

available at www.sciencedirect.comwww.elsevier.com/locate/brainres**BRAIN
RESEARCH****Research Report****Modulation of brain regions involved in word recognition by homophonous stimuli: An fMRI study**Randy Lynn Newman^{a,*}, Marc F. Joanisse^b^aDepartment of Psychology, Acadia University, Wolfville, NS, Canada^bDepartment of Psychology, The University of Western Ontario, London, ON, Canada

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ABSTRACT

We used rapid event-related fMRI to explore factors modulating the activation of orthographic and phonological representations of print during a visual lexical decision task. Stimuli included homophonous word and nonword stimuli (MAID, BRANE), which have been shown behaviorally to produce longer response times due to phonological mediation effects. We also manipulated participants' reliance on orthography by varying the extent to which nonword foils were orthographically typical (wordlike context) or atypical (non-wordlike context) of real words. Key findings showed that reading low-frequency homophones in the wordlike context produced activation in regions associated with phonological processing (i.e., opercular region of the left inferior frontal gyrus [IFG; BA 44]), the integration of orthography and phonology (i.e., the inferior parietal lobule (IPL), and lexicosemantic processing (i.e., left middle temporal gyrus, [MTG]). Pseudohomophones in the wordlike context produced greater activity relative to other nonword trials in regions engaged during both phonological processing (i.e., left IFG/precentral gyrus; BA 6/9), and semantic processing (triangular region of the left IFG; BA 47). Homophonous effects in the non-wordlike context were primarily isolated to medial extrastriate regions, hypothesized to be involved in low level visual processing and not reading-related processing per se. These findings demonstrate that the degree to which phonological and orthographic representations of print are activated depends not only on homophony, but also on the word-likeness of nonword stimuli. Implications for models of visual word recognition are discussed.

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1. Introduction

English provides two possibilities for computing a printed word's meaning. Readers can rely directly on the word's printed form (i.e., orthography), or they can translate letters into their phonological percepts and use the resulting phonological representation to compute meaning. While there is an emerging consensus that phonology does play a role in reading,

theories continue to differ in the importance they assign to this mechanism, compared to a direct print-to-meaning route. The so-called dual-route theory (Coltheart et al., 1977, 2001) views reading as taking place via two distinct routes; a direct route that allows for the direct mapping of orthographic representations onto lexical word forms, and an the indirect route for translating orthographic input into a phonological form prior to accessing the word's lexical form. Because of the strong

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role assigned to lexical access in recognizing familiar forms, phonology is deemed to play a weaker role. Instead, the extent of phonology's influence on word recognition is dependent on factors such as word type (e.g., regular, irregular) and word frequency. The original dual-route model held that words (or nonwords) were processed by only one of the two routes; however, the most recent implementation of the dual-route model suggests that words are processed in parallel along both the direct and the indirect route (Coltheart et al., 2001).

In contrast to the dual-route theory of reading, strong phonological theories deny the existence of a direct pathway from orthography to semantics; instead, such theories argue that computation of word meaning is always phonologically mediated (for review see Frost, 1998). An alternative to both weak and strong phonological theories is the connectionist "triangle" model of visual word recognition (Harm and Seidenberg, 2004; Seidenberg and McClelland, 1989). The model proposes a single mechanism for visual word recognition, in which computation of word meaning is achieved via a distributed pattern of activation across orthographic, phonological and semantic units. Recognizing a single word is thus the result of the dynamic interplay between these three sources of information processing. The relative weighting of these units may be altered, thus influencing the extent to which a given process (i.e., phonology, orthography) contributes to word recognition. The triangle model differs from the most recent version of the dual-route model in that the latter posits discrete, word specific representations of each familiar word. In contrast, the triangle model represents each word as a unique distributed pattern of activation across phonological, orthographic, and semantic units.

Many of the experimental manipulations performed to investigate phonological influences on reading have involved homophones and/or pseudohomophones. Homophones are words that share identical phonologies while possessing different orthographic and semantic representations (e.g., STEAL/STEEL; KNIGHT/NIGHT). Similarly, pseudohomophones are nonwords that sound like real words (e.g., BRANE). The interest in homophones stems from the assumption that if phonological processes mediate word recognition, then a homophone (or pseudohomophone) will activate orthographic and/or semantic information associated with the homophonic partner (or the pseudohomophone's base word). As a result, task performance should be reduced compared to other words and nonwords of similar length and orthographic neighborhood (and frequency in the case of homophones).

Evidence for homophone and pseudohomophone effects comes from a variety of experimental contexts. In a semantic categorization task, Van Orden (1987) found that participants made more false positive errors when targets (e.g., ROWS) were homophonic to the prompted category (e.g., *type of flowers*), compared to when an orthographically similar form was presented from a different semantic category (e.g., ROBS). Van Orden et al. (1988) extended these findings to pseudohomophone foils, where more false alarms were observed for pseudohomophones (e.g., ROZE) in a similar context, compared to controls (e.g., BOZE). Homophone and pseudohomophone effects have also been observed in other types of tasks including lexical decision, where response times to homo-

phones tend to be slower than to non-homophonous control words (Ferrand and Grainger, 2003; Pexman et al., 2001; Rubenstein et al., 1971). Similarly, lexical decisions to pseudohomophones are slower and more error prone than to non-pseudohomophone nonwords (McCann et al., 1988; Seidenberg et al., 1996; VanHoy and Van Orden, 2001).

Homophone and pseudohomophone effects like these are often attributed to phonological decoding processes that result in the activation of orthographic and/or semantic features of the homophonous partner or base word (Pexman et al., 2001; Seidenberg et al., 1996). Recent research has focused on defining the various aspects of lexical structure (e.g., frequency, orthographic familiarity) that modulate these effects. Homophone effects have been shown to be dependent on frequency, such that greater homophone effects occur for low-frequency homophones with high-frequency partners (MAID-MADE; Ferrand and Grainger, 2003; Pexman et al., 2001). The influence of word frequency on the size of the homophone effect has been attributed to a spelling check mechanism that involves semantic to orthographic feedback (Van Orden, 1987). According to the spelling check account, once the phonological representation of the homophone has activated the meaning associated with both homophones, the spelling of both meanings is retrieved and compared with the orthographic representation of the presented word to determine which meaning is correct. Van Orden (1987) proposed that the spelling check procedure is less efficient for low-frequency homophones leading to slower and more error prone responses.

Aside from the influence of homophone frequency, studies have shown that processing of homophones and pseudohomophones are influenced by the orthographic nature of nonword foils. Pexman et al. (2001) found that homophone effects in a lexical decision task were attenuated when word trials (i.e., homophones and controls) were presented in the context of nonwords that were comprised of less word-like word bodies (e.g., OLPH in TOLPH). In contrast, when word bodies were more word-like (e.g., ADE in CADE), homophone effects, particularly for low-frequency homophones with high-frequency partners, were observed. Similarly, in both speeded naming and lexical decision tasks, Vanhoy and Van Orden (2001) observed larger pseudohomophone effects when stimuli had word bodies more frequently encountered in the English language (e.g., BOCKS) compared to novel word bodies (e.g., BAWX). In accounting for their results, Pexman et al. (2001) suggested that when words are easily discriminated from nonwords on the basis of visual information, less phonological processing will be required hence attenuating homophone effects.

In summary, studies of homophone effects for both homophones and pseudohomophones have shown that phonological representations of printed words and nonwords influence lexical and semantic decisions during reading. The data suggest that phonological representations are activated in an automatic way during reading, but that this might be influenced by task-related factors such as the context in which words are being presented.

In the current study, we introduce new data on this topic by examining homophone and pseudohomophone effects within the context of a functional magnetic resonance

imaging (fMRI) study. By identifying which regions are activated by the presence of homophonous stimuli, and furthermore by examining those factors which modulate the extent of homophonous effects in the brain, we add to the existing literature pertaining to the location of brain regions sensitive to phonological and orthographic processing of print. Prior to outlining the specifics of the current study, we briefly review the neuroimaging literature pertaining to reading-related brain regions.

