation would be that word and pseudoword reading dissociated only to the degree to which semantic processing was involved.

Functional neuroimaging comparisons of word and pseudoword reading have not demonstrated a clear double dissociation in lexical and sublexical processing [Binder et

Contract grant sponsors: Wellcome Trust; Ministry of Education and Science; Contract grant numbers: BSO2003-01135; SEJ2004-07680-C02-02/PSIC (to M.C.); Contract grant sponsor: Secretaría de Estado de Educación y Universidades (Spain); Contract grant number: PR2004-0563 (to M.C.); Contract grant sponsor: National Institutes of Health; Contract grant number: MH64445 (to A.M.).

*Correspondence to: Manuel Carreiras, Departamento de Psicología Cognitiva, Facultad de Psicología, Universidad de La Laguna, 38205 Tenerife, Spain. E-mail: mcarreir@ull.es

Received for publication 27 September 2005; Accepted 22 December 2005

DOI: 10.1002/hbm.20236

Published online 20 April 2006 in Wiley InterScience (www.interscience.wiley.com).

al., 2003; Fiebach et al., 2002; Fiez and Petersen, 1998; Fiez et al., 1999; Hagoort et al., 1999; Herbster et al., 1997; Ischebeck et al., 2004; Mechelli et al., 2003, 2005; Paulesu et al., 2000; Price et al., 1996; Rumsey et al., 1997; Tagamets et al., 2000; Xu et al., 2001]. Although the majority of studies have shown increased left inferior frontal activation for pseudowords compared to words, this is unlikely to reflect sublexical processing because the same region is also activated by words with irregular relative to regular spellings [Fiez et al., 1999; Mechelli et al., 2005]. We recently proposed that three different inferior frontal regions are differentially activated by words and pseudowords [Mechelli et al., 2005] with 1) a ventral inferior frontal and anterior fusiform system more engaged by lexico-semantic processing; 2) a left precentral and posterior fusiform system more engaged when phonology is retrieved directly from orthography; and 3) a region in the pars triangularis that is more engaged for pseudowords and irregular words than regular words. Critically, however, this dissociation was explained in terms of semantic and phonological processing, not lexical and sublexical processing.

An alternative approach for dissociating lexical and sublexical processes involved the manipulation of lexical and sublexical frequency in polysyllabic words [see Alvarez et al., 2001; Barber et al., 2004; Carreiras et al., 1993; Conrad and Jacobs, 2004; Mathey and Zagar, 2002; Perea and Carreiras, 1998]. These studies have shown that, during lexical decision, the effect of word frequency is facilitatory and the effect of syllable frequency is inhibitory. Thus, response times are faster and N400 amplitudes are smaller when word frequency is high and syllable frequency is low. For speech production tasks, however, the effect of syllable frequency is reversed, with faster response times for high syllable frequency during reading aloud [Carreiras and Perea, 2004; Perea and Carreiras, 1998], picture naming [see Alario et al., 2004], and pseudo-word production [Cholin et al., 2006; Levelt and Wheeldon, 1994].

A number of potential explanatory factors of the syllable frequency effect have been discarded: neither bigram frequency [Carreiras et al., 1993], orthographic neighborhood density/frequency [Álvarez et al., 2001; Perea and Carreiras, 1998], or morpheme frequency [Álvarez et al., 2001] can account for the findings. To explain the inhibitory effect of high-frequency syllables during lexical decision, Carreiras et al. [1993] proposed that it reflects competition between the larger number of lexical candidates that are generated from high-frequency syllables than low-frequency syllables. In contrast, at the speech production level articulatory processing is facilitated for syllables that are in frequent use [Levelt and Wheeldon, 1994; see also Levelt, 1989; Levelt et al., 1999].

The present study used functional MRI (fMRI) to examine whether the dissociations of lexical frequency and syllable frequency observed in behavioral and electrophysiological measures can be mapped onto different areas of the brain. In addition, we investigated the interaction of these effects with task: lexical decision or reading aloud. On the basis of the

previous findings discussed above, we predicted greater activation for words with 1) low relative to high lexical frequency; 2) high relative to low syllable frequency during lexical decision; and 3) low relative to high syllable frequency during reading aloud. The hemodynamic response can provide additional details of the processing stage at which these effects are arising. First, taking into account previous fMRI findings that left inferior frontal activation is likely to be greater for low relative to high lexical frequency words. Second, if words with high-frequency syllables produce more lexical competition than those with low-frequency syllables in the lexical decision task [Carreiras et al., 1993], then we would expect increased activation within the frontal or temporal regions that have been associated with lexico-semantic processing. Third, as the facilitatory syllable frequency effect in speech production tasks has been associated with faster access to articulatory-phonetic syllable programs for high-frequency syllables, we predict that syllable effects during reading aloud will be in areas associated with articulatory planning.

PATIENTS AND METHODS

Participants

A total of 16 right-handed volunteers (6 men, 10 women), native speakers of Spanish, ages 22–46 years, participated in the study. This project was approved by the “National Hospital for Neurology and Neurosurgery and the Institute of Neurology Joint Research Ethics Committee,” Ethics code 00/N032. Informed consent was obtained from each participant.

