Syllable Congruency and Word Frequency Effects on Brain Activation

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Abstract: This article investigates the neural representation of the processes involved in recognizing multisyllabic words in Spanish asking whether lexical and sublexical processes are reflected in a different neuronal activation pattern. High and low frequency words were presented for lexical decision in two different colors. In the congruent condition the color boundaries matched the limit of the first syllable, whereas in the incongruent condition color boundaries and syllable boundaries did not match. The results revealed robust and dissociable brain activations for lexical frequency and syllable-color congruency, but no interaction between the two. We interpreted the greater activation for low relative to high frequency words in the left pre/SMA region, and in the insula/inferior frontal cortex bilaterally to reflect a differential recruitment of lexico-phonological and/or semantic processes. In contrast, we considered two interpretations for the greater deactivation in the precuneus for both lexical frequency and syllable-color congruency words, and in the thalamus and a frontal area for syllable-color congruency words only. The deactivations may reflect the differential engagement of semantic processing or may result from the differential allocation of attentional resources. Importantly, while a differential deactivation pattern was observed in the precuneus region for lexicality and syllable-color congruency, BOLD deconvolution revealed a remarkable difference in timing of the two effects with a much earlier deactivation peak for the syllable-color congruency factor. Thus, effects of lexical frequency and syllable-color congruency on brain activation show an important dissociation between lexical and sublexical processes during visual word recognition of multisyllabic words. *Hum Brain Mapp* 30:3079–3088, 2009. © 2009 Wiley-Liss, Inc.

Key words: lexical processes; sublexical processes; syllable; word recognition; functional magnetic resonance imaging

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INTRODUCTION

Reading is one of the most important acquired cultural skills. How we recognize words—a major step in reading—has been the focus of a myriad of investigations employing a range of different methodologies. There are still under-researched questions in word recognition, however, such as the processing of multisyllabic words. Whereas most words contain several syllables, most previous research efforts have sought to understand how we recognize mono-syllabic words [e.g., Coltheart et al., 1993; Grainger and Jacobs, 1996; McClelland and Rumelhart, 1981]. Recognizing multisyllabic words may be fundamentally different. For instance, are multisyllabic words parsed into syllables before their meaning is accessed? This article investigates the cortical representation of the processes involved in recognizing multisyllabic words in Spanish, a language with clearly defined syllabic boundaries and a transparent orthography, using functional magnetic resonance imaging, with the main goal to scrutinize whether lexical and sublexical processes (e.g., syllabic parsing) are reflected in different neuronal activation patterns.

Behavioral and event-related brain potential (ERP) evidence seems to show that multisyllabic words are parsed into syllables during reading. One important piece of evidence supporting syllabic processing in visual word recognition has been obtained by manipulating the syllabic congruency between primes and targets with masked priming techniques [Álvarez et al., 2004; Carreiras and Perea, 2002; Carreiras et al., 2005b] or with parafoveal preview during reading [Ashby and Rayner, 2004]. As an example of the former experimental strategy, Carreiras and Perea [2002; Experiment 3] used monosyllabic (ZINC) and disyllabic words (RA.NA) as targets (Note that the dots represent syllables boundaries and were not displayed in the original stimuli) that were preceded by masked primes. The results showed a significant syllabic priming effect for the disyllabic words (*ra.jo*-RA.NA relative to *cu.fo*-RA.NA). In contrast, monosyllabic words were not affected by related primes that shared the first two letters with the target (*ziel*-ZINC vs. *flur*-ZINC). Likewise, Álvarez et al. [2004] found a significant advantage for disyllabic prime-target pairs that shared the first three letters and the first consonant-vowel (CV) syllable (e.g., *ju.nas*-JU.NIO) relative to disyllabic pairs that shared the first three letters but not the first syllable (*jun.tu*-JU.NIO). Another key finding supporting syllabic processing in visual word recognition is the syllable frequency effect that pertains to the fact that words composed of high-frequency syllables are responded to more slowly than words composed of two low-frequency syllables in lexical decision [Spanish: Álvarez et al., 2001; Carreiras et al., 1993; Conrad et al., in press; Perea and Carreiras, 1998; German: Conrad and Jacobs, 2004; French: Mathey and Zagar, 2002]. The syllable-frequency effect is generally interpreted as evidence for an automatic syllabic segmentation of visually presented words: after a syllabic segmentation of the input, the first

syllable activates the representations of words sharing this syllable in identical position and competition between these words is responsible for the observed delay in the processing of words with high-frequency initial syllables [e.g., Perea and Carreiras, 1998]. However, effects of syllable frequency have mainly revealed late inhibitory processes resulting from competition by syllabic neighbors, whereas syllabic congruency effects seem to reflect early processes of syllabic parsing during visual word recognition.