1.1. Neural bases of reading

Evidence from a number of neuroimaging has begun to converge on a set of brain regions, primarily within the left cerebral hemisphere, that are involved in the different aspects of visual word recognition. Regions associated with phonological processing of visual word forms include the left prefrontal cortex, particularly the inferior frontal gyrus (IFG, BA 44/45) and precentral gyrus (BA 6; Bodke et al., 2001; Fiez et al., 1999; Gold et al., 2005; Poldrack et al., 1999), as well as the left supramarginal gyrus (SMG; McDermott et al., 2003; Sandak et al., 2004) and left posterior superior temporal gyrus (STGp; Simos et al., 2002). The left intraparietal lobule (IPL) is proposed to support the mapping to orthographic representations to phonological representations during reading (Booth et al., 2002; Cao et al., 2006; Chen et al., 2002). Processing within the semantic domain has been found to involve more ventral areas of left IFG (BA 47; Devlin et al., 2003; Poldrack et al., 1999; Wagner et al., 2000), as well as the left posterior middle temporal gyrus (MTGp; Gold et al., 2005; Pugh et al., 1996; Simos et al., 2002).

On the other hand, evidence of an area uniquely specialized for processing words' visual form (compared to other types of visual objects) is somewhat more controversial. Some have argued there is a so-called visual word form area (VWFA) within the left occipitotemporal/mid-fusiform cortex (hereafter referred to as the OT region), which is specialized for computing visual word forms (Cohen et al., 2002; McCandliss et al., 2003). However, this view has been challenged largely on the basis that activation in the OT region has occurred in tasks that do not involve visual word recognition, such as perceiving or naming visual objects (Moore and Price, 1999; Van Turennout et al., 2000). An alternative hypothesis is that the OT region supports the integration of orthographic features of a stimulus with higher order properties such as its sound and meaning (Devlin et al., 2006).

Techniques such as magnetoencephalography (MEG) and electroencephalography (EEG) serve as complementary measures to fMRI by providing information about the timing of the component processes involved in visual word recognition. MEG studies, which have the added benefit of providing spatial, in addition to temporal, information, have shown evidence for early activation in OT regions (~150 ms post stimulus onset) that is hypothesized to support visual word form processing (Simos et al., 2002, 2009; Wilson et al., 2007). Activation associated with phonological processing of print has been found to occur later in the STGp, anterior IFG (Wilson et al., 2007), and MTGp (Simos et al., 2002). A recent MEG study suggested, however, that under certain task requirements activation in the STGp and IFG may occur too late to be

involved in phonological processes that are involved, for instance, in assessing a letter string's lexicality (Simos et al., 2009).

Several EEG studies are particularly relevant to the current study, as they involved the use of homophonous stimuli to assess phonology's role in reading-related tasks (Braun et al., 2009; Newman and Connolly, 2004; Niznikiewicz and Squires, 1996; Ziegler et al., 1999). While the majority of these studies found evidence of homophonous effects, the timing of such effects varied considerably across studies, ranging from effects occurring as early as 150 ms post-stimulus (Braun et al., 2009) to those occurring at 400 ms and even later (Newman and Connolly, 2004; Ziegler et al., 1999). There are a number of plausible explanations for these mixed results, including task differences (e.g., semantic categorization versus lexical decision) as well as the influence of factors discussed above that are known to influence homophonous effects, such as word frequency and the orthographic nature of nonword foils.

Results of MEG and fMRI studies have been argued to support a dual mechanism account of reading (Fiebach et al., 2002; Jobard et al., 2003; Wilson et al., 2007). In a representative study, Jobard et al. (2003) used the dual route framework for interpreting the results of a large meta-analysis conducted on neuroimaging studies of word reading. The meta-analysis suggested that mechanisms underlying the operation of the direct route are most consistently associated with activation in the OT region, the inferior and middle temporal gyri, and the triangular region of the IFG. In contrast, operation of the phonologically mediated route was proposed to involve activation of the STG, the SMG, and the opercular regions of the IFG. The data used in the meta-analysis were from studies that involved dichotomous comparisons, such as words versus nonwords. The rationale, for example, was that according to the dual-route theory, words have a stored visual representation and should therefore reveal brain regions involved in direct access to the lexicon. On the other hand, nonwords, which lack a lexical representation, should reveal those regions involved in phonological mediation. The limitation of such comparisons is that they do not speak to the existence of interactive effects during reading. For instance, while a nonword may not have a lexical representation, its orthographic similarity to a word can modulate the degree to which phonology is activated (Pexman et al., 2001). Furthermore, modeling work has shown that nonwords, and more specifically, pseudohomophones that are orthographically similar to their base word and that come from a large orthographic neighborhood, are capable of activating their base word's semantic representations via direct connections from orthography to semantics (Harm and Seidenberg, 2004). Likewise, comparing words and nonwords does not directly assess the potential for feedback between, for instance, phonological and orthographic units, which many models of visual word recognition now incorporate into their structures (Coltheart et al., 2001; Harm and Seidenberg, 2004). The present study was designed to allow for examination of interactive effects, including the potential for feedback effects that have been purported to occur during reading (Pexman et al., 2001; Van Orden, 1987). We used an fMRI paradigm designed to examine whether the extent of phonological mediation, and not the absolute occurrence, is influenced by

homophone frequency and orthographic familiarity (i.e., the word-likeness of nonwords). As already mentioned, both of these factors have been shown to produce interactive effects in behavioral studies (Pexman et al., 2001; Vanhoy and Van Orden, 2001).

There is good evidence to suggest that homophonous effects can indeed illustrate how the reading-related brain regions described above interact during reading (Edwards et al., 2005; Gitelman et al., 2005; Simos et al., 2002). A study by Edwards et al. (2005) examined visual word processing strategies during a lexical decision task involving homophonous stimuli. This particular study was conducted in response to mixed behavioral results obtained in lexical decision tasks (LDT) when pseudohomophones were presented as nonword foils. While some studies found that the presence of pseudohomophone foils allows participants to strategically de-emphasize the activation of phonology (Davelaar et al., 1978; Pugh et al., 1994), other findings support the automatic activation of phonological codes during the LDT, regardless of whether or not pseudohomophones are presented as stimuli (Pexman et al., 2001; Ziegler et al., 2001). In an effort to resolve the debate, Edwards et al. (2005) presented word trials (homophones and control words) in the context of one of three different foil types: pseudowords (BLINT), consonant strings (BVRNT), or pseudohomophones (BRANE). A block design was implemented, such that words and only one of the foil types were intermixed within a block of trials. For example, in the pseudohomophone block, words were presented in the context of pseudohomophones only. Results identified a region in the left IFG (BA 44/45) that was modulated by foil type. Activation was greatest when words were presented in the context of pseudohomophones, intermediate when words were intermixed with pseudowords, and least when words were intermixed with consonant strings. These results suggest that the presence of pseudohomophones does not cause participants to alter their response strategy with respect to the activation of phonological mechanisms. The authors interpreted results as supporting the automatic activation of phonological units from orthographic units, with the existence of feedback activation from phonological to orthographic units in order to resolve the ambiguity resulting from the presentation of a homophonous stimulus.

1.2. Current study

The current study builds upon the experimental framework employed in Edwards et al. (2005) to more closely examine the brain basis of reading. Of particular interest is the extent to which phonological information is activated during reading of different word types. We capitalized on factors predicted to modulate phonological activation, namely homophone frequency and the word-likeness of nonword foils. The implementation of a block design in the Edwards et al. (2005) study prevented direct examination of homophone effects; thus, the current study employed a rapid event-related imaging protocol, which permitted the segregation and comparison of homophonous and non-homophonous items. Furthermore, trials were presented at short SOAs (as quickly as once every 2 s), to more closely approximate the behavioral testing paradigms upon which this experiment was modeled.