Design and Task

The $2 \times 2 \times 2$ factorial design manipulated: task (lexical decision vs. reading aloud), word frequency (high vs. low), and syllable frequency (high vs. low). In the reading aloud task, participants were instructed to read each stimulus, whispering their sounds into a microphone. In the lexical decision task they were instructed to make finger press responses to indicate whether the letter string was a real word or not. In addition to the eight activation conditions, the design included two task-specific baseline conditions that involved viewing strings of false fonts. For the reading aloud baselines, participants were instructed to whisper the Spanish word FALSO, “false.” For the lexical decision baseline, the participants made a keypad response to indicate that the stimulus was not a word. Accuracy was recorded in the reading aloud task. Dubious cases were scored as errors. Accuracy and response time were recorded in the lexical decision task.

All 10 activation and baseline conditions were counterbalanced within each participant.

Data were acquired in two different runs, each with 32 blocks of items. Half the blocks (henceforth, lexical blocks) presented strings of letters in a normal font (Ariel 80), the other half presented false fonts. Within the false font blocks,

TABLE I. Means of word frequency and syllable frequency per million and number of neighbors of the stimuli

	Word frequency	Syllable 1	Syllable 2	N
High-frequency words				
High-frequency syllables	38.8	1788	1168	11.7
Low-frequency syllables	40.8	312	1149	10.3
Low-frequency words				
High-frequency syllables	2.5	1804	1000	11.3
Low-frequency syllables	2.8	261	914	11.3

seven stimuli were presented one after the other at a rate of 1 per 1.8 s. Within the lexical blocks, 14 stimuli were presented (also at a rate of 1 per 1.8 s) with seven words randomly intermixed with seven pseudowords. The lexical and syllable frequency of the words remained constant within a block, making four different types of lexical blocks: (1) high lexical frequency/high syllable frequency; (2) high lexical frequency/low syllable frequency; (3) low lexical frequency/high syllable frequency; and (4) low lexical frequency/low syllable frequency.

The 16 lexical blocks alternated with the 16 blocks of false fonts throughout each run.

The task and frequency conditions were also counterbalanced within runs. One task was performed during the first and the last eight blocks of the run (two blocks for each of the four frequency conditions), while the other task was performed during the other 16 blocks in the middle of the run (two blocks for each of the four frequency conditions). The assignment of the two tasks to blocks of items was counterbalanced within participants across runs. In the second run the same stimuli were presented again, but with a different task.

Each trial started with the fixation point—a cross in the middle of the screen—that lasted for 1,300 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 2,500 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 one task while in black for the other task. The assignment of the colors to the two tasks was counterbalanced across participants.

Stimuli

A list of 112 disyllabic words, all of them of four or five letters, was selected from a Spanish standard corpus [Sebastián et al., 2000]. Half of them were of high word frequency and the other half of low word frequency. In addition, within each group of word frequency half contained a first syllable of high frequency and the other half a first syllable of low frequency (Table I). As in previous studies [e.g., Barber et al., 2004; Perea and Carreiras, 1998], syllable frequency was manipulated in the first syllable only. The fre-

quency of the intersyllable bigrams was always greater than the frequency of the intrasyllable bigrams. The syllabic structure, the frequency of the second syllable, and the number of orthographic neighbors—the number of words that can be created by changing one letter of the stimulus item preserving letter positions—were matched across conditions (see Table I for the characteristics of the materials). In addition, 112 pseudowords were created by changing one or two letters from of an existing word, none of which were presented as words in the present experiment, without violating any phonotactic constraints of Spanish.

Data Acquisition

A Siemens 1.5 T scanner was used to acquire T2*-weighted echo-planar images with BOLD (blood oxygen level-dependent) contrast. Each echo-planar image comprised 35 axial slices of 2-mm thickness with 1-mm slice interval and 3 × 3 mm in-plane resolution. Volumes were acquired with an effective repetition time (TR) of 3.15 s/volume and the first six (dummy) volumes of each run were discarded to allow for T1 equilibration effects. A total of 432 volume images were taken in two separate runs. After the two functional runs, a T1-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, Sherbon, 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 et al., 1995a] 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 et al., 1995b].

Statistical Analysis

At the first level, data were analyzed in a participant-specific fashion, with each word type, baseline, and

TABLE II. Means and standard deviations (in parentheses) of lexical decision times (in ms) and percentage of errors (in italics) for lexical decision and reading aloud

	Word frequency	
	High	Low
Syllable frequency: lexical decision		
High	709 (105) <i>1.7 (0.7)</i>	778 (121) <i>8.9 (1.6)</i>
Low	723 (98) <i>1.7 (1.0)</i>	770 (116) <i>8.9 (2.4)</i>
Syllable frequency: reading aloud		
High	<i>0.07</i>	<i>0.10</i>
Low	<i>0.10</i>	<i>0.10</i>

pseudowords modeled separately and convolved with a canonical hemodynamic response function (HRF). The data were highpass-filtered using a set of discrete cosine basis functions with a cutoff period of 128 seconds. The contrasts of interest were each of the eight word conditions (2 task \times 2 word frequency \times 2 syllable frequency) relative to the task specific baseline. These contrast images were then entered into a second-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 second-level analysis, we report the effects of: (1) low vs. high lexical frequency; (2) low vs. high syllable frequency; (3) the interaction of lexical and sublexical frequency; and (4) the interaction of all these effects with task.

In addition to looking for frequency effects that are significant across the whole brain ($P < 0.05$, corrected for multiple comparisons), we also reduced our search space and tested for frequency effects within the set of voxels that were activated by the main effect of all words relative to the false font conditions (i.e., the average of all eight reading aloud and lexical decision conditions). Within this reduced search space, there were two criteria that were both required for significance: (i) more than 25 voxels surpassed a statistical threshold of $P < 0.001$ in the effect of frequency; and (ii) the conjunction of the frequency contrast and average word contrast was significant at $P < 0.05$ corrected for multiple comparisons.

