

Phonological Priming in Visual Word Recognition for English Words: An Event-Related Functional MRI Study

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Functional magnetic resonance imaging (fMRI) was used to explore the nature of the mappings between orthography, phonology, and semantics in reading English words. Stimulus pairs were arranged in a priming paradigm with lexical decision to understand the neural correlates of phonological processes. Homophonic targets varied in the regularity of the mapping from spelling to sound (e.g., *feet-feat*, *bare-bear*). There were three main findings. First, the results revealed that the left middle temporal gyrus (BA 21) showed increased neural activity for phonologically primed irregular pairs consistent with increased semantic involvement in making lexical decisions when the mapping between orthography and phonology is made difficult. Second, the left supramarginal gyrus (BA 40) was associated with reduced neural activity for phonologically-identical pairs with regular spelling to sound correspondences, when the mapping between orthography and phonology is made easy. Third, the visual association cortex including the left fusiform gyrus (BA 37) showed more activation in the homophone pairs compared to the unrelated pairs

and more activation for pseudoword targets compared to word targets, suggesting that this region may have been involved in a spelling check on lexical decisions. These three findings show how phonological priming effects on behaviour can result from a complex interaction of several processing phases involving both increases and decreases of activity.

Keywords: *language, priming, regularity, fMRI*

The mental 'lexicon', a long term store of words and their meanings, is the core of the human language system. Cognitive accounts of the mental lexicon have traditionally described three distinct, yet closely linked sets of representations that contain information crucial to the comprehension and production of written language - that is knowledge of orthography (the written form of words), phonology (the spoken or auditory form of words) and semantics (the meanings of words) on visual word recognition (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Plaut, McClelland, Seidenberg, & Patterson, 1996). While these cognitive accounts have been influential, evidence for

the neural systems involved in representing these three distinct forms of word knowledge is far from complete (Price, 2000). In this paper, we conducted an event-related fMRI study that used repetition priming to investigate the neural system involved in accessing the sound of words from their printed form.

Repetition priming refers to improvements in performance (increases in speed/accuracy of responses) when items are presented twice. These behavioural priming effects can be accompanied by *reductions* in the amount of neural activation relative to unprimed task performance. This concept of repetition can be extended to a design in which prime-target relations take various forms, such as semantic, graphemic, or phonological repetitions in the field of language (Naccache & Dehaene, 2001). Priming effects often show anatomic specificity to brain regions involved in particular cognitive processes, for example, reductions in left prefrontal regions are associated with conceptual priming (Schacter & Buckner, 1998). The underlying neural mechanism may be that less neural activity is required for the second item (the target) to reach threshold due to partial activation by a preceding item (the prime) or because response thresholds are reached more rapidly as pathways are more easily utilised (Mummary, Shallice, & Price, 1999). One issue that remains unclear in these studies is whether reductions in reaction times (and error rates) associated with priming always correspond to reductions in the neuro-imaging signal. Studies have found that priming is accompanied by decreased activity in a variety of cortical regions when materials are presented within modality (e.g., visual-visual), are tested after recognition or consist of familiar stimuli, whereas increased activity has been observed when materials are presented across modalities (e.g., visual-auditory), are tested before recognition or consist of unfamiliar stimuli (Henson, Shallice, & Dolan, 2000; James, Humphrey, Gati, Menon, & Goodale, 2000; Schacter, Badgaiyan, & Alpert, 1999). It may be that response times reflect the net outcome of sev-

eral processing stages, and the benefit of brain imaging is that it may be able to measure each processing stage separately (Naccache & Dehaene, 2001). Even where reductions in both response time and neural signal coincide, regional specialisation may not be observed because reductions in activity in decision processes could be responsible for reduced neural activity (Dobbins, Schnyer, Verfaellie, & Schacter, 2004). In this study, we used a priming manipulation in which repetition of the phonological form of a word increased response times and error rates in a behavioural task. In the context of this behavioural interference, we can be more confident that reductions in neural activity reflect the priming of systems involved in processing phonological information in written words.