Of particular relevance to the present fMRI study are event-related potential data of syllabic congruency that further support a role of syllabic parsing in word recognition. Carreiras et al. [2005a] presented high and low frequency words and pseudowords in two colors (red and green) for a lexical decision task such that in the congruent condition the first syllable was in one color and the second syllable in the other color (i.e., the color matched the syllable boundary), whereas in the incongruent condition, color and syllable boundaries did not match. The rationale for this manipulation was that if syllabic processing is an important early and automatic process during visual word recognition, the incongruent condition should interfere with stimulus recognition compared with the congruent condition, and the effects of syllable-color congruency should differ from those of lexical frequency or lexicality. Whereas syllable-color congruency modulated the ERPs in the P200 and the N400 windows, lexical frequency and lexicality effects were observed in the N400 window only. Moreover, syllable-color congruency and lexical frequency influenced the ERP in the N400 time-range with a different topographical distribution that further supports the independence of these two processes. Thus, these experiments support the view that the initial syllable may mediate between the letter and word levels, at least in Romance languages. The activation and inhibition of lexical candidates obtained for syllable congruency has also been captured in other studies manipulating syllable frequency and employing ERPs: the higher the frequency of the syllables embedded in words, the lower the amplitude of the P200 and the higher the amplitude of the N400 [Barber et al., 2004; Hutzler et al., 2004]. However, no topographical differences were obtained with the syllable frequency manipulation between the P200 and the N400 effects, suggesting that a longer-lasting negative shift was superimposed on these two peaks. Also, there was no topographical difference between syllable frequency and word frequency effects at the N400. Taken together, this is providing a weaker empirical basis for claiming that two independent processes (lexical vs. sublexical) are at work. For instance, the same lexical mechanism (e.g., competition) operating on syllabic neighbors and on lexical neighbors could account for the effects of syllable and word frequency on ERPs.

Functional magnetic resonance imaging is a very appropriate method to investigate how multisyllabic words are processed, because it allows us to address whether lexical (e.g., lexical frequency) and sublexical (e.g., syllabic structure) manipulations produce different patterns of brain

activation (i.e., whether they are dissociable). The dissociation of lexical frequency and syllable congruency brain activation patterns will strongly suggest that syllables are important sublexical units computed during visual word recognition. Since in Carreiras et al.'s [2005a] study both syllabic and lexical effects modulated the N400 component with a different topographical distribution, and in addition, the syllabic effects also modulated the P200 component, it is very relevant to ask whether syllabic and lexical effects influence activation in different brain areas by using fMRI, a technique with a much better spatial resolution than ERPs. The majority of the studies reported to date have focused on the comparison of word and pseudoword processing [e.g., Binder et 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; Paulesu et al., 2000; Price et al., 1996; Rumsey et al., 1997; Tagamets et al., 2000; Xu et al., 2001], with only a few studies comparing words of high and low frequency [Carreiras et al., 2006; Chee et al., 2002, 2003; Fiebach et al., 2002; Fiez et al., 1999; Joubert et al., 2004] or regular and irregular words [Fiez et al., 1999; Herbster et al., 1997; Mechelli et al., 2005; Rumsey et al., 1997]. Nevertheless, the results appear to converge by showing greater left inferior frontal activation for pseudowords compared to words, low relative to high frequency words; and words with irregular relative to regular orthography. More recently, Carreiras et al. [2006] examined whether the dissociations of lexical frequency and syllable frequency documented in behavioral and electrophysiological measures could be mapped onto different areas of the brain. They showed a corresponding dissociation in the brain regions sensitive to these two manipulations. During lexical decision, words with low lexical frequency showed increased activation in left frontal, anterior cingulate, and pre-SMA regions relative to words with high lexical frequency. In contrast, words with high frequency syllables showed increased activation in a left anterior inferior temporal region relative to words with low frequency syllables. They proposed that the contrasting effects of word and syllable frequency reflect two different cognitive processes in visual word processing. Specifically, while differential demands on lexical-phonological processes may underlie the effects of lexical frequency, words with high frequency syllables may increase lexical competition in the inferior temporal lobe. However, lexical competition occurs in later stages of the process of visual word recognition. In particular, lexical competition is assumed to be a late consequence of prior syllabic parsing. A more straightforward way to look into the sublexical versus lexical distinction is to manipulate the syllable congruency that seems to tap into early syllabic segmentation processes, that is, sublexical processes taking place prior to accessing the whole word form. Some previous work [e.g., Carreiras et al., 2008] suggests that syllable frequency and syllable congruency indeed tap into two different mechanisms of visual word recognition, since syllable congruency effects but not