RESULTS

Behavioral Data

Incorrect responses (5.8%) 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.

Participant and item ANOVAs based on the participants and items response latencies and percentage of errors (see Table II) in the lexical decision task were conducted based on a 2 (lexical frequency: high vs. low) \times 2 (syllable fre-

quency: high vs. low) within participants (F_1) but between items (F_2) design.

The ANOVA on the latency data showed a main effect of lexical frequency ($F_1(1,15) = 41.47$, $P < 0.0001$, mean squared error [Mse] = 1303; $F_2(1,108) = 43.07$, $P < 0.0001$, Mse = 2393), reflecting faster responses to high-frequency words than low-frequency words. Neither the main effect of syllable frequency ($F_1 < 1$; $F_2(1,108) = 1.35$, $P > 0.1$, Mse = 2393), or the interaction ($F_1(1,15) = 2.46$, $P > 0.1$, Mse = 857; $F_2 < 1$) were significant. The ANOVA on the error data showed again only a significant effect of word frequency ($F_1(1,15) = 21.77$, $P < 0.001$, Mse = 2.58; $F_2(1,108) = 20.92$, $P < 0.0001$, 1.54), indicating that fewer errors were produced responding to high-frequency words than to low-frequency words. The main effect of syllable frequency and the interaction were not significant (all $F < 1$).

The percentage of errors in the reading aloud task was negligible. None of the frequency effects on accuracy were significant in the reading aloud task (all $F < 1$).

fMRI Data

Effects of lexical frequency

In the lexical decision task only, low-frequency words increased activation relative to high-frequency words in the left dorsal opercularis, pre-supplemental motor area (SMA), and the sulcus between the anterior cingulate and SMA (see Table III, Fig. 1, for details). There were no significant effects of low $>$ high lexical frequency in the reading aloud task, or high $>$ low lexical frequency in either task.

Effects of syllable frequency

In the reading aloud task only, low-frequency syllables increased activation in relation to high-frequency syllables in the left anterior insula (see Table IV, Fig. 2A–B for details). There were no other effects of low $>$ high syllable frequency for either task.

In the lexical decision task, high-frequency syllables increased activation in relation to low-frequency syllables in the left inferior temporal region, but this effect was limited to low-frequency words only (see Table IV, Fig. 2C–D for details). As shown in Figure 2D, activation in the left anterior inferior temporal region was higher for lexical decision on words with high syllable frequency and low lexical frequency than in any other condition.

There were no other significant effects of syllable frequency or interactions with lexical frequency and/or task.

DISCUSSION

As predicted, word and syllable frequency produced different effects on regional brain activation. Effects of lexical frequency were observed in the left dorsal opercularis, pre-SMA, and the sulcus between the anterior cingulate and SMA—where activation was increased for low relative high lexical frequency but only in the lexical decision task. In contrast, effects of syllable frequency modulated activation

TABLE III. Effects of lexical frequency (LFW > HFW) during lexical decision and reading aloud

Region and effect	<i>x, y, z</i>	Lexical decision (LFW > HFW)		Reading aloud (LFW > HFW)	Interaction with task (LFW > HFW)	
		Z	Voxels		Z	Voxels
Left dorsal opercularis	-46, 18, 22	4.2	122	n.s.	3.8	16
Anterior cingulate/SMA	-4, 22, 42	4.1	83	n.s.	3.6	9
Pre-SMA	-2, 10, 58	4.0	28	n.s.	4.0	33

x, y, z = coordinates of local maxima; Z = Z scores; voxels = number of voxels at $P < 0.001$ uncorrected. Z scores significant at $P < 0.05$ (corrected for multiple comparisons) when search limited to those areas activated over and above baseline, and cluster size significant at $P < 0.05$ (corrected for multiple comparisons) are reported in bold. HFW: high-frequency words. LFW: low-frequency words. n.s. indicates not significant if did not reach at least the combined uncorrected threshold criteria of height $P < 0.001$ and voxel extent $P < 0.05$. The effects of HFW > LFW were not significant in lexical decision and in reading aloud.

in two other brain areas—a left anterior inferior temporal region and the left anterior insula. In the left anterior inferior temporal region, lexical decision on low-frequency words with high-frequency syllables increased activation relative to all other conditions. In the left ante-

rior insula, reading aloud words with high-frequency syllables reduced activation relative to all other conditions (Fig. 2). Therefore, high-frequency syllables increased activation in some conditions while reducing activation in other conditions.