This study examined the phonological priming effect for visually presented word pairs in a lexical decision task (real/non-word discrimination). In the literature, the use of priming to investigate language systems has focused on lexical-semantic information (Copland et al., 2003; Kotz, Cappa, von Cramon, & Friederici, 2002; Rissman, Eliassen, & Blumstein, 2003; Rossell, Price, & Nobre, 2003; Wagner, Maril, & Schacter, 2000). Not many imaging studies of repetition priming have investigated prime-target relationships in terms of phonology. Most studies have used rhyme matching tasks to identify brain regions involved in phonological processes, including the left supramarginal gyrus (SMG, BA 40) and left inferior frontal gyrus (IFG, BA 44 and 45) (Poeppel, 1996; Price, 1997). Those studies of phonological priming that have been reported have used a blocked design (Haist, Song, Wild, Faber, Popp, & Morris, 2001) or have used a naming task (de Zubicaray, McMahon, Eastburn, & Wilson, 2002). These studies have observed active regions in the left SMG, left IFG, left middle temporal gyrus, and left inferior temporal gyrus. The left SMG has previously been associated with mappings between orthography and phonology. For example, cross-modal conversion is required in spelling tasks with auditory input and rhyming

tasks with written input; both of these tasks produce activation in this region (Booth et al., 2002a, 2003). Since visually presented words in the current study are readily converted to phonological representations during recognition, we predict that phonologically related pairs (e.g., *stare-stair*) would lead to reduced activity in neural systems involved in processing the sound form of written words. Thus, we predicted the left SMG (BA 40), a system that may be involved in mapping between orthography and phonology (Booth et al., 2003, 2004), would show a priming effect in this study.

Accurate performance in lexical decision may require activity in semantic representations to be monitored from a parallel and distributed processing (PDP) approach (Plaut & Booth, 2000). Since homophones have a one-to-many mapping between phonological and semantic representations, we anticipate slower settling into stable patterns of semantic activations and hence slower lexical decision responses (Rodd, Gaskell, & Marslen-Wilson, 2002; Pexman, Lupker, & Jared, 2001). Moreover, within the PDP framework Harm and Seidenberg (2004) point out that lexical semantics can be activated by both visual (orthography to meaning) and phonologically mediated (orthography to phonology to meaning) processes during visual word recognition. When the mapping between orthography and phonology is made difficult, reading for meaning places a greater demand on activation in the lexical-semantic system (also see Strain, Patterson, & Seidenberg, 1995; Rodd, 2004). Previous studies have associated activity in left middle temporal gyrus (MTG, BA 21) with semantic processing, including judging whether a word is abstract or concrete, living or non-living, determining its category (Friederici, Opitz, & Cramon, 2000; Price, Moore, Humphreys, & Wise, 1997; Pugh et al., 1996). Thus, since homophonic words place an increased load on semantic processes, we might anticipate activation in the left middle temporal gyrus to be influenced by homophonic priming.

One important variable in the mapping of

orthography to phonology is the degree of regularity/consistency in this mapping. For instance, a word like *leak* is regular by virtue of sharing the relationship between orthography and phonology with its neighbours (e.g., *peak*, *weak*). By contrast a word like *pint* is irregular/inconsistent because its orthographic neighbours (e.g., *mint*) are not pronounced in the same way. Cognitive accounts of reading aloud largely agree that regularly spelt words are more readily converted from orthography to phonology (Coltheart et al., 2001; Plaut et al., 1996). In contrast, irregularly spelt words place greater demands on the lexical system because of the inconsistent mappings between orthography and phonology. We therefore expected the left SMG (BA 40) and left MTG (BA 21) involved in priming to be modulated by regularity. In particular, we expected that homophone priming may facilitate the mapping of regular targets and therefore result in less activation in the SMG, whereas for irregular words there may be greater involvement of semantics in the MTG because the mapping between orthography and phonology is made difficult. Furthermore, previous studies using overt and covert reading (Fiez, Balota, Raichle, & Petersen, 1999; Herbster, Mintun, Nebes, & Becker, 1997; Joubert, Beauregard, Walter, Bourgouin, Beaudoin, Leroux, Karama, & Lecours, 2004; Paulesu et al., 2000) or lexical decision (Fiebach, Friederici, Muller, & von Cramon, 2002; Pugh, Shaywitz, B. A., Shaywitz, S. E., Shankweiler, Katz, Fletcher, Skudlarski, Fulbright, Constable, Bronen, Lacadie, & Gore, 1997; Rumsey, Horwitz, Donohue, Nace, Maisog, & Andreason, 1997) have found regularity effects in left inferior frontal gyrus (IFG, BA 45) so we expected that regularity might also modulate priming effects in this region.