syllabic frequency effects are preserved in Alzheimer patients. Effects of syllable congruency seem to correspond to early structural parsing stages of word recognition, namely syllabification, while the syllable frequency effect seems to be the end result of a late lexical inhibitory process.

In sum, we will investigate whether syllable-color congruency and word frequency map onto different areas of the brain using the same paradigm and the same stimuli as used in Carreiras et al. [2005a] with fMRI. The ultimate goal is to demonstrate a dissociation of lexical and sublexical processes. Effects of color/syllable congruency are assumed to reflect early sublexical processes of syllabic parsing, while effects of lexical frequency are assumed to reflect later stages of word recognition.

METHOD

Participants

Twenty volunteers (10 women) participated in the study. They were all native Spanish speakers, right-handed, and with no history of neurological or psychiatric disorders according to a structured interview. Ages ranged from 19 to 42 years (mean = 25.6 years). All subjects gave their written informed consent and were paid for participation. All procedures were cleared with the Ethical Review Board of the University of Magdeburg.

Task and Stimuli

A lexical decision task was employed. Participants were instructed to make finger press responses to indicate whether the current letter string was a legitimate Spanish word or not. For half of the participants, the right button was used to signal the "yes" response and the left button was assigned to the "no" response. For the remaining participants, the order was reversed. A fast event-related design was used. Stimuli were presented on a black screen for 225 ms. The interstimulus interval was jittered varying between 2 and 8 s. A fixation point (a cross) was presented before each stimulus during the ISI.

A total of 320 stimuli were presented, divided into two blocks of 160. Half of the stimuli in each block were words and the other half were pseudowords. One-hundred-sixty bi-syllabic and tri-syllabic words with CV.CV and CV.CV.CV structures, respectively were selected from the Spanish word pool LEXESP [Sebastián-Gallés et al., 2000] composed of six and a half million tokens extracted from different sources of written material. Eighty words were of low lexical frequency and the other eighty were of high lexical frequency. The mean frequency of the low frequency set was 4.3 (range: 2–7) per million, whereas the mean frequency for the high frequency group was 57.8 (range: 19–206) per million. The 160 pseudowords were created for the purpose of the lexical decision task by changing one letter from existing words in Spanish and preserving the phonotactic and orthotactic rules of Spanish. Half of them had a CV.CV structure and the other half

a CV.CV.CV structure. All stimuli (words and pseudowords) appeared in two colors (red and green): In the congruent condition the first syllable was in one color and the rest of the word in the other color; that is, the color boundaries matched the limit of the first syllable, whereas in the incongruent condition color boundaries and first syllable did not match. Half of the stimuli (80 words and 80 pseudowords) were presented with a congruent color arrangement and the other half were shown in incongruent colors. Four versions of each item were created by combining syllable-color congruency (congruent vs. incongruent) and order of colors (red-green vs. green-red), for example, *maleta*, *maleta*, *maleta*, *maleta* (suitcase; italic font stands for red, bold font for green). Thus, four lists of items were created such that each item appeared in all four counterbalanced conditions across lists, but only in one condition within each list. Since each participant was assigned only to one list, she/he saw only one version of each item. The frequency of the first syllable as well as the bigram frequency was controlled: The bigram frequency (i.e., the frequency of co-occurrence of two consecutive letters) intrasyllable was always less or equal to the bigram frequency of the letters between the first and the second syllables. Letters within syllables tend to co-occur in the written language more often than letters that mark syllable boundaries. Consequently, syllable boundaries are typically marked by a pattern of bigram frequencies that can be referred to as a “trough”: The letter pair preceding the syllable boundary will often have a higher frequency than the bigram that straddles the boundary. Therefore, it is important to control for intersyllable and intrasyllable bigram frequency, as we did in the present experiment, to make specific claims about syllabic processing.