In order to investigate the extent to which activation of phonological information is reliant on homophone frequency, high-frequency homophones with low-frequency homophone mates were presented as stimuli. These were compared to non-homophonous control words matched for word frequency and orthographic neighborhood. To assess the role of word-likeness on phonological activation, word stimuli were presented in the context of pseudohomophone and non-pseudohomophone (hereafter referred to as pseudowords) foils that either did or did not possess word bodies typical of English orthography (hereafter referred to as wordlike and non-wordlike). In the wordlike context, the word bodies of nonwords resembled English words (e.g., pseudohomophones such as HEET, and pseudowords such as GEET). In the non-wordlike context, nonwords were comprised of novel word bodies (e.g., TOLPH/GOLPH) that were nevertheless phonotactically legal.

We anticipated that activation in brain regions typically involved in phonological processing of print would be modulated by homophone frequency and the word-likeness of nonwords foils. Behavioral evidence for frequency dependent homophone effects as well as pseudohomophone effects provided the basis for our predictions regarding planned contrasts between (a) homophones and control words and (b) pseudohomophones and pseudowords. For the contrast comparing homophones to non-homophonous control words, we expected to observe activation associated with increased involvement of the phonologically mediated pathway for homophones, and in particular for low-frequency homophones, as well as activity related to the process of disambiguating homophones. Similarly, the comparison of pseudohomophones to pseudowords was expected to reveal activity related not only to increased involvement of phonological processing, but also activity associated with mapping the phonological representation of a pseudohomophone to its base word's semantic representation. In addition to contrasts involving homophonous stimuli, those examining context effects (i.e., wordlike vs. non-wordlike) were also performed.

2. Results

2.1. Behavioral results

Table 1 displays the reaction time (RT) and error rates for word and nonword trials. For each subject, responses times (RTs) more than two standard deviations above or below the mean in all conditions were considered outliers, and were excluded from the analysis. In addition, only those trials in which participants responded correctly were included in the analysis.

2.1.1. Word trials

For the RT analysis of word trials, we conducted a $2 \times 2 \times 2$ ANOVA with Context [Wordlike, Non-wordlike], Homophony [Homophone, Control], and Frequency [High, Low] treated as a within subjects factors. The main effect of Frequency was significant ($F(1,10)=29.67, p<0.05$), indicating that participants responded faster to high-frequency compared to low-frequency words. No other effects were significant. The mean RTs for homophones compared to non-homophonous controls were in the expected direction for the wordlike context,

Table 1

Stimulus	RT ms (SD)	% Error (SD)	Homophone/ pseudohomophone effect	
			RT difference	% Error difference
Wordlike context				
Homophones (HiFreq+LoFreq)	876 (118)	1.2 (1.3)	+6	-0.2
Non-Homophones (HiFreq+LoFreq)	871 (130)	1.4 (1.4)		
HiHom	844 (136)	0.8 (1.5)	+7	-0.8
HiCtl	837 (116)	0.6 (0.8)		
LoHom	909 (99)	1.6 (1.1)	+5	-0.6
LoCtl	904 (144)	2.2 (2.1)		
Pseudohomophones	946 (108)	3.4 (2.3)	+35	+2.9
Pseudowords	911 (122)	0.5 (0.9)		
Non-Wordlike context				
Homophones (HiFreq+LoFreq)	808 (81)	1.1 (1.2)	-1	-0.2
Non-Homophones (HiFreq+LoFreq)	809 (72)	1.3 (1.3)		
HiHom	763 (87)	0.5 (0.8)	+0	-0.1
HiCtl	763 (71)	0.4 (0.7)		
LoHom	853 (75)	1.8 (1.6)	-2	-0.4
LoCtl	855 (72)	2.2 (1.9)		
Pseudohomophones	846 (68)	1.0 (1.4)	+24	+0.6
Pseudowords	822 (64)	0.4 (0.8)		

Mean response times and error rates for lexical decisions in the wordlike (top) and non-wordlike (bottom) contexts. Homophone/pseudohomophone effects are expressed as the difference in RT/errors between homophones/pseudohomophones and their respective controls. Standard deviations are presented in parentheses.

but not for the non-wordlike context. This trend towards attenuated homophone effects in the non-wordlike context is consistent with behavioral findings in Pexman et al. (2001); however, our statistical power was limited by the inclusion of fewer trials and participants than what is typical of behavioral lexical decision paradigms. We did not observe a trend towards larger homophone effects for low-frequency homophones with higher-frequency partners. In the wordlike context, the homophone effect for low-frequency homophones was 5 ms, while that for high-frequency homophones was 7 ms. It is noteworthy that one participant responded much slower to low-frequency control items than to low-frequency homophones (200 ms difference). Had this participant not been included in the data analysis, the homophone effect for low-frequency items would have been 21 ms compared to 6 ms for high-frequency homophones.

We also performed a similar $2 \times 2 \times 2$ ANOVA on error rates. For this analysis the main effect of frequency was significant ($F(1,10)=18.73, p<0.001$), and was due to higher error rates for low-frequency items compared to high-frequency items. None of the other effects were significant.

2.1.2. Nonword trials

Response times for nonwords trials were analyzed with a 2×2 (Context [Wordlike, Non-wordlike] \times Homophony [Pseudoho-

mophone, Pseudoword] ANOVA. The main effect of Context ($F(1,10)=15.27, p<0.001$) was significant, as participants responded more slowly to wordlike nonwords compared to non-wordlike nonwords. The main effect of Pseudohomophony ($F(1,10)=5.85, p<0.05$) was also significant, and was attributable to slower responses for pseudohomophones compared to pseudowords. Although the magnitude of the pseudohomophone effect was larger in the wordlike compared to the non-wordlike context, the interaction between Context and Pseudohomophony was not significant ($p > 0.05$).

Analysis of error rates revealed a main effect of Context ($F(1,10)=11.01, p<0.001$), a main effect of Pseudohomophony ($F(1,10)=20.28, p<0.001$), as well as an interaction between these two variables ($F(1,10)=42.25, p<0.001$). Further analysis revealed that participants made significantly more errors for pseudohomophones compared to pseudowords in the wordlike context; however, no such effect was observed in the non-wordlike context. These results are consistent with Vanhoy and Van Orden's (2001) finding that pseudohomophone effects during lexical decision are attenuated when orthographically dissimilar nonwords are presented as foils.