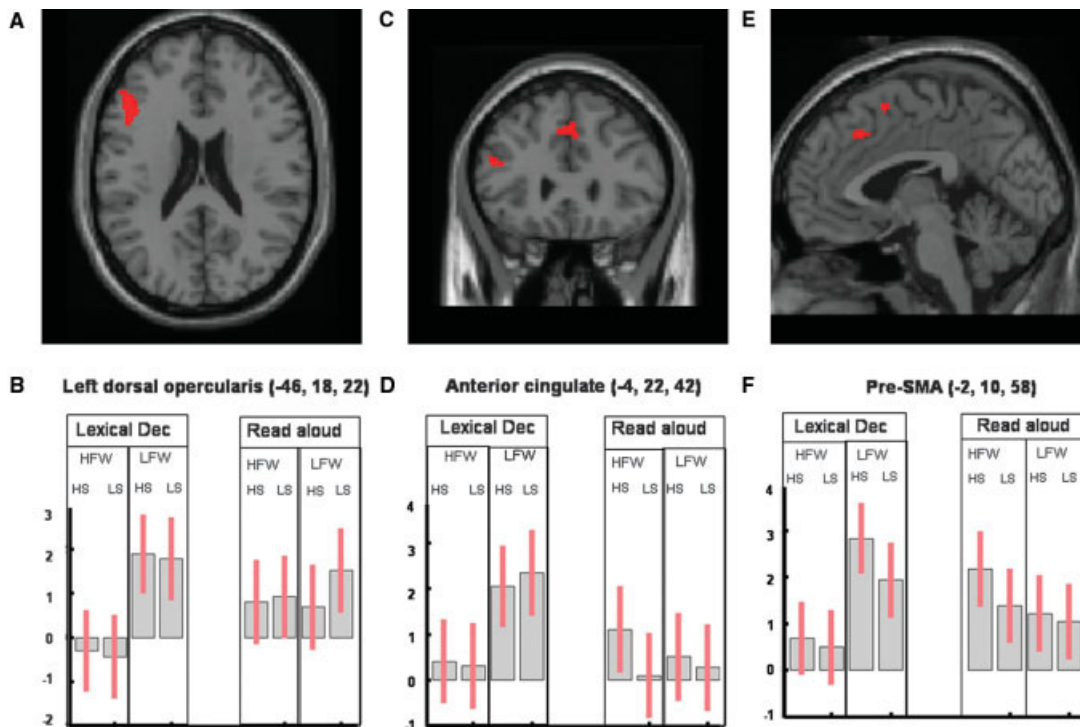


Figure 1.

A,C,E: Axial, coronal, and sagittal sections. Voxels colored red depict brain activation for low-frequency words as compared to high-frequency words in the lexical decision task. All contrasts depicted at $P < 0.001$, uncorrected. **B,D,F:** Graphs of contrast estimates and 90% confidence intervals for the areas left dorsal opercu-

laris, the sulcus between the anterior cingulate and SMA, and the pre-SMA. HFW: high-frequency words; LFW: low-frequency words; HS: high-frequency syllable; LS: low-frequency syllable. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

TABLE IV. Effects of syllable frequency during lexical decision and reading aloud

Region and effect	<i>x, y, z</i>	Lexical decision, Z (vox)			Reading aloud, Z(vox)			T x SF, Z(vox)	T x SF x WF, Z(vox)
		All	LFW	HFW	All	LFW	HFW		
LFS > HFS									
Left anterior insula	-40, 16, 14	n.s.	n.s.	n.s.	4.6(62)	n.s.	4.5(37)	3.6 (14)	n.s.
HFS > LFS									
Left inferior temporal	-42, -12, -32	n.s.	4.2(28)	n.s.	n.s.	n.s.	n.s.	3.4(5)	3.5(8)

x, y, z = coordinates of local maxima; Z = Z scores; Vox = number of voxels at $P < 0.001$ uncorrected. Z scores significant at $P < 0.05$ (corrected for multiple comparisons) when search limited to those areas activated over and above baseline are reported in bold. T x SF: Interaction of task by syllable frequency. T x SF x WF: Interaction of task by syllable frequency by word frequency. HFS: high-frequency syllable. LFS: low-frequency syllable. LFW: low-frequency words. n.s. = Not significant if did not reach at least the combined uncorrected threshold criteria of height $P < 0.001$ and voxel extent $P < 0.05$. For these effects, only voxel numbers above the extent threshold of $P < 0.05$ are shown in the table.

With respect to the behavioral responses, lexical decision was slower and less accurate to words with low than high lexical frequency but, contrary to previous behavioral studies, there was no significant effect of syllable frequency. We

suggest that the syllable frequency effects in our behavioral data do not replicate previous reports because we (1) did not use a self-paced paradigm (stimuli were presented at regular intervals of 1.8 s); (2) only included 16 participants, which is