Data Acquisition and Analysis

Acquisition

Data were acquired in a 3-Tesla Siemens Magnetom Trio Scanner. First, structural images of the brain were obtained by means of a T1-weighted MPRAGE sequence: 256×256 matrix; field of view (FOV) = 256 mm; 192 1-mm sagittal slices. Subsequently, functional images were obtained in two runs implementing an echo-planar-imaging sequence. The pulse-sequence parameters were as follows: time to repeat (TR) = 2,000 ms; time to echo (TE) = 30 ms; FOV = 224 mm; flip angle (FA) = 80° ; matrix = 64×64 ; slice thickness = 4 mm. Thirty-two transversal slices ($3.5 \times 3.5 \times 4$ mm voxel) were obtained parallel to the anterior commissure-posterior commissure (AC-PC).

Analysis

Data analysis included preprocessing (3D motion correction, slice scan time correction, high-pass temporal filtering, and spatial smoothing with an 8-mm Gaussian filter), coregistration, and normalization to Talairach stereotaxic

space using Brain Voyager QX. We performed a random-effects analysis [Holmes and Friston, 1998] on the functional data. Both at the individual and group level, the variable under analysis was the % of BOLD signal change calculated relative to the prestimulus baseline that corresponds to periods of the fixation cross. For each individual participant, a design matrix was defined that included the following four predictors: word congruent high frequency, word congruent low frequency, word incongruent high frequency, and word incongruent low frequency. Pseudowords were considered as another predictor in the first level analysis to extract variance from the model, but they will not be discussed here because words and pseudowords required different responses (yes vs. no). Predictors were convolved with a two-gamma hemodynamic response function. At the group level, a random-effects analysis [Holmes and Friston, 1998] on the functional data was performed including the design matrices and functional data of all participants. To correct for Type I error inflation due to the large number of voxels involved, a correction method for multiple comparisons was implemented. For each statistical contrast, the statistical maps were corrected using the False Discovery Rate (FDR) set at 5% [Genovese et al., 2002]. Statistical contrasts involved comparisons between predictors (e.g., high frequency vs. low frequency words or congruent vs. incongruent words), and no baseline condition was included in the model. For a given contrast, the surviving statistically significant voxels after FDR correction constituted the voxels comprising the volumes of interest (VOIs) used to study the time course of the BOLD response in a subsequent step (see below).

To adequately study those brain areas showing significant effects for specific statistical contrasts, additional analyses of the time course of the BOLD response were conducted. These analyses required first the definition of a VOI comprising those voxels with suprathreshold t -values that had survived the correction for multiple comparisons by means of the FDR. Second, in the context of the fast event-related design with jittered stimulus presentation used, a linear deconvolution was performed. This deconvolution analysis used the averaged signal across voxels in the VOI and yielded for each subject and run the values of the β weights of the different predictors defined in the GLM (corrected for serial correlations) along time and for a given VOI. The obtained β weights were used to generate the event-related deconvolution plots and also as input for serial analyses of variance conducted to study the time course of the syllable-color congruency effect and the lexical frequency effects. As prestimulus baseline for the plots, β values in the interstimulus interval were used.

RESULTS

Behavioral Data

Incorrect responses (4.0%) were excluded from reaction time analyses. Reaction time data (see Table I) were

TABLE I. Means and standard deviations (within parentheses) of lexical decision times (in ms) and percentage errors (in italics)

Lexical frequency	Congruency	
	Congruent	Incongruent
High	685 (82) <i>0.9 (1.7)</i>	675 (74) <i>1.4 (1.9)</i>
Low	756 (88) <i>7.9 (6.0)</i>	764 (93) <i>5.1 (4.4)</i>

subjected to a two-way within-subjects ANOVA with lexical frequency (high vs. low) and congruency (congruent vs. incongruent) as factors. A significant effect of lexical frequency was observed [$F(1,19) = 145, P < 0.001$]. Responses to high frequency words were faster than responses to low frequency words. Neither the main effect of congruency [$F(1,19) < 1$] nor the interaction between congruency and lexical frequency were significant [$F(1,19) = 2.65, P > 0.1$]. The ANOVA on the error data including omissions and commission showed again an effect of lexical frequency [$F(1,19) = 25.31, P < 0.001$]. Error rates were higher for low frequency than for high frequency words. Although no overall effect of congruency was found [$F(1,19) = 2.91, P > 0.1$], there was a significant interaction between lexical frequency and congruency [$F(1,19) = 9.41, P < 0.01$]. Paired t -tests showed that the congruency effect was restricted to the low frequency words ($t(19) = 2.43, P < 0.05$).