2.2. fMRI results

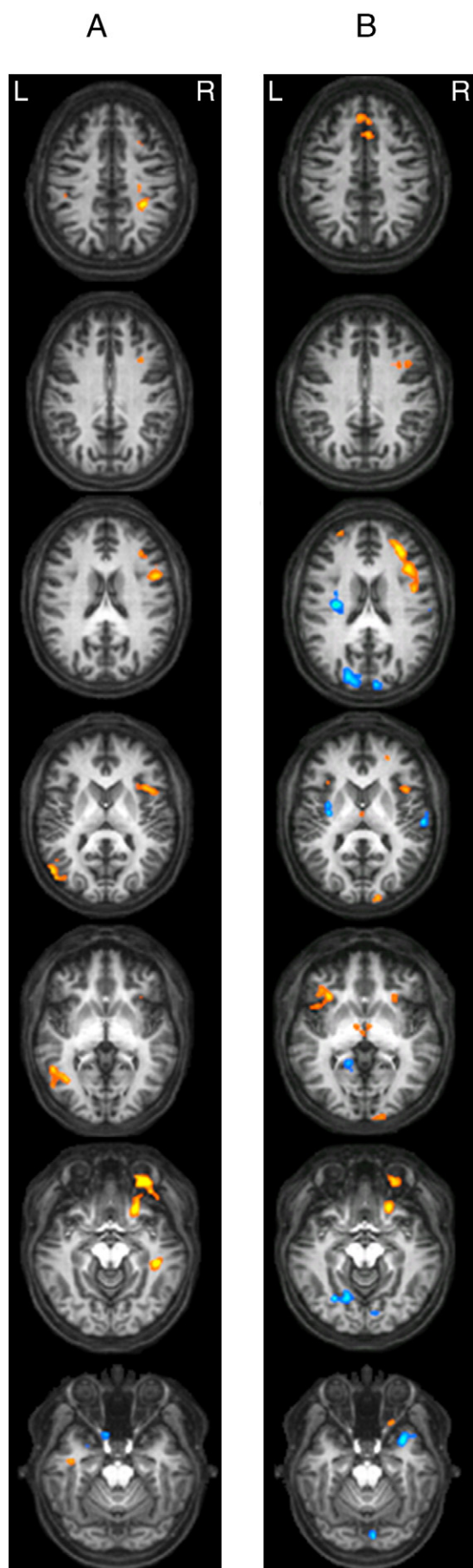
2.2.1. Context effects

Fig. 1, panel A, illustrates brain regions showing a main effect of List Context for word trials. Reading words in the wordlike context compared to the non-wordlike context was associated with activation in the left middle frontal gyrus (MFG; BA 6) and the left posterior middle temporal gyrus (MTG; BA 37). Significant activation increases were also observed in a number of right hemisphere regions including the right IFG (BA 44/45), the right precentral gyrus extending into the insula (BA 44/13), the right MFG (BA11/47), the right parahippocampal gyrus of the limbic lobe (BA 36), and the right inferior parietal lobule (IPL; BA 40). The only activation that was stronger for words in the non-wordlike context than words in the wordlike context was a sub-gyral region in the left temporal lobe (BA 20), which was only marginally above the cluster threshold.

Nonwords presented in the wordlike context caused stronger activation than nonwords presented in the non-wordlike context in a number of regions (cf. Fig. 1, panel B). In the frontal cortex, increases were observed bilaterally in the IFG (BA 47) and the superior frontal gyri (BA 10), in the left middle frontal gyrus (BA 46), and in the pre-motor region of the right superior frontal gyrus. In the occipital lobe, activation was observed in the cuneus (BA 17/18) region of the occipital lobe. Nonwords in the non-wordlike context caused greater activation than nonword trials in the wordlike context in the left posterior aspect of the insula (BA 13), and in the lingual gyrus and cuneus region of the occipital lobe. In the right hemisphere, stronger activation was observed in the inferior frontal gyrus extending into the superior temporal cortex, in the transverse temporal gyrus (BA 41/42) and in the posterior lobe of the cerebellum.

2.2.2. Homophone and pseudohomophone effects

The red regions in Fig. 2, panel A illustrate those regions respecting the predicted 3-way interaction (i.e., greater

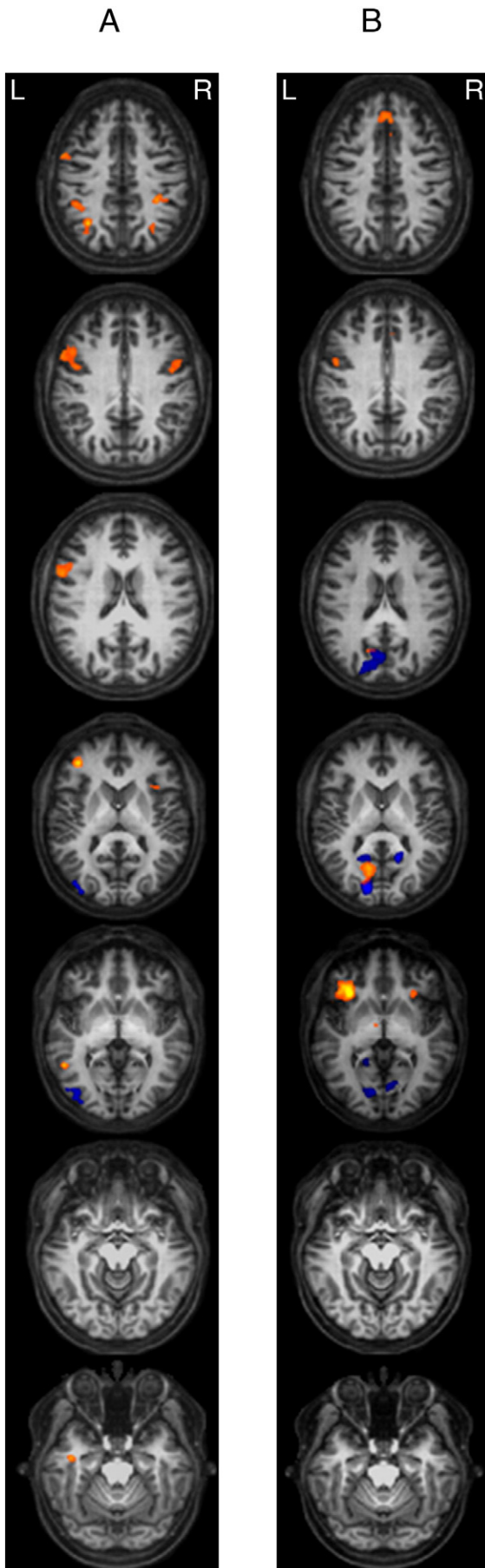


activation for the low-frequency homophones presented in the wordlike context, compared to all other conditions). Low-frequency homophones presented in the wordlike context yielded widespread activation in the left IFG encompassing BA 44 and the left IFG/MFG (BA 10/46). Reading low-frequency homophones was also associated with greater activation in the left MTG (BA 22), and the left IPL (BA 40). A number of right hemisphere regions were also activated, including the IFG (BA 9), the insula, the IPL (BA 40), and the SPL (BA 7). In order to highlight the role that context plays in the engagement of reading-related brain regions, the blue regions in panel A illustrate those regions where low-frequency homophones presented in the non-wordlike context exhibited greater activation than all other word trials. The only area showing reliable activation was the middle occipital gyrus (BA 19). Also illustrated in Fig. 2, panel B, are those regions respecting the predicted Homophony x Context interaction such that wordlike pseudohomophones showed greater activity compared to all other nonwords. Wordlike pseudohomophones (cf. red regions Fig. 2B) exhibited activation in the left IFG (BA 9) extending into the precentral gyrus (BA 6), and the middle and superior frontal gyri (BA 6/8). The most extensive region of activation for wordlike pseudohomophones, however, was observed in the ventral aspect of the left IFG (BA 47/45). Finally, the left posterior cingulate gyrus extending into the cuneus region of the occipital lobe (BA 31/30) showed greater activation for wordlike pseudohomophones. As was the case for homophone effects, context played a key role in the presentation of homophonous effects. Reading non-wordlike pseudohomophones (cf. blue regions Fig. 2B) compared to all other nonword trials caused activation in the thalamus and in visual processing regions, specifically the left cuneus (BA 17/18) and the right lingual gyrus (BA 18/19).

3. Discussion

The present study has revealed the interplay of brain regions subserving phonological, orthographic and semantic features of words during a lexical decision task. Of particular interest

Fig. 1 – Effects of list context on neural activity for the contrast involving (A) words presented in the wordlike context compared to words in the non-wordlike context, and (B) nonwords presented in the wordlike context compared to nonwords in the non-wordlike context. For A and B, red regions represent those regions where the wordlike context exhibited greater activation than the non-wordlike context; blue regions represent the opposite pattern of activation. The statistical maps have been thresholded at $p < 0.001$ uncorrected with a minimum cluster size of 300 mm^3 . The z coordinates for the axial slices shown from top to bottom are as follows: +40, +30, +20, +10, 0, -10, -20. L and R indicate left and right hemisphere, respectively. Talairach coordinates and cluster size are given in Appendix B.



was the phonological mediation of print recognition due to homophony. It has been theorized that activation of a homophonous item's phonological representation also leads to activation of the orthographic and semantic representations associated with its homophone partner or base word. However, the word-likeness of nonwords also appears to modulate these effects (Pexman et al., 2001; Vanhoy and Van Orden, 2001).

Our study examined the influence of word frequency on homophone effects and also the neural basis of pseudohomophone effects. We predicted that reading homophones of varying frequency would modulate activation in brain regions involved in phonological processing. More specifically, evidence of greater phonological activation was anticipated for low-frequency homophones relative to their higher-frequency mates. We also predicted that the word-likeness of nonword foils would influence the degree to which phonological codes are activated following the presentation of a homophonous stimulus. Specifically, we anticipated that regions involved in processing the phonological form of homophones would be less activated when word trials were presented in the context of less word-like nonwords. Similarly, we anticipated that neural correlates of pseudohomophone effects would be reduced when pseudohomophones themselves were less word-like. At a more general level, we anticipated that reading-related regions involved in the processing of words and nonwords would be affected by the word-likeness of nonword stimuli.