Homophones are pairs of words that sound the same but are spelt differently (e.g., *feet-feat*). Behavioural studies have found homophone interference in tasks that require word versus pseudo-word judgment (Chou & Marslen-Wilson, 2001; Davelaar, Coltheart, Besner, & Jonasson, 1978; Ferrand & Grainger, 1996, 2003; Pexman et al.,

2001; Rubenstein, Lewis, & Rubenstein, 1971). Although a shared sound between word pairs would facilitate performance, some have suggested that the two different orthographic representations activated by the same sound create competition at the orthographic level resulting in longer settling times for orthographic activation (Ferrand & Grainger, 2003; Pexman et al., 2001). This orthographic competition cancels out the phonological facilitation and results in longer response times, as lexical decisions seem to be affected by the summed activity of phonological and orthographic processing (Ferrand & Grainger, 1996; McClelland & Rumelhart, 1981). When pseudo-homophones (e.g., *hoam*) are included as stimulus foils, orthographic processing is even stronger because participants may have to set a more strict activation criterion for discriminating words from nonwords (Ferrand & Grainger, 2003; Pexman et al., 2001). Participants may also have greater reliance on orthographic coding by using a spell checking mechanism or familiarity judgements to make lexical decisions, producing longer response times (Davelaar et al., 1978; Norris, 1984; Rubenstein et al., 1971) or greater brain activation for pseudo-homophones (Cappa, Perani, Schnur, Tettamanti, & Fazio, 1998; Hagoort et al., 1999; Horwitz, Rumsey, & Donohue, 1998; Rumsey et al., 1997). Once pseudo-homophones are removed or orthographic activation gets settled quicker, phonological facilitation emerges (Chou & Marslen-Wilson, 2001; Ferrand & Grainger, 1996). Since pseudohomophones were included as target foils in the homophone priming conditions in this study, we expected bilateral fusiform gyri (BA 37) to be activated for homophone primes or for lexical decisions to pseudohomophones. Imaging studies have found activation related to the processing of letter strings for pseudowords in bilateral fusiform gyri (Cappa et al., 1998; Hagoort et al., 1999). Other studies have found this area active during lexical decisions to pseudowords (Rumsey et al., 1997).

The first goal of the present study was to examine the influence of phonological priming on

activation in the left supramarginal gyrus (SMG) implicated in mapping between orthography and phonology and in the left middle temporal gyrus (MTG) implicated in semantic processing. The second goal was to determine whether these priming effects had differential influences on processing regular versus irregular targets. The third goal was to explore if interference due to including homophones and pseudo-homophones was related to activation in the fusiform gyrus.

Materials and methods

Subjects

Twelve volunteers, ages 19-35 years, (seven females), from the subject panel of the Medical Research Council Cognition and Brain Sciences Unit, Cambridge, UK participated in the experiment. All were right-handed, native British English speakers with normal or corrected-to-normal vision, free from past or current neurological disorders, brain injury, or psychiatric disability. Informed written consent was obtained from each volunteer prior to scanning. All procedures were approved by the Addenbrookes Hospital Research Ethics committee.

Stimuli

Stimuli consisted of two categories, the word category (300 word-word pairs) and the pseudo-word category (300 word-pseudoword pairs). The pseudowords were orthographically legal and pronounceable. Each category had three sets of item pairs, 100 homophonic (e.g., piece-peace or grief-greef), 100 orthographic (e.g., coach-coast or blame-blail), and 100 unrelated (e.g., bribe-toast or dress-kirth) pairs (Table 1). The evaluation of phonological priming needed to disentangle the orthographic influence, because homophone pairs were usually visually similar in English. Thus, the orthographic priming condition was included. Orthographic primes were generated by preserving common letters in common positions between

Table 1

Stimulus characteristics for primes and targets in the three priming conditions for the word and pseudoword category, and for regular and irregular targets in the two priming conditions for the word category (standard deviations in parentheses). Frequency counts were derived from CELEX (1 million words, lemma frequency). Neighbours were derived from the MRC psycholinguistic database (University of Western Australia).

Words	Frequency		Word Length		Neighbours	
	Prime	Target	Prime	Target	Prime	Target
Homophonic	106 (245)	62 (120)	4.3 (0.7)	4.5 (0.8)	7.7 (4.2)	7.1 (5.6)
Orthographic	96 (188)	48 (102)	4.4 (0.7)	4.4 (0.7)	6.3 (4.5)	8.1 (5.6)
Unrelated	47 (48)	52 (101)	4.5 (0.7)	4.5 (0.7)	6.0 (4.9)	6.9 (5.0)
Pseudowords						
Homophonic	134 (310)		4.5 (0.6)	4.4 (0.7)	6.2 (4.6)	4.9 (4.5)
Orthographic	136 (290)		4.4 (0.6)	4.4 (0.6)	6.3 (4.4)	5.0 (4.5)
Unrelated	70 (142)		4.4 (0.7)	4.4 (0.6)	5.9 (5.0)	5.1 (3.7)
Regular						
Homophonic	128 (196)	51 (99)	4.4 (0.6)	4.4 (0.7)	7.7 (3.9)	7.6 (5.3)
Unrelated	44 (49)	41 (54)	4.4 (0.7)	4.5 (0.7)	6.4 (5.5)	7.3 (4.6)
Irregular						
Homophonic	86 (285)	73 (139)	4.1 (0.7)	4.6 (0.9)	7.6 (4.6)	6.6 (5.9)
Unrelated	50 (47)	62 (132)	4.7 (0.8)	4.5 (0.7)	5.5 (4.1)	6.5 (5.4)