fMRI Data

The second level analysis of the fMRI data was performed on the four contrast of interest corresponding to lexical frequency and color/syllable congruency. Thus, from this second level analysis, we report the effects of (1) low versus high lexical frequency, (2) color/syllable congruency versus incongruency, and (3) the interaction of lexical frequency and congruency. These analyses highlighted brain areas showing significant main effects of lexical frequency and of color/syllable boundary congruency after correction for multiple comparisons by means of the FDR (at the 0.05 level). Only correctly responded trials were included in the analysis (virtually identical results were obtained when including trials with errors, which were relatively few). The interaction between the two factors was not significant anywhere in the brain. The lexical frequency main effect was observed in the left pre/SMA region, and in the insula/inferior frontal cortex bilaterally. These regions showed an increased BOLD response for low compared to high frequency words. Additionally, an area showing a decrease in BOLD response for low compared to high frequency words was found in the precuneus (see Table II and Fig. 1A).

A congruency main effect was observed in four different brain regions. A decrease of the BOLD response was greater for incongruent than for congruent words (see Table III and Fig. 1B). The largest cluster was found in the paracentral gyrus/precuneus, followed in extension and absolute magnitude of the t -values by the left and the right thalamus and lastly by a small area in the frontal lobe. Figure 1B shows the main suprathreshold cluster superimposed on an anatomical image.

Since the precuneus/paracentral gyrus region showing congruency effects (i.e., a significant incongruent > congruent contrast) overlapped with the area showing lexical frequency effects, a study of the time course of the BOLD response was conducted on this area. First, a VOI was defined including all suprathreshold voxels of the incongruent > congruent contrast, because this was the contrast of main theoretical interest. Second, a deconvolution analysis was performed on this VOI for each study participant. Third, the event-related deconvolution plots representing the β weight values along time for each of the four stimulus types (high frequency congruent, high frequency incongruent, low frequency congruent, low frequency incongruent) and each participant were generated relative to the prestimulus baseline. The average plots (across participants) of the β weight values along time for each stimulus type are presented in Figure 1C. A new analysis defining the VOI according to an inclusive mask with the low > high frequency contrast was also performed showing very similar results. The time course of the β weights shows a deactivation of the precuneus/paracentral gyrus relative to the prestimulus baseline for the four depicted conditions. Instead of considering null events as a baseline condition to measure increases (activation) and decreases (deactivation) of activation, similarly to ERPs, a prestimulus baseline of four seconds duration (two volumes) was taken into account. The magnitude of the deactivation was modulated by both, the syllable-color congruency and the lexical frequency factors. This is further highlighted by the difference waves shown in the lower panel. Interestingly, the word incongruent–word congruent difference wave goes lower and peaks earlier than the low–high lexical frequency difference wave. Table IV shows the results of the serial ANOVAs performed on the β weights at each

TABLE II. Main brain regions showing significant changes in BOLD response for the contrast low frequency–high frequency words (corrected for multiple comparisons at FDR = 0.05)

Region	Coordinates	N voxels	Max t value
Pre/SMA	−3, 17, 45	13,765	8.41
Precuneus	9, −55, 40	21,969	−7.61
Left inferior frontal/insula	−37, 28, 4	26,032	7.21
Right inferior frontal/insula	42, 17, 4	9,327	6.81

Coordinates (x,y,z) are in Talairach space and indicate local maxima.

A. Low > High Frequency **B. Incongruent > Congruent** **C. Time course** **Figure 1.**

(A) Low frequency words > high frequency words contrast. Low frequency words lead to more activity (red color) in the pre SMA and the left and right inferior frontal/insula and deactivation (blue colors) in the precuneus/paracentral gyrus region. Results shown corrected for multiple comparisons using a FDR = 0.05. For t -values consult labels on the left of the color scale.