3.1. Homophone effects

A number of studies have shown that in the course of making lexical decisions on homophones, activation of phonological information leads to activation of the semantic representations associated with the presented homophone as well as the homophone partner. Resolving the resulting semantic ambiguity has been argued to involve a spelling check mechanism in which the orthographic form of the presented

Fig. 2 – (A) Red regions represent regions where low-frequency homophones presented in the wordlike context exhibited greater activation than all other word trials; blue regions represent regions where low-frequency homophones presented in the non-wordlike context exhibited greater activation than all other word trials. (B) Red regions represent regions where wordlike pseudohomophones exhibited greater activation than other nonwords items; blue regions represent regions where non-wordlike pseudohomophones exhibited greater activation than all other nonword trials. The statistical threshold was $p < 0.001$ (uncorrected) with a minimum cluster size of 300 mm^3 . The z coordinates for the axial slices shown from top to bottom are as follows: +40, +30, +20, +10, 0, -10, -20. L and R indicate left and right hemisphere, respectively. Talairach coordinates and cluster size are given in Appendix B.

word is compared to those of the activated meanings (Van Orden, 1987). Alternatively, parallel input from the orthographic pathway (orthographic-semantics) could provide disambiguating information that results from processing along the phonological pathway (Harm and Seidenberg, 2004). At the behavioral level, the ambiguity caused by phonological mediation results in delayed and more error prone responses, a finding often referred to as a homophone effect. In the current study, we observed a neural correlate of a homophone effect in several reading-related regions including the left IFG encompassing BA 44 and 45, the left posterior MTG, and the left inferior parietal lobule. It has been established that the pars opercularis of the left IFG (BA 44) supports aspects of phonological processing (Bodke et al., 2001; Fiez et al., 1999; Gold et al., 2005; Poldrack et al., 1999), and for that reason has been linked to processing subserved by the phonological route (Fiebach et al., 2002; Jobard et al., 2003). In contrast to the pars opercularis, the pars triangularis of the left IFG (BA 45) has been associated with semantic processes (Devlin et al., 2003; Poldrack et al., 1999; Wagner et al., 2000) such as selection from amongst competing representations (Thompson-Schill et al., 1997) and has been linked to processing along the lexicosemantic/direct route (Fiebach et al., 2002; Jobard et al., 2003). Activation of both these regions in the current study suggests that processing of low-frequency homophones presented in the wordlike context involves phonological and semantic processing. The pars opercularis may be involved in the assembly of the phonological form of the printed word; an operation supported by the phonological pathway. In contrast, the pars triangularis may be involved in processes related to resolving the ambiguity that results from phonologically mediated activation of a homophone's semantic forms. That is, activation of the phonological form of a homophone (e.g., bare) results in the activation of multiple semantic representations (e.g., naked and animal). Resolving this ambiguity necessitates the selection of the appropriate semantic form from amongst competing representations, a process that is not inconsistent with past arguments regarding the role of the pars triangularis (Thompson-Schill et al., 1997). Our results, however, do not allow us to differentiate whether the process of selecting the correct semantic representation involves a spelling check mechanism (i.e., semantic to orthographic feedback) or alternatively, one that involves parallel activation of the direct route.

In addition to increased activation of the left IFG, reading low-frequency homophones was associated with increased activation in the posterior MTG. This region has been previously associated with semantic processing (Gold et al., 2005; Jobard et al., 2003; Pugh et al., 1996; Sandak et al., 2004; Simos, et al., 2002) and with processing along the direct (or lexicosemantic) route in particular (Fiebach et al., 2002; Jobard et al., 2003). While all word trials would be expected to produce activation of this region, the semantic ambiguity resulting from presentation of a homophone may have increased processing demands, which in turn would account for the higher activation in the posterior MTG observed for low-frequency homophones relative to other word trials. While we do not dispute the link between posterior MTG activation and semantic processing, our results do not preclude the possibility that posterior MTG activation is associated with pho-

nologically mediated activation of semantics, rather than semantic activation resulting directly from orthographic representations.

The left inferior parietal lobule (IPL) was activated more strongly for low-frequency homophones in the wordlike context compared to other word trials. This region has been linked to the process of mapping orthographic representations to phonological representations (Booth et al., 2002; Cao et al., 2006; Chen et al., 2002). A recent study showed increased activation in the IPL as participants performed visual rhyming and spelling judgement tasks involving word pairs that possessed conflicting phonology and orthography (e.g., jazz-has; pint-mint; Bitan et al., 2007). The same visual rhyming task was later employed in a study examining the effective connectivity between left hemisphere regions, including the left IPL, in children with and without reading difficulties (Cao et al., 2008). Findings showed that children with reading difficulties exhibited weaker modulatory effects involving connections to and from the left IPL, especially for conflicting word pairs (e.g., jazz-has). Children with reading difficulties almost invariably exhibit phonological processing deficits, which include poor phonological decoding skills (i.e., orthographic to phonological mapping; Stanovich and Siegel, 1994). Cao et al.'s (2008) observation of weak modulatory effects from the left IPL to the left IFG was hypothesized to represent a deficit in function of the phonological pathway. That is, children with poor reading skills exhibit a deficit in mapping orthographic to phonological representations. In the same study typically developing children showed a positive correlation between reading skill and modulatory effects from the left IFG to the left IPL, which the authors suggested may represent top-down modulation of orthographic to phonological integration.

The hypothesis that the IPL plays a role in the integration of orthographic and phonological information is supported by the current results. There is ample evidence from the behavioural literature attributing homophone effects to phonological decoding processes, and in the current study we observed activation of both the left IFG and the left IPL for low-frequency homophones in the wordlike context. Furthermore, phonological decoding of a homophone creates a conflict, not entirely unlike the conflicting word pairs (e.g., jazz-has) employed by Cao et al. (2008), whereby a single phonological representation corresponds to more than one orthographic representation. While our results certainly support the idea that the left IPL supports phonological decoding mechanisms, we cannot determine if the activation we observed in the left IPL is correlated with activation we observed in the left IFG.

Activation of reading-related regions by low-frequency homophones was dependent on list context. When low-frequency homophones presented in the non-wordlike context were compared to other word trials, the only region exhibiting significant activation was the left middle occipital gyrus (MOG). The activation we observed is not proximal to the portion of the left fusiform/occipitotemporal gyrus that is frequently referred to as the visual word form area, a region purportedly specialized for processing the orthographic form of words or word-like stimuli (Cohen et al., 2002; McCandliss et al., 2003). Activation of the left MOG region has been activated in studies involving a variety of contrasts (see Jobard et al., 2003) and has not been linked to visual word recognition

processes per se. Rather, this medial extrastriate region has been linked to low-level visual processes, such as visual complexity, and not necessarily to higher-level processes involved in reading or word identification (Jobard et al., 2003). The lack of activation of reading-related regions by low-frequency homophones presented in the non-wordlike context supports previous behavioral (Pexman et al., 2001) and neuroimaging findings (Edwards et al., 2005), which found less evidence for phonological processing when nonword trials were comprised of non-wordlike items compared to nonwords with common word bodies. It was argued that the presence of non-wordlike nonwords allows nonwords to be detected on the basis of a superficial visual analysis. Our results corroborate this hypothesis insofar as activation of the left medial extrastriate region may represent a surface analysis of visual information, and not necessarily one that involves an analysis of a word's orthographic structure.