the experimental and control primes, as closely as possible (as in Rastle & Coltheart, 1999). For the word category, the target words of the three stimulus sets were matched for lemma frequency, type frequency (Forster & Taft, 1994), word length, and number of neighbours (NN) from the CELEX database (Baayen, Piepenbrock, & van Rijn, 1993). For the pseudoword category, the target

words of the three stimulus sets were matched for word length and NN. One-way ANOVAs revealed that there were no significant differences between the three word categories for the targets on any of these measures. Pseudo-homophones were included as pseudoword targets in the homophone condition, so that lexical decision for homophone primes for both word and pseudoword targets could not be based on sound overlap. A pilot study showed an effect of regularity on priming for the comparison between the homophonic and unrelated word pairs. Therefore, the 100 homophonic pairs and 100 unrelated pairs in the word category were split into 50 pairs with regularly-spelt targets and 50 pairs with irregular targets. Regularity was defined by grapheme-phoneme correspondences, determined by the REGCELEX database (Coltheart et al., 2001). Thus, the regularity in English was defined in terms of the relationship between phonological segments and orthographic segments that were either graphemes or “bodies”. Primes were regularly-spelt words for all conditions. Lemma frequency, type frequency, word length, and NN were matched between regular and irregular targets (Baayen et al., 1993). 2 target (regular, irregular) x 2 prime (homophonic, unrelated) ANOVAs indicated that there were no main effects or interactions involving these variables. Despite attempts to match these lexical characteristics for the primes across conditions, and due to the limited number of available words and the specific structure of the conditions, the lemma frequency of the homophone and orthographic primes was significantly higher than the unrelated condition for both the word and pseudoword categories. Word length and NN of the primes were matched for both the word and pseudoword categories. The regularity by prime interaction indicated that there were no main effects or interactions involving these variables except for the main effect of frequency measure (Table 1). 150 null-events (fixation crosses) were also included.

Apparatus and procedure

Stimulus presentation and response measurement was controlled using DMDX software (Forster, K. I., & Forster, J. C., 2003). Subjects lay in the scanner and viewed letter strings that were projected onto a screen via a mirror attached to the inside of the headcoil (viewing distance ~50cm). Words subtended a visual angle of approximately 4°. Trials lasted 2500ms and consisted of a fixation cross (1750 ms), followed by the first (prime) stimulus (250 ms), and second (TARGET) stimulus for 500 ms. The duration of the prime was chosen from one of our pilot studies that showed a regularity effect and this short duration should prevent strategic expectancy based processes (Lesch & Pollatsek, 1993; Neely, 1977; Rossell, Bullmore, Williams, & David, 2001). Subjects were told that they would see pairs of letter strings, and were instructed to respond to the second, uppercase stimulus by pressing a response key to indicate if this was a real English word or not. On occasional 'null-event' trials, there was a longer gap (2500-7500ms) between trials and subjects were instructed to watch the screen attentively. Stimuli were presented in a pseudorandom order with the constraint that within any five trials the mean of the repetitions of any of the six conditions (2 word categories by 3 priming types) was statistically the same. Thus, trials of the same condition were not lumped together in a particular time section. Each subject performed two 16-minute functional runs of this word-reading task followed by a high resolution structural scan of the brain.

Imaging acquisition and analysis

Images were acquired on a Bruker Medspec (Ettlingen, Germany) 3-Tesla MR System with a head gradient set, using interleaved whole brain EPI acquisition. Echo-planar image volumes (21 slices) were collected parallel to the AC-PC plane with TR = 3 s, TA = 2.3 s, slice thickness = 4 mm, interslice interval = 1 mm, FOV = 25 (25 cm, matrix size = 128 (128. Each of two sessions used