(B) Incongruent > congruent contrast. Incongruent words show deactivation (blue color) in the precuneus/paracentral gyrus region, the left and right thalamus and the superior frontal gyrus. Results shown corrected for multiple comparisons using a FDR = 0.05. For t -values consult labels on the right of color scale.

(C) Left: Event-related deconvolution plots showing the time course of the β weights in the precuneus/paracentral gyrus cluster. Right: β weight difference waves illustrating the timing of the effects of lexical frequency and syllable/color congruency.

measurement point (every 2 s) from stimulus presentation until 18 s poststimulus. The congruency effect is an early effect that is seen from seconds 2 to 6, whereas the lexical frequency effect has a later onset and lasts from seconds 6

TABLE III. Brain regions showing significant decreases in BOLD response for the contrast incongruent–congruent words (corrected for multiple comparisons at FDR = 0.05)

Region	Coordinates	N voxels	Max t value
Precuneus/Paracentral gyrus	3, -47, 52	7,703	-8.1
Left thalamus	-7, -22, 10	1,169	-7.9
Right thalamus	10, -22, 10	656	-6.1
Superior frontal gyrus	3, 46, 10	1,001	-5.1

Coordinates (x,y,z) are in Talairach space and indicate local maxima.

to 8. Furthermore, the peak F value is larger for the congruency than for the lexical frequency effect.

DISCUSSION

The present investigation revealed robust and dissociable brain activations for lexical frequency and syllable-color congruency, but no interaction of the two factors was observed. With regard to lexical frequency, greater activation was obtained for low relative to high frequency words in the left pre/SMA region, and in the insula/inferior frontal cortex bilaterally. In addition, an enhanced deactivation in the precuneus was observed for low relative to high frequency words. With regard to syllable-color congruency, deactivation in the precuneus/paracentral gyrus, the left and the right thalamus and in a small area in the frontal lobe was greater for incongruent than for congruent stimuli. Although a deactivation pattern was observed for the precuneus region for both, the lexuality and syllable-color congruency factors, BOLD deconvolution revealed a remarkable difference in timing of the two effects. Thus, the two main effects of lexical frequency and syllable-color congruency on brain activation show an important dissociation between lexical and sublexical processes.

Behavioral responses confirmed previous data: Lexical decision was slower and less accurate to words with low compared to high lexical frequency, as predicted by models of visual word recognition, and replicated in many studies. On the other hand, effects of congruency were observed only for accuracy in low frequency words. Thus, low frequency words were more sensitive to syllabic effects. This is consistent with previous findings with the

TABLE IV. Serial ANOVAs performed from 2 to 14 s following stimulus presentation

Time point (s)	2.0	4.0	6.0	8.0	10.0	12.0	14.0
Congruency, $F(1,19)$	4.92	18.27	5.28	1.04	2.80	1.58	3.23
Frequency, $F(1,19)$	1.09	2.54	4.98	9.24	1.84	0.95	0.01
Con $\times$ Freq	0.16	0.45	0.09	0.14	0.22	0.03	0.28

$P < 0.05$; $P < 0.01$; $P < 0.001$.

same stimuli showing that early ERP effects of syllable-color congruency were only obtained for low frequency words [e.g., Carreiras et al., 2005a]. Nonetheless, the fMRI data showed no interaction but two main effects. The absence of an interaction between the two variables is also consistent with other behavioral experiments that showed similar syllabic effects for low and high frequency words [e.g., Carreiras et al., 1993; Perea and Carreiras, 1998]. Thus, it seems that syllabic effects for low frequency words are very robust, but for high frequency words are more elusive and very much depend on the strength of the manipulation, the paradigm, and/or the particular dependent measure used. Therefore, these effects suggest that syllabic processing seems to be mandatory when reading multisyllabic words in languages such as Spanish, although weaker and thus not always visible for high frequency words, which can be accessed faster than low frequency words through a direct lexical route.

In the subsequent sections we will first discuss lexical frequency effects, followed by discussion of the main and novel findings of the present study regarding the syllable-color congruency effects.