3.2. Pseudohomophone effects

Presentation of wordlike pseudohomophones was associated with activation of several notable regions including the left anterior IFG encompassing BA 47 (pars orbitalis) and 45 (pars triangularis), the left precentral gyrus, and the left posterior cingulate gyrus. Like the pars triangularis, the more ventrally located pars orbitalis has also been tied to semantic processes (Devlin et al., 2003; Poldrack et al., 1999; Wagner et al., 2000). We propose that the activation observed in the anterior IFG to pseudohomophones most likely reflects phonologically mediated activation of the base word's semantic form. Such activation would not be expected for pseudowords, since their phonological form cannot be linked to a semantic representation. Alternatively, activation in the left anterior IFG could reflect the direct activation of semantic information from orthographic input (i.e., input from the direct pathway). For instance, Harm and Seidenberg (2004) observed in their model that a pseudohomophone (BRANE) could activate the base word's semantic form (BRAIN) even when connections to/from the phonological layer have been severed. The fact that these effects were contingent on the pseudohomophone's word-likeness appears to support the direct activation account. However, we matched the word bodies of pseudohomophones to the pseudowords, such that pseudowords would also have been capable of activating the base word's semantic form via the direct pathway. The fact that we observed increased activation in the anterior IFG for pseudohomophones argues against the direct connection view. Instead, it seems more likely that the pseudohomophone effects observed in the anterior IFG are attributable to phonologically mediated activation of the base word's semantic representation.

As was the case for low-frequency homophones, pseudohomophones presented in the non-wordlike context did not yield activation of areas linked specifically to reading, rather non-wordlike pseudohomophones yielded higher activation in the thalamus and in regions tied to early visual processing (i.e., left cuneus, right lingual gyrus). Once again, these results suggest that the engagement of regions involved in processes (e.g., phonology, semantics) linked to reading are dependent on the word-likeness of nonword trials.

3.3. Context effects

We reasoned that if context modulates the extent to which phonological representations are accessed during word recognition, then we should observe increased activation in brain regions that mediate phonological and semantic processing when words are presented in the context of nonwords that are word-like (i.e., the wordlike context) compared to words presented in the context of non-wordlike nonwords (i.e., the non-wordlike context). Our imaging results provided at least partial support for this hypothesis. Reading words presented in the wordlike context was associated with increased activation in the left MTG, a region purportedly involved in semantic processing (Gold et al., 2005; Pugh et al., 1996; Simos et al., 2002). The present data also show that the orthographic typicality of pseudohomophones and pseudowords themselves will influence the degree to which semantic mechanisms are engaged insofar as activation in the left IFG (47/45) was greater for wordlike nonwords versus non-wordlike nonwords. Results of these contrasts would seem to suggest that the atypical orthography of nonwords in the non-wordlike context, enabled participants to make lexical decisions based on a superficial analysis of orthography, and thus participants did not activate the semantic representation of words/nonwords in the wordlike context to the same extent as they did in the wordlike context.

A number of right hemisphere regions, notably regions of the prefrontal cortex, insula, and the right IPL, showed increased activation for the contrast involving words in the wordlike context versus words in the non-wordlike context. These regions are homologous to those in the left hemisphere associated with phonological processing, such as the left IFG and the left IPL. Moreover, previous imaging studies have also found activation in regions of the right prefrontal cortex during tasks requiring phonological processing (Edwards et al., 2005; Fiebach et al., 2002). The fact that we did not see significant activation in the left IFG or left IPL for this contrast likely reflects the fact that we collapsed over factors, namely word frequency and homophony, that have been shown to influence the engagement of phonological processes.

3.4. Implications for models of visual word recognition

Many previous neuroimaging studies have observed regional differences in activation between words and nonwords, which have been interpreted in terms of dual route theories of reading (Fiebach et al., 2002; Jobard et al., 2003). Original versions of the dual-route model proposed that visual word recognition was achieved via one of two processing routes: a direct route that links a visual word with discrete, lexical entries (bypassing phonology altogether) and a non-direct route in which words are decomposed into constituent phonemes (Coltheart et al., 1977). Previous neuroimaging studies have observed the engagement of putative lexical brain regions by words (i.e., left MTG) and phonologically tuned regions by nonwords (i.e., left IFG), which has been taken as evidence that words are read by the direct route while nonwords are processed via the non-direct route (Fiebach et al., 2002; Fiez et al., 1999; Jobard et al., 2003).

The present study observed similar effects, whereby the left IFG appears to support phonological processing, while

regions in the left MTG appear to support lexical/semantic processing. However, a critical finding in our study was that the magnitude of activation in these regions, left IFG and left MTG, was influenced by homophone frequency and the word-likeness of stimuli. The demonstration of such interactive effects is consistent with the connectionist “triangle” model of reading (Harm and Seidenberg, 2004; Seidenberg and McClelland, 1989), according to which homophone effects arise due to phonologically mediated activation of semantic units associated with both homophones (or with the pseudohomophone’s base word). The frequency dependent homophone effect we observed in the left IFG and left MTG is consistent with the model’s proposal of increased input from the phonological pathway (i.e., left IFG) required to compute the meaning of a low-frequency word, with parallel input from the direct pathway (i.e., left MTG) required to resolve the ambiguity produced by presentation of a homophone. Recent implementations of the dual-route model also support the notion that both pathways may be activated in parallel, thus accounting for the homophone effects we observed here (Coltheart et al., 2001). However, both the triangle and dual-route models also incorporate feedback connections between orthographic, phonological, and semantic units, thereby permitting, for instance, a spelling check mechanism (Van Orden, 1987) to disambiguate homophones.

3.5. Conclusions

A great deal of headway has been made in understanding the cognitive mechanisms of reading using both behavioral paradigms and neuroimaging. Lexical decision studies of homophone effects have represented an especially useful avenue of inquiry in the behavioral literature as they allow us to tease apart the relative contribution of orthographic, phonological, and semantic information during skilled reading. In the present study, we used rapid event-related fMRI to examine how homophonous items influence the activation of brain regions known to play key roles in on-line visual word recognition. The results do indicate a significant degree of interactivity among regions believed to support phonologically-mediated (“sublexical”) and whole-word (“lexical”) processes in word reading. A key finding of our study is that such effects are strongly influenced by homophony and the word-likeness of nonword trials. Our results indicate that the orthographic structure of nonword foils strongly influenced the extent to which readers engaged reading-related brain regions, such as the left IFG and the left posterior MTG. These results support past arguments that less-wordlike nonwords may allow readers to base lexical decisions on a more superficial analysis of familiar orthographic patterns (Pexman et al., 2001; Edwards et al., 2005).

Neuroimaging studies aimed at identifying regions involved in phonological and semantic processing have often contrasted patterns of brain activation for words and nonwords. Even if activation patterns to nonwords are not of primary interest in such studies, they often serve as filler items when comparing activation patterns to different word types (e.g., words with regular vs. irregular spellings). The findings presented here suggest some caution in interpreting such findings, however, given that nonword foils strongly

influenced the neuroimaging results. The orthographic word-likeness of stimuli appeared to alter the implicit or explicit strategies adopted by participants by encouraging them to access different levels of representation of the word stimuli. The data emphasize the importance of considering the nature of nonword foils used to examine visual word recognition, and the influence that these can have on the word stimuli they accompany.

Finally, despite the large number of behavioral investigations that have taken advantage of homophony to investigate phonology’s role in reading, few neuroimaging studies have employed homophonous stimuli to study their impact on reading-related brain regions. Thus, a key novelty of this study was the observation of neural correlates of homophone and pseudohomophone effects, and the finding that homophone frequency influences the degree to which brain regions supporting the direct (i.e., orthography-semantics) and phonologically mediated pathways (i.e., orthography-phonology-semantics) are activated.

4. Experimental procedures

4.1. Participants

Thirteen right-handed English-speaking adults (Mean age = 26.1 years [range = 21–33]; 5 females) participated in this study. None of the participants reported a history of neurological or psychiatric disorder or a learning disability. All had normal or corrected to normal vision. Written consent was given by participants prior to the commencement of the study, and all received monetary compensation for participating. All procedures were approved by The University of Western Ontario Office of Research Ethics.