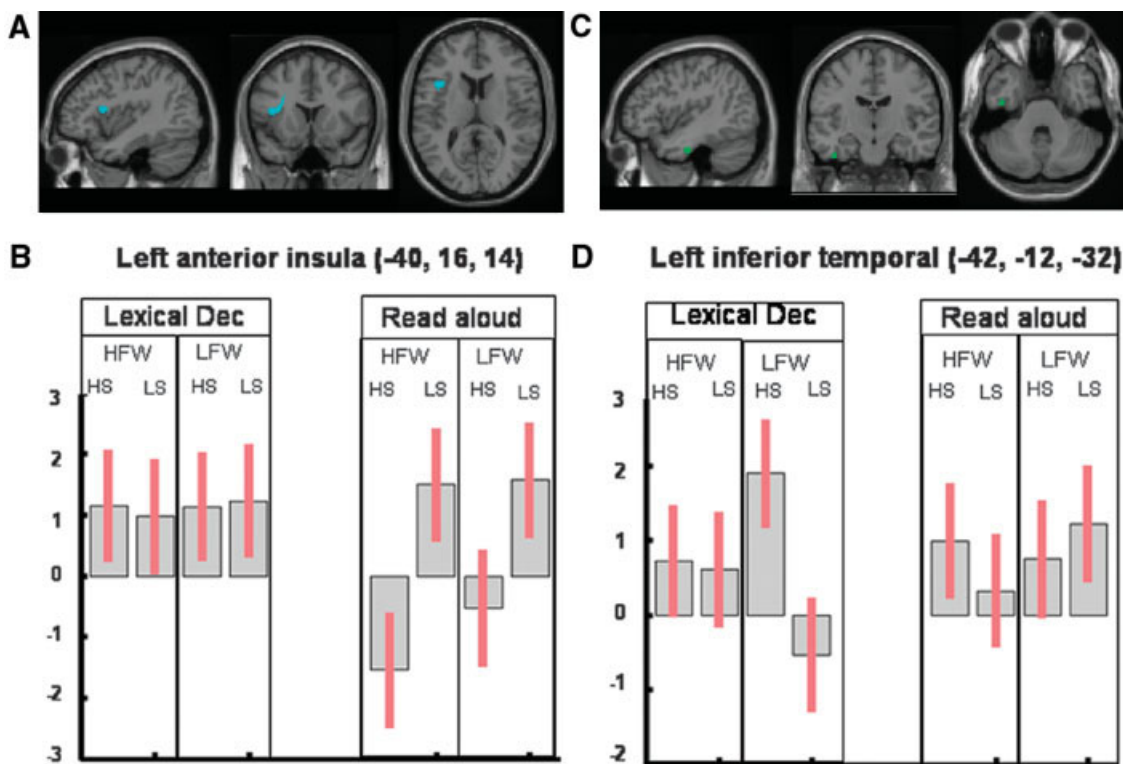


Figure 2.

A–B: Sagittal coronal and axial sections, and graph of contrast estimates and 90% confidence intervals in the left anterior insula. Voxels colored in light blue depict action for words with low-frequency syllables as compared to high-frequency syllables during reading aloud. **C–D:** Sagittal coronal and axial sections, and graph of contrast estimates and 90% confidence intervals in the left inferior temporal. Voxels colored green depict activation of low-

frequency words with high-frequency syllables as compared to low-frequency syllables in the lexical decision task. All contrasts depicted at $P < 0.001$, uncorrected. HFW: high-frequency words; LFW: low-frequency words; HS: high-frequency syllable; LS: low-frequency syllable. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

much lower than the previous behavioral experiments; and (3) blocked rather than randomized the event types. It has been demonstrated [e.g., Perea et al., 2004] that participants change their decision criteria when word frequency is blocked, so that in pure blocks of high-frequency words decisions can be made based on familiarity more than on unique word identification. Since the inhibitory effect of syllable frequency requires that the identification of a particular word candidate has taken place, and therefore the active suppression of other candidates, it is not surprising that familiarity-based criteria produced a facilitative trend of syllable frequency in the high-frequency word condition. This may also explain why the effects of high vs. low syllable frequency in the hemodynamic response during lexical decision were restricted to low-frequency words. Nevertheless, the effects of syllable frequency that we observe in the imaging data are consistent with the previous behavioral literature. For example, words with high-frequency syllables produce shorter latencies during speech production tasks [Carreiras and Perea, 2004; Cholin et al., 2006; Levelt and Wheeldon, 1994; Perea and Carreiras, 1998] but longer latencies during lexical decision [e.g., Carreiras et al., 1993; Perea and Carreiras, 1998] with larger effects of syllable frequency for low-frequency words than high-frequency words. Likewise, our imaging results show that high-frequency syllables reduce activation during reading aloud and increase activation during lexical decision when the words have low lexical frequency. It might be argued that the lack of behavioral effects—reaction times (RTs) and accuracy—for syllable frequency in the present study undermines our interpretation of the brain activation patterns. However, the contrasting effects of syllable frequency that we observed for lexical decision and reading aloud in the imaging data are consistent with many previous behavioral studies. Therefore, although our paradigm was more sensitive to the neuronal effect than to the behavioral effect, we believe the neuronal effect contributes to our understanding of the syllable frequency manipulation.

The location of the effects that we observe in our imaging data helps to interpret the processing stage at which lexical and sublexical frequency effects arise. As we will argue below, the task-dependent effects of syllable frequency may reflect two different cognitive processes in visual word identification: a lexical competition process and articulatory facilitation.

Increased Activation for High- vs. Low-Frequency Syllables

The increased left anterior inferior temporal activation for lexical decision on low-frequency words with high-frequency syllables is consistent with previous behavioral data showing that words—especially low-frequency words—with high-frequency syllables produce longer latencies than words with low-frequency syllables in lexical decision tasks [e.g., Carreiras et al., 1993; Perea and Carreiras, 1998] and

more negative amplitudes in the N400 time window [Barber et al., 2004]. This syllable frequency effect has been interpreted in terms of competition among word units in an interactive activation model. The competition includes both orthographic neighbors (i.e., words that share all letters but one) and syllabic neighbors (i.e., words that share a syllable with the target word, especially the *first* syllable). Thus, a word's higher frequency syllabic neighbors may be partially activated during word processing and these syllabic neighbors may later interfere (because of lateral inhibition) with the unique identification of the target word. Interestingly, the left anterior inferior temporal area that we identified as sensitive to this competition process (−40, −14, −32) is just posterior to the area associated with semantic priming during lexical decision [Mummery et al., 1999 (−40, 4, −28); Rossell et al., 2003 (−40, 14, −34); see also Rossell et al., 2001]. The same anterior temporal area has also been identified in other functional imaging studies of semantic association [Damasio et al., 1996; McCarthy et al., 1995; Mummery et al., 1998; Price et al., 1997; Vandenberghe et al., 1996, 2002] and intracranial recordings of visual word recognition in humans [e.g., McCarthy et al., 1995; Nobre and McCarthy, 1994, 1995; Nobre et al., 1994]. Thus, our finding that the left inferior temporal lobe is sensitive to syllable frequency during lexical decision is consistent with the effect arising at the level of lexical competition among orthographic and syllabic neighbors.