Lexical Frequency Effects

The increase of activation for low as compared to high frequency words in left pre/SMA region, and in the insula/inferior frontal cortex bilaterally, is replicating previous fMRI experiments that reported activity in similar areas during reading of irregular low frequency words and/or pseudowords, but not of high frequent words [e.g., Carreiras et al., 2006, 2007; Fiebach et al., 2002, 2007; Fiez et al., 1999; Mechelli et al., 2003, 2005]. This has been interpreted as indicating an involvement of this region in phonological processing or phonological retrieval [see also Bookheimer, 2002]. In fact, the behavioral data (errors and reaction time) indeed suggest that low frequency words are more difficult to process. Other reasons seem to favor an interpretation in terms of differential recruitment of lexico-phonological processes: First, there is a large amount of data suggesting that activation of the inferior frontal area is driven by grapheme-to-phoneme mapping. Second, it has been demonstrated with other techniques that lexico-phonological processes are recruited in the processing of multisyllabic stimuli. Therefore, it seems likely that lexico-phonological processes are differentially involved in the visual word recognition of low and high frequency words that is reflected in different activation levels of the insula/inferior frontal cortex and the pre-SMA. This is consistent with cognitive models of lexical decision, which 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.

On the other hand, explanations in terms of less effortful retrieval for high frequency words [e.g., Chee et al., 2002] or semantic processing [e.g., Devlin et al., 2003] have also

been proposed, and on the bases of the present data we cannot exclude such accounts. In fact, in the left prefrontal cortex, a double dissociation has been observed in ventral and dorsal regions for semantic and phonological tasks, respectively [Devlin et al., 2003; McDermott et al., 2003; Roskies et al., 2001]. Specifically, it has been proposed that the left pars triangularis is activated by semantic more than phonological tasks; and the left premotor cortex is activated by phonological more than semantic tasks. More recently, Mechelli et al. [2005] suggested that different inferior frontal regions are engaged in different semantic and phonological processes. In particular, they proposed that three different inferior frontal regions are differentially activated by words and pseudowords with (1) a ventral inferior frontal area more engaged by lexico-semantic processing, (2) a left precentral area 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. Thus, importantly, the inferior frontal activation in the present experiment for low frequency words compared to high frequency words 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].

For the greater decrease of activation for low versus high frequency words in the precuneus region, we would like to consider two interpretations. First, the finding may reflect the differential engagement of semantic processing by low and high frequency words. The precuneus has been found activated by the recollection of words [Fletcher et al., 1995; Krause et al., 1999], and when words were contrasted to letter strings [Jessen et al., 1999]. This has been interpreted in the sense that the precuneus is part of a network processing semantic associations. In our case, the differential activation for high and low frequency words could reflect the more pronounced semantic associations of high frequency words.

As an alternative interpretation, we would like to offer that high and low frequency words differentially engage attentional resources (see below for a description of how activity in of the precuneus may be related to the allocation of attentional resources).

In sum, the differential activation for low versus high frequency words in the inferior frontal region, pre/SMA, and precuneus cannot be accounted by sublexical processes, but seem to entail areas recruited for semantic and/or lexico-phonological processes.

Syllable Color Congruency Effects

At the outset of our discussion of syllable-color congruency effects, it is important to recall that the color manipulation was completely irrelevant to the lexical decision task. The observation that syllable-color congruency is reflected by brain activations therefore suggests that syllable information is registered early and automatically. A

more pronounced deactivation has been found for the syllable-color incongruent condition in the precuneus/paracentral gyrus, the left and the right thalamus, and in a small area in the frontal lobe. As stated above, the precuneus has been related to semantic processes in prior work [Fletcher et al., 1995; Jessen et al., 1999; Krause et al., 1999]. Deactivation of this region has also been observed when pragmatically anomalous sentences and morphosyntactic anomalous sentences were compared to a low-level fixation condition [Kuperberg et al., 2003]. Although these findings seem to suggest that this region is involved in specific aspects of language processing, it has also been reported as deactivated in a variety of cognitive tasks, because it has a high resting baseline activity [Binder et al., 1999; Mazoyer et al., 2001; Raichle et al., 2001; Shulman et al., 1997]. The medial parietal/precuneus region is one of the four principal regions that show “task independent decreases” (TIDs) according to Gusnard and Raichle [2001]. The other three regions showing TIDs whenever the brain is engaging in some kind of demanding cognitive activity are the superior and inferior medial frontal regions, and posterior lateral parieto-occipital cortex. Correlated activity between these areas has been demonstrated, leading to the notion of a default mode network [e.g., Biswal et al., 1995; Fox et al., 2005; Greicius et al., 2003; Raichle and Snyder, 2007; Sorg et al., 2007].