4.2. Stimuli

A total of 160 words and 176 nonwords were selected from the stimuli used in a behavioral study by Pexman et al. (2001; see Table 2 and Appendix A for details of stimuli). Note that a greater number of nonwords than stimulus words were presented so as to produce a balanced number of trials at each presentation SOA, as described below. Word items consisted of 40 homophone pairs and 80 non-homophonic control words. Homophones consisted of high-frequency words (frequency greater than 40 per million, Kucera and Francis, 1967) that had low-frequency homophone partners (frequency less than 30 per million). Control words were matched to the Homophones for frequency, number of letters, initial letter, and neighborhood size (Coltheart et al., 1977). There were 176 nonwords: 88 pseudohomophones taken from the Pexman et al. study, derived from a real word that had a frequency greater than 10 per million to help ensure that participants were familiar with its base word, and 88 “pseudo-words” consisting of nonword items that do not have a valid pronunciation that is homophonous with an existing English word. The two sets were matched for number of letters and word body (RADE/CADE; GOLPH/TOLPH). The orthographic familiarity of nonword foils was manipulated to create two “contexts” in which real-word items had to be recognized. All

Table 2

	No. letters	Mean frequency	Coltheart's N
Words			
HiHom (MADE)	4.6 (1.0)	160.0 (183)	8.2 (5.8)
LoHom (MAID)	4.7 (1.0)	7.4 (6.7)	8.0 (5.4)
HiCtl (MUST)	4.6 (1.0)	160.0 (183)	7.4 (5.2)
LoCtl (MESS)	4.7 (1.0)	6.5 (5.4)	7.0 (5.0)
P (HiHom–LoHom)	ns	< 0.001	ns
P (HiCtl–LoCtl)	ns	< 0.001	ns
P (HiHom–HiCtl)	ns	ns	ns
P (LoHom–LoCtl)	ns	ns	ns
Nonwords			
Wordlike context			
PsHom (RADE)	4.5 (0.63)		6.27
PsW (CADE)	4.4 (0.62)		5.93
P (PsHom–PsW)	ns		ns
Non-Wordlike context			
PsHom (GOLPH)	4.8 (0.58)		1.68
PsW (TOLPH)	4.8 (0.58)		0.75
P (PsHom–PsW)	ns		< 0.05
Word and nonword conditions, including mean number of letters, frequency per million words (Kucera and Francis, 1967) and orthographic neighborhood size (Coltheart's N; Coltheart et al., 1977). Homophones and their controls were matched for frequency, letter length, and orthographic neighborhood size. Nonword trials were matched for word body and number of letters.			

nonwords were pronounceable forms that obeyed basic principles of English spelling. However, in the wordlike context, the word bodies of pseudohomophones and pseudowords matched that of at least one English word (e.g., BRANE, FRANE), whereas in the non-wordlike context, the foils were composed of novel word bodies (e.g., GOLPH, TOLPH).

Four lists of 84 items were created. Each list consisted of 40 words: 10 high-frequency non-homophonous controls (HiCtl), 10 low-frequency non-homophonous controls (LoCtl), 10 high-frequency homophones (HiHom), 10 low-frequency homophones (LoHom); and 44 nonwords: 22 pseudohomophones (PsHom), and 22 pseudowords (PsW). Context was manipulated between-lists, such that two contained only wordlike nonword foils, and two contained only non-wordlike foils. Lists of the same context were presented sequentially with order of context counterbalanced across participants. Both the high- and low-frequency members of a homophone pair were presented to participants, but order was counterbalanced across participants and only one member of each pair was presented in a single list. Participants only viewed one instance of a word; however, presentation was again counterbalanced across participants so that each word item could appear in either the wordlike and non-wordlike contexts.

4.3. Stimulus presentation

During scanning, stimuli were projected in black lower-case letters against a white background onto the centre of a screen positioned at the opening of the scanner bore (approximately 1 m from participants head). Participants viewed the screen

via a mirror positioned above their eyes. They were instructed to determine whether the letter string was a word or nonword and respond by pressing one of two buttons on an fMRI-compatible numeric keypad. Ten practice trials were provided within the scanner before starting the experiment, using items not included in the actual testing phase. During the experiment, a trial began with presentation of a stimulus item on the center of the screen. The item remained on the screen until the participant responded, in which case a blank screen appeared until the next trial began. The stimulus onset asynchrony (SOA) of trials was varied at 2 s, 4 s, or 6 s, and was randomized across trials. This jittered stimulus presentation paradigm improved our ability to detect regions of BOLD signal changes by introducing predictable variability in the hemodynamic responses evoked by each trial type (Serences, 2004). Each SOA was used twenty-eight times, yielding a mean interval of 4 s. The duration of each run (i.e., each list) was 6 minutes, for a total of 24 minutes per subject.

4.4. fMRI imaging parameters

Functional magnetic resonance imaging was performed at 4.0 Tesla on a Varian/Siemens system, located at the Robarts Research Institute, London, Ontario. A custom quadrature head coil was used for signal transmission and reception. Foam padding was placed between the head and coil in order to minimize head motion. Functional images were collected using a T2*-weighted, navigator-corrected, two-shot spiral pulse sequence (TR=2000; TE=15 ms; field of view 220×220 mm; flip angle=40°). A total of 193 functional volumes were acquired in each run, and 4 runs total were acquired for each participant. The first five volumes collected were discarded to compensate for magnetic saturation effects and to allow participants to acclimate to scanner noise. Stimulus presentation did not begin until after these five preparatory scans. Stimuli were presented in sets of 21 trials, interspersed with 10 s rest intervals. Each functional volume consisted of nineteen, 5 mm thick 64×64 transverse slices (no gap; 3.44×3.44 mm in-plane resolution).

Anatomical coverage of functional slices ranged (in the inferior-superior direction) from the lateral plane of occipitotemporal cortex to superior aspects of parietal cortex (verified for each subject using a sagittal scout image acquired before the experiment began). This choice of slice prescription permitted the acquisition of volumes at a relatively high temporal resolution, necessary for rapid event-related trials. Although it did not cover the entire cortex (the most superior portion of parietal and frontal lobes as well as portions of the cerebellum were not imaged), it ensured that areas known to participate in visual word recognition and phonology were imaged, including the middle and inferior frontal gyri, the superior, middle, and inferior temporal gyri, the occipitotemporal junction including the fusiform gyrus, as well as the inferior parietal lobe (angular gyrus, supramarginal gyrus). Functional scans were aligned with a high resolution T1-weighted anatomical image acquired in the same session using a 3D FLASH spiral pulse sequence (TR: 10 ms; TE=5.5 ms; matrix size=256×256×108; voxel size=0.9×0.9×1.5 mm; FOV=220 mm×220 mm×162; TE=15 ms).

4.5. fMRI data analysis

Data analysis was performed using BrainVoyager QX software (Brain Innovation B.V., Maastricht NL, Max Planck Society). Prior to analysis, functional images were motion corrected in three dimensions using a rigid-body transformation and underwent spatial filtering using a Gaussian filter (full width half maximum=4 mm) as well as temporal filtering to remove linear drift. Functional images were then resampled to 1 mm³ resolution and transformed to the three-dimensional stereotaxic space of Talairach and Tournoux (1988).

Statistical analyses used a random effects general linear model (GLM) consisting of independent predictors defined for each condition (HiHom, LoHom, HiCtl, LoCtl, PsHom, and PsW) within both the wordlike and non-wordlike contexts. A hemodynamic predictor function modeled a canonical blood oxygen level dependent (BOLD) response as a gamma function (delta, 2.5; tau, 1.25, assuming a stimulus duration of one volume, aligned to the onset of each trial). For word stimuli, a 2x2x2 ANOVA was constructed for the effects of Frequency (high, low), Homophony (homophones, control words) and List Context (wordlike, non-wordlike). A statistical parametric map was constructed for the three-way interaction, with significant voxels limited to those respecting the predicted effect of greater activity for the low-frequency homophones in the wordlike context, compared to all other conditions. To identify brain regions specifically influenced by the word-likeness of nonword stimuli, we also constructed a map showing regions where low-frequency homophones in the non-wordlike context caused stronger activation than all other word trials. Finally, statistical maps were also constructed for the main effects of List Context for word trials (i.e., words in the wordlike context compared to words in the non-wordlike context).