Reduced Activation for High- vs. Low-Frequency Syllables

The reduced left anterior insula activation for reading aloud words with high- as compared to low-frequency syllables is more likely to reflect sublexical output processes. For example, cognitive models have proposed that the facilitative effect of syllable frequency could result from faster access to the syllabary for high-frequency syllables [see Levelt, 1989; Levelt et al., 1999]. The location of the effect in the left anterior insula is consistent with sublexical motor plans because this area has been associated with planning speech articulation processes [Gorno-Tempini et al., 2004; Dronkers, 1996; Nestor et al., 2003; Wise et al., 1999; but see Hillis et al., 2004; Indefrey and Levelt, 2000, 2004] as well as nonverbal motor planning [Ackerman and Rieker, 2005]. Critically, the response in the left anterior insula dissociated from that in the left inferior frontal cortex. While the left anterior insula was sensitive to syllable frequency, the left inferior frontal cortex was sensitive to lexical frequency [see also Fiebach et al., 2002; Fiez et al., 1999; Hagoort et al., 1999; Herbster et al., 1997]. Future studies are required to determine whether the left anterior insula receives inputs directly from the left inferior frontal cortex, or whether each area functions independently.

On the other hand, Hagoort et al. [1999] suggested that cerebral areas, SMA, and premotor cortex may be involved in accessing precompiled articulatory routines for high-frequency syllables and in the segment-to-segment assembly for low-frequency syllables. In their study, however, syllable

frequency was confounded with lexicality effects because, as the authors acknowledge, their pseudowords contained higher-frequency syllables than words. Future studies are necessary to investigate the contribution of these areas (SMA, motor, premotor, and cerebral areas) and of the left anterior insula and left inferior frontal cortex to the network involved in speech planning.

Lexical Frequency Effects

Lexical frequency effects were only obtained in the lexical decision task. This is not surprising, given that lexical frequency had a greater influence on performance during lexical decision than reading aloud (Table II). The lexical decision task places more of an emphasis on frequency-familiarity information in making the word/nonword discrimination [Balota and Chumbley, 1984; Ratcliff et al., 2004], whereas the reading aloud task emphasizes the onset of the appropriate articulation. Critically, the left inferior frontal region responds both to low- and high-frequency words in reading aloud [see, however, Ischebeck et al., 2004]; and to low-frequency words during lexical decision but not to high-frequency words during lexical decision (Fig. 1). This is consistent with cognitive models of lexical decision that all propose that lexical search for high-frequency words requires less phonological mediation because high-frequency words can be rapidly identified on the basis of visual word information.

Although the behavioral data (errors and reaction time) suggest that lexical decision was more difficult for low- than high-frequency words, it was not simply the case that words with low-frequency increased activation throughout the whole reading network. To the contrary, we only detected lexical frequency effects in the left dorsal opercularis, pre-SMA, and anterior cingulate/SMA but not in the left fusiform gyrus, reported to be sensitive to frequency effects by Kronbichler et al. [2004]. We therefore propose that the slower RTs and the greater activation in the left inferior frontal, anterior cingulate/SMA, and pre-SMA reflect greater demands on lexico-phonological processes. However, we cannot rule out the hypothesis that these effects are caused by general difficulty instead of an increased phonological mediation for low-frequency words. Future studies are required to determine precisely how the left inferior frontal, anterior cingulate/SMA, and pre-SMA regions contribute to phonological processing, as many other studies have shown that these areas are involved in nonverbal tasks. In addition, the fact that we did not replicate effects of lexical frequency in the left fusiform gyrus and on the left inferior frontal gyrus in reading aloud suggest that the effect of lexical frequency on brain activation is dependent on the experimental design; this will require further investigation.

CONCLUSIONS

Our results have shown two important dissociations between lexical frequency and syllable frequency, and

between syllable frequency in the reading aloud and lexical decision tasks. This suggests that lexical and sublexical—input and output—processes of word reading activate different brain networks. Increased left anterior inferior temporal activation for lexical decision on low-frequency words with high-frequency syllables can be explained in terms of semantic competition during word selection. Reduced left anterior insula activation for reading aloud words with high-frequency syllables is consistent with facilitation of motor planning during the speech production process. Finally, reduced activation in the left inferior frontal, anterior cingulate/SMA, and pre-SMA for lexical decision on high-frequency words suggests reduced demands on lexico-phonological processes. Thus, the present results indicate that—at least in languages with shallow orthographies, transparent spelling-to-sound correspondences, and clear syllabic boundaries—the computation of lexical and input-output sublexical processes modulates different brain areas. It remains to be seen how these regions are functionally connected during the process of word recognition.

ACKNOWLEDGMENTS

M.C. thanks the Institute of Cognitive Neuroscience, University College of London, where he was a visitor while the work was carried out.