This led to the hypothesis that differential deactivation of this region in association with various tasks may reflect differentially focused attention to such tasks. Thus, in the present experiment the degree of activation may result in the differential allocation of attentional resources devoted to process color syllable congruent and incongruent stimuli. If this is the case, differences would not be specific to processes related to visual word recognition, but they would suggest that syllable-color congruent and incongruent stimuli (as well as high and low frequency words) need different amounts of attentional resources to be processed. Enhanced deactivation could be caused by the more difficult conditions in the contrasts of low versus high frequency words and of color/syllable incongruent stimuli versus congruent stimuli. In any case, perceptual/linguistic match or mismatch has processing consequences in the brain that only would occur if the system processes syllables in the first place. Although both lexical frequency and syllable-color congruency led to differential deactivations, we will turn to important differences in the timing of the two effects in the next section, which, we suggest, place them in two different processing stages: sublexical and lexical.

Before addressing the timing differences, we would like to briefly consider an alternative interpretation of the activation differences in the precuneus. It could be that they reflect semantic association differences for high versus low frequency words and for syllable-color congruent versus incongruent stimuli. Carreiras et al. [2005a] in an ERP experiment using similar stimuli have found effects of both congruency and lexical frequency on the N400 component. In particular, the larger amplitude of the N400 for

syllable-color congruent stimuli was interpreted as the result of an inhibitory process, because a higher number of lexical candidates must be inhibited in this condition compared to the syllable-color incongruent condition. In this regard, it is interesting to note that the thalami (found more active in congruent relative to incongruent stimuli in the current experiment) are involved in multiple processes that directly or indirectly support cortical language functions. For instance, the thalamus has been shown to be part of a fronto-striato-thalamic loop involved in working memory, monitoring of tasks performance, object recall, and lexical retrieval [Crosson et al., 1999, 2003; Kraut et al., 2002]. In particular, it has been suggested that the thalamus is involved in selective engagement of cortical mechanisms necessary to perform language tasks, having its greatest effects on lexical retrieval [Crosson, 1999]. Selective engagement mechanisms can be used to hold lexical-semantic information on line in the service of working memory, in addition to facilitating the selection of a precise lexical item [Nadeau and Crosson, 1997]. Following this reasoning, the different activation for syllable-color congruent and incongruent stimuli may reflect differences in the inhibition-selection of lexical candidates in connection with the processing of frontal regions. This may explain the activation of the left and right thalamus and the frontal region as well.

Time Course for Syllabic and Lexical Effects

The fact that two different neural systems were modulated by lexical frequency and syllable-color congruency provides new evidence for how the brain makes the distinction between lexical and sublexical effects. However, both variables modulated activation in a common area, the precuneus. Therefore, we analyzed the effect of the two variables in this region in greater depth looking for similarities and differences in the pattern of de-activation. The time courses of β -weights (Fig. 1C) showed that the peaks of de-activation for lexical frequency and syllable-color congruency in the precuneus have a remarkably different latency with a much earlier deactivation peak for the latter. This suggests that the two variables are influencing processes with a different time course. Interestingly, even though the temporal resolution of the BOLD signal is much poorer than the ERP signal, it is striking that both show the same relative time course for the two variables, although on a very different temporal scale. Carreiras et al. [2005a] have shown earlier effects of syllable-color congruency than of lexical frequency in the ERP signal. Thus, the present data support the idea of sublexical—syllabic—processing during visual word recognition of multisyllabic words.

CONCLUSION

The present results show a dissociation between lexical and sublexical processes by manipulating lexical frequency

and color/syllable congruency. Lexical and sublexical processes during visual word recognition activated different brain networks. Lexical frequency activated inferior frontal areas bilaterally, left pre/SMA and precuneus suggesting engagement in lexical-phonological and/or in semantic processes. In contrast, color/syllable congruency enhanced deactivation in the precuneus/paracentral gyrus and in the left and the right thalamus for incongruent compared to congruent stimuli. Interestingly, the time course of the BOLD response in the precuneus depending on whether the effect was caused by the color/syllable congruency or the lexical frequency manipulation peaked earlier for colour/syllable congruency, suggesting that the computation of sublexical and lexical processes modulates different brain areas with an earlier computation of sublexical processes. Further research will uncover how these regions are functionally connected during the process of word recognition.

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