A 2x2 ANOVA was next conducted for the nonword items, with Homophony (pseudohomophones, pseudowords) and List Context as repeated measures factors. A statistical map was constructed for the two-way interaction, with significant voxels limited to those reflecting the predicted effect of greater activity of pseudohomophones in the wordlike list context. We also constructed a statistical map showing voxels activated more strongly by non-wordlike pseudohomophones compared to all other nonword trials. Finally, a map was constructed for the main effect of List Context, comparing nonwords presented in the wordlike context to nonwords presented in the non-wordlike context. For all contrasts, the voxel-wise significance threshold was set at p<0.001 with a minimum cluster size of 300 mm³. Anatomical information was obtained for center of gravity of activation clusters using the Talairach Daemon software (Lancaster et al., 2000), using a search range of 5 mm³.

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Appendix A. Stimuli used in the wordlike and non-wordlike context

High-frequency homophones	Low-frequency homophones	High-frequency control words	Low-frequency control words
aid	aide	ask	arch
allowed	aloud	applied	aloof
beat	beet	boat	bait
blue	blew	bill	boil
board	bored	black	baked
break	brake	broad	bleed
chance	chants	choice	champs
council	counsel	concern	costume
course	coarse	church	cheese
dear	deer	draw	deed
die	dye	dog	den
fair	fare	fast	fake
feet	feat	five	flip
grown	groan	grass	graze
hair	hare	hard	hack
hall	haul	hope	hoop
higher	hire	having	heap
horse	hoarse	heart	hearse
latter	ladder	larger	locate
least	leased	large	loomed
loan	lone	lake	lace
made	maid	must	mess
main	mane	mass	maze
manner	manor	middle	manic
mind	mined	miss	mused
minor	miner	model	molar
morning	mourning	million	mounting
none	nun	note	nap
pain	pane	post	pest
pair	pear	pick	perk
pale	pail	page	peep
read	reed	rest	rail
real	reel	rate	rude
rose	rows	rock	rags
sale	sail	soil	silk
seem	seam	soon	seep
size	sighs	step	skids
soul	sole	safe	seal
thrown	throne	twelve	thrill
wine	whine	wide	whack

Nonword stimuli used in the wordlike and non-wordlike contexts.

Wordlike Pseudohomophones	Wordlike Pseudowords	Non-Wordlike Pseudohomophones	Non-Wordlike Pseudowords
bleek	fleek	bahrn	mahrn
bor	klor	bawx	vawx
chace	nace	boarn	foarn
cheef	meef	braive	claive
deel	geel	breth	creth
durt	furt	daize	taize
goast	loast	darck	varck
greef	deef	dowt	howt
hed	ped	dyve	byve
heer	zeer	falce	balce

(continued on next page)

Appendix A (continued)

Wordlike Pseudohomophones	Wordlike Pseudowords	Non-Wordlike Pseudohomophones	Non-Wordlike Pseudowords
jale	lale	fawlt	dawlt
keap	meap	fawx	yawx
kerse	ferse	fayze	thayze
koast	foast	gloab	woald
laff	naff	golph	tolph
lern	sern	graive	draive
mait	swait	hedd	chedd
meel	greel	hoarn	goarn
murge	turge	jooce	tooce
neet	reet	joynt	roynt
neem	creem	looce	fooce
nife	pife	nayvy	layvy
noze	broze	nerce	lerce
rade	cade	nyne	hyne
rane	tane	perce	berce
rong	shong	plaie	blaie
rore	prore	pleez	bleez
sain	blain	pruve	bruve
scail	spail	pryze	chryze
scoar	floor	raige	taiga
shair	jair	rayk	vayk
shurt	murt	redd	gedd
smoak	loak	runn	cunn
speek	jeek	shoart	hoart
squair	gair	soald	goald
swet	shet	spoart	choart
teech	weech	stahr	slahr
thret	fet	stawp	dawp
tite	jite	taip	baip
trale	drale	taks	kaks
tutch	rutch	tayk	yayk
vurse	blurse	troab	gloab
wheal	treal	woond	loond
yung	shung	wurld	murld

Appendix B

Clusters of significant activation for each of the contrasts performed. ($p < 0.001$ uncorrected; $300 \times 1 \text{ mm}^3$ contiguous voxels). BA: Brodmann area closest to cluster's center of gravity, based on a 5-mm^3 search range. Coordinates are based on Talairach and Tournoux (1988), and were obtained using the automated Talairach Atlas (Lancaster et al., 2000).

Contrast/region	x	y	z	Cluster size
Words (wordlike context) > words (non-wordlike context)				
L. mid. frontal gyrus, BA 6	-26	-4	51	955
L. mid. temporal, BA 37	-47	-57	4	2532
R. inf. frontal gyrus, BA 44/45	48	15	17	3747
R. mid. frontal gyrus, BA 11/47	27	37	-10	2316
R. precentral gyrus/insula, BA 44/13,	43	13	9	3906
R. inf. parietal lobule, BA 40	37	-36	47	3575
R. limbic lobe, parahipp. gyrus, BA 36	40	-31	-10	959
Words (non-wordlike context) > words (wordlike context)				
L. temporal lobe, sub-gyral, BA 20	-42	-9	-17	354

Appendix B (continued)

Contrast/region	x	y	z	Cluster size
Nonwords (wordlike context) > nonwords (non-wordlike context)				
L. frontal lobe, sub-gyral, BA 6	-25	1	54	1326
L. insula/inf. frontal gyrus, BA 47/45	-37	22	3	1483
L. mid. frontal gyrus, BA 46	43	19	20	4822
L. sup. frontal gyrus, BA 10	-28	55	17	536
R. inf. frontal gyrus, BA 47	22	26	-8	1270
R. sup. frontal gyrus, BA 6	4	8	51	2924
R. mid/sup. frontal gyrus, BA 10/11	26	53	-12	795
R. occipital gyrus, cuneus/BA 17/18	14	-96	5	1023
Nonwords (non-wordlike context) > nonwords (wordlike context)				
L. insula, BA 13	-31	-7	17	2467
R. inf. fron/sup. temporal gyrus, BA 47/38	35	16	-19	465
R. transverse temporal gyrus, BA 41/42	58	-18	11	689
L. occipital gyrus, lingual gyrus, BA 19	-16	-57	-6	2680
L. occipital gyrus, cuneus, BA 18	-16	-84	21	1640
R. posterior lobe, cerebellum	7	-77	-14	768
LoHom (wordlike context) > all other word trials				
L. inf./mid. frontal gyrus, BA10/46	-39	42	10	729
L. inf. frontal gyrus, BA 44/45	-50	13	23	3592
L. mid. temporal gyrus, BA 22	-52	-47	1	355
L. sup/inf. parietal lobule, BA 7	-30	-57	43	661
L. inf. parietal lobule, BA 40	-40	-40	40	560
R. insula, BA 13	31	20	6	339
R. precentral/inf. frontal gyrus, BA 9	44	3	33	698
R. temporal gyrus/sub-gyral, BA 37	48	-45	-6	330
R. precuneus/sup. parietal lobule, BA 7	25	-55	50	2160
R. inf. parietal lobule, BA 40	34	-35	42	578
LoHom (non-wordlike context) > all other word trials				
L. mid. occipital gyrus, BA 19	-39	-80	5	1232
Wordlike PsH > all other nonwords trials				
L. inf. frontal gyrus, BA 47/45	-36	25	2	2743
L. mid/sup frontal gyrus, BA 6/8	-1	29	41	2040
L. precentral/inf. frontal gyrus, BA 6/9	-47	4	28	513
L. pos. cingulate gyrus/cuneus, BA 31/30	-13	-65	14	2341
Non-wordlike PsH > all other nonwords trials				
L. thalamus	-5	-9	7	895
L. occipital lobe, cuneus, BA 17/18	-13	-76	13	4949
R. lingual gyrus, BA 18/19	7	-68	-1	511

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