REFERENCES

- Ackerman H, Rieker A (2004): The contribution to the insula to motor aspects of speech production: a review and a hypothesis. *Brain Lang* 89:320–328.
- Alario FX, Ferrand L, Laganaro M, New B, Frauenfelder, UH, Segui J (2004): Predictors of picture naming speed. *Behav Res Methods Instrum Comput* 31:531–552.
- Álvarez CJ, Carreiras M, Taft M (2001): Syllables and morphemes: contrasting frequency effects in Spanish. *J Exp Psychol Learn Mem Cogn* 27:545–555.
- Balota DA, Chumbley JI (1984): Are lexical decisions a good measure of lexical access? The role of word frequency in the neglected decision stage. *J Exp Psychol Hum Percept Perform* 10:340–357.
- Barber H, Vergara M, Carreiras M (2004): Syllable-frequency effects in visual word recognition: evidence from ERPs. *Neuroreport* 15:545–548.
- Binder JR, McKiernan KA, Parsons ME, Westbury CF, Possing ET, Kaufman JN, Buchanan L (2003): Neural correlates of lexical access during visual word recognition. *J Cogn Neurosci* 15:372–393.
- Carreiras M, Perea M (2004): Naming pseudowords in Spanish: effects of syllable frequency. *Brain Lang* 90:393–400.
- Carreiras M, Álvarez CJ, de Vega M (1993): Syllable frequency and visual word recognition in Spanish. *J Mem Lang* 32:766–780.
- Coltheart M, Curtis B, Atkins P, Haller M (1993): Models of reading aloud: dual-route and parallel distributed-processing approaches. *Psychol Rev* 100:589–608.
- Conrad M, Jacobs A (2004): Replicating syllable frequency effects in Spanish in German: one more challenge to computational

- models of visual word recognition. *Lang Cogn Process* 19: 369–390.
- Cholin J, Levelt WJM, Schiller N (2006): Effects of syllable frequency in speech production. *Cognition* 99:205–235.
- Damasio H, Grabowski TJ, Tranel D, Hichwa RD, Damasio AR (1996): A neural basis for lexical retrieval. *Nature* 380:499–505.
- Dronkers NF (1996): A new brain region for coordinating speech articulation. *Nature* 384:159–161.
- Fiebach CJ, Friederici AD, Müller K, von Cramon DY (2002): fMRI evidence for dual routes to the mental lexicon in visual word recognition. *J Cogn Neurosci* 14:11–23.
- Fiez JA, Petersen SE (1998): Neuroimaging studies of word reading. *Proc Natl Acad Sci U S A* 14:11–23.
- Fiez JA, Balota DA, Raichle ME, Petersen SE (1999): Effects of lexicality, frequency, and spelling-to-sound consistency on the functional anatomy of reading. *Neuron* 24:205–218.
- Friston KJ, Ashburner J, Frith CD, Poline JB, Heather JD, Frackowiak RSJ (1995a): Spatial registration and normalization of images. *Hum Brain Mapp* 2:1–25.
- Friston KJ, Holmes A, Worsley KJ, Poline J-B, Frith CD, Frackowiak RSJ (1995b): Statistical parametric maps in functional imaging: a general linear approach. *Hum Brain Mapp* 2:189–210.
- Gorno-Tempini ML, Dronkers NF, Rankin KP, Ogar JM, Phengrasamy L, Rosen HJ, Johnson JK, Weiner MW, Miller BL (2004): Cognition and anatomy in three variants of primary progressive aphasia. *Ann Neurol* 55:335–346.
- Hagoort P, Brown C, Indefrey P, Herzog H, Steinmetz H, Seitz R (1999): The neural circuitry involved in the reading of German words and pseudowords: a PET study. *J Cogn Neurosci* 11:383–398.
- Herbster AN, Mintun MA, Nebes RD, Becker JT (1997): Regional cerebral blood flow during word and nonword reading. *Hum Brain Mapp* 5:84–92.
- Hillis AE, Work M, Barker PB, Jacobs MA, Breese EL, Maurer K (2004): Reexamining the brain regions crucial for orchestrating speech articulation. *Brain* 127:1479–1487.
- Holmes AP, Friston KJ (1998): Generalisability, random effects and population inference. *Neuroimage* 7:5754.
- Indefrey P, Levelt WJM (2000): The neural correlates of language production. In: Gazzaniga M, editor. *The New Cognitive Neurosciences*. Cambridge, MA: MIT Press.
- Indefrey P, Levelt WJM (2004): The spatial and temporal signatures of word production components. *Cognition* 92:101–144.
- Ischebeck A, Indefrey P, Usui N, Nose I, Hellwig F, Taira M (2004): Reading in a regular orthography: an fMRI study investigating the role of visual familiarity. *J Cogn Neurosci* 16:727–741.
- Jesper LR, Andersson JLR, Hutton C, Ashburner J, Turner R, Friston K (2001): Modeling geometric deformations in EPI time series. *Neuroimage* 13:903–919.
- Kronbichler M, Hutzler F, Wimmer H, Mari A, Staffen W, Ladurner G (2004): The visual word form area and the frequency with which words are encountered: evidence from a parametric fMRI study. *Neuroimage* 21:946–953.
- Levelt WJM (1989): *Speaking: from intention to articulation*. Cambridge, MA: MIT Press.
- Levelt WJM, Wheeldon L (1994): Do speakers have access to a mental syllabary? *Cognition* 50:239–269.
- Levelt WJM, Roelofs A, Meyer AS (1999): A theory of lexical access in speech production. *Behav Brain Sci* 22:1–38.
- Marshall JC, Newcombe F (1973): Patterns of paralexia: a psycholinguistic approach. *J Psycholinguist Res* 2:175–199.
- Mathey S, Zagar D (2002): Lexical similarity in visual word recognition: the effect of syllabic neighborhood in French. *Curr Psychol Lett* 8:107–121.
- McCarthy G, Nobre AC, Bentin S, Spencer DD (1995): Language-related field potentials in the anterior-medial temporal lobe. I. Intracranial distribution and neural generators. *J Neurosci* 15: 1080–1089.
- Mechelli A, Gorno-Tempini ML, Price CJ (2003): Neuroimaging studies of word and pseudoword reading: consistencies, inconsistencies, and limitations. *J Cogn Neurosci* 15:260–271.
- Mechelli A, Crinion J, Long S, Friston KJ, Lambon-Ralph MA, Patterson K, McClelland JL, Price CJ (2005): Dissociating reading processes on the basis of neuronal interactions. *J Cogn Neurosci* 17:1753–1765.
- Mummery CJ, Patterson K, Hodges JR, Price CJ (1998): Functional neuroanatomy of the semantic system: divisible by what? *J Cogn Neurosci* 10:766–777.
- Mummery CJ, Shallice T, Price CJ (1999): Dual-process model in semantic priming: a functional imaging perspective. *Neuroimage* 9:516–525.
- Nestor PJ, Graham NL, Fryer TD, Williams GB, Patterson K, Hodges JR (2003): Progressive non-fluent aphasia is associated with hypometabolism centred on the left anterior insula. *Brain* 126: 2406–2418.
- Nobre AC, McCarthy G (1994): Language-related ERPs: scalp distributions and modulation by word type and semantic priming. *J Cogn Neurosci* 6:233–255.
- Nobre AC, McCarthy G (1995): Language-related field potentials in the anterior-medial temporal lobe. II. Effects of word type and semantic priming. *J Neurosci* 15:1090–1098.
- Nobre AC, Allison T, McCarthy G (1994): Word recognition in the human inferior temporal lobe. *Nature* 372:260–263.
- Paap KR, Noel RW (1991): Dual-route models of print to sound: still a good horse race. *Psychol Res* 53:13–24.
- Patterson KE, Morton J (1985): From orthography to phonology: an attempt at an old interpretation. In Patterson K, Marshall JC, Coltheart M, editors. *Surface Dyslexia*. London: Erlbaum. p 335–359.
- Paulesu E, McCrory E, Fazio F, Menoncello L, Brunswick N, Cappa SF, Cotelli M, Cossu G, Corte F, Lorusso M, Pesenti S, Gallagher A, Perani D, Price C, Frith CD, Frith U (2000): A cultural effect on brain function. *Nat Neurosci* 3:91–96.
- Perea M, Carreiras M (1998): Effects of syllable frequency and syllable neighborhood frequency in visual word recognition. *J Exp Psychol Hum Percept Perform* 24:134–144.
- Perea M, Carreiras M, Grainger J (2004): Blocking by word frequency and neighborhood density in visual word recognition: a task-specific response criteria account. *Mem Cogn* 32:1090–1102.
- Price CJ, Wise RJS, Frackowiak RSJ (1996): Demonstrating the implicit processing of visually presented words and pseudowords. *Cereb Cortex* 6:62–70.
- Price CJ, Moore CJ, Humphreys GW, Wise RJS (1997): Segregating semantic from phonological processes during reading. *J Cogn Neurosci* 9:727–733.
- Ratcliff R, Gomez P, McKoon G (2004): A diffusion model account of the lexical decision task. *Psychol Rev* 111:159–182.
- Rossell SL, Bullmore ET, Williams SCR, David AS (2001): Brain activation during automatic and controlled processing of semantic relations: a priming experiment using lexical-decision. *Neuropsychologia* 39:1167–1176.
- Rossell SL, Price CJ, Nobre AC (2003): The anatomy and time course of semantic priming investigated by fMRI and ERPs. *Neuropsychologia* 41:550–564.

- Rumsey JM, Horwitz B, Donohue C, Nace K, Maisog JM, Andreason P (1997): Phonological and orthographic components of word recognition: a PET-rCBF study. *Brain* 120:739–759.
- Sebastián-Gallés N, Martí MA, Carreiras M, Cuetos F (2000): *Lexesp: una base de datos informatizada del español*. Universitat De Barcelona, Spain, 2000.
- Seidenberg MS, McClelland JL (1989): A distributed developmental model of word recognition and naming. *Psychol Rev* 96: 523–568.
- Tagamets M-A, Novick JM, Chalmers ML, Friedman RB (2000): A parametric approach to orthographic processing in the brain: an fMRI study. *J Cogn Neurosci* 12:281–297.
- Vandenberghe R, Price C, Wise R, Josephs O, Frackowiak RS (1996): Functional anatomy of a common semantic system for words and pictures. *Nature* 383:254–256.
- Vandenberghe R, Nobre AC, Price C (2002): The response of left temporal cortex to sentences. *J Cogn Neurosci* 14:550–560.
- Wise RJS, Greene J, Büchel C, Scott SK (1999): Brain regions involved in articulation. *Lancet* 353:10057–10061.
- Xu B, Grafman J, Gaillard WD, Ishii K, Vega-Bermudez F, Pietrini P, Reeves-Tyler P, DiCamillo P, Theodore W (2001): Conjoint and extended neural networks for the computation of speech codes: the neural basis of selective impairment in reading words and pseudowords. *Cereb Cortex* 11:267–277.