320 image volumes. Pre-processing used statistical parametric mapping (SPM99, Wellcome Department of Cognitive Neurology, London, UK) to realign to the first (non-discarded) volume of the first run to correct for subject motion (no subject had more than 4 mm of movement in any plane). Images were corrected for differences in slice-acquisition time using sinc interpolation, and corrected for geometric distortion (Cusack, Brett, & Osswald, 2003). Functional images were normalised to the Montreal Neurological Institute (MNI) template brain and resliced into $3 \times 3 \times 3$ mm voxels. Regions of susceptibility artefact were masked to reduce tissue distortion (Brett, Leff, Rorden, & Ashburner, 2001), and then smoothed with a Gaussian kernel of 12mm FWHM suitable for random effects analyses (Xiong et al., 2000). Data from each subject was entered into a general linear model using an event-related analysis procedure (Josephs & Henson, 1999). Word pairs were treated as individual events for analysis and modelled using a canonical HRF (with temporal and dispersion derivatives). Separate columns were included for each of 8 types of prime-target pairs (homophonic regular words, homophonic irregular words, orthographic words, unrelated regular words, unrelated irregular words, homophonic pseudowords, orthographic pseudowords, and unrelated pseudowords). An additional event type was included for error trials which were excluded from analysis. The time series were high-pass filtered with cutoff period 120 seconds, and intrinsic correlations were modelled using an AR(1) function. No global normalisation was applied. Realignment parameters were used as regressors of no interest. Parameter estimates from contrasts of the canonical HRF in single subject models were entered into random-effects analysis using one-sample t-tests across all participants to determine whether activation during a contrast was significant (i.e., parameter estimates were reliably greater than 0).

Due to our a priori hypotheses regarding left middle temporal gyrus (BA 21), supramarginal gyrus (BA 40), inferior frontal gyrus (BA 45) and

bilateral fusiform gyri (BA 37), the small volume correction of SPM99 was used to search the volume of a sphere of 10 mm radius, which was centred at the average of peak voxels from previous studies in MNI coordinates: (-53,-23,-4) for semantic judgements in BA 21 (Booth, Burman, Meyer, Gitelman, Parrish, & Mesulam, 2002b; Jernigan, Ostergaard, Law, Svarer, Gerlach, & Paulson, 1998; Moore & Price, 1999; Price, Wise, & Frackowiak, 1996); (-57,-47,25) for phonological judgements in BA 40 (Booth et al., 2002a, 2003; Jobard, Crivello, & Tzourio-Mazoyer, 2003; Menard, Kosslyn, Thompson, Alpert, & Rauch, 1996); (-47,17,17) for regularity effects in BA 45 (Fiebach et al., 2002; Fiez et al., 1999; Jobard et al., 2003; Joubert et al., 2004); and (\pm 39,-50,-11) for spelling judgements in BA 37 (Booth et al., 2003; Cohen, Lehericy, Chochon, Lemer, Rivaud, & Dehaene, 2002; Fiez et al., 1999; Hagoort et al., 1999). Coordinates from previous studies are all within the corresponding 10-mm spheres in this study. The voxelwise threshold was set to $p < .005$, and regions surviving correction at $p = .05$ for multiple comparisons across the small volume are reported. Voxels that were outside of our regions of interest and passed a moderately conservative uncorrected threshold ($p < .005$ at the voxel level with a cluster size greater than 25 voxels) are also reported to see activated regions, but interpreted with caution given they may be false-positives produced by multiple comparisons.

Results

Behavioural: phonological priming

Response-time (RT) data were inverse transformed to reduce the influence of outlying responses (Ratcliff, 1993). The mean non-inverse RTs are illustrated in Figure 1(a). Results of a 2 (lexicality: word vs. pseudoword) \times 3 (priming: homophone, orthographic, unrelated) ANOVA showed no main effect of prime type, $F(2, 22) = 1.78, p = .19$, but a main effect of lexicality, $F(1, 11) = 7.31, p < .05$, resulting from longer reaction times for the pseu-

doword targets than the word targets. The interaction between lexicality and priming was significant, $F(2, 22) = 7.96, p < .01$. A simple main effects analysis showed that homophone word pairs were slower than unrelated word pairs [$F(1, 22) = 6.87, p < .05$] and that orthographic word pairs were slower than unrelated word pairs [$F(1, 22) = 19.58, p < .01$]. The difference between homophone and orthographic word pairs did not reach significance. In addition, there were no significant differences in reaction time between the priming conditions for the pseudoword targets.

Target errors were analysed in the same way as with the RT analyses (see Figure 1b). Although there were no main effects, a two way ANOVA showed a significant interaction of lexicality and priming, $F(2, 22) = 20.49, p < .01$. A simple main effects analysis showed that word targets primed with homophones showed more errors than did word targets primed with unrelated controls, $F(1, 22) = 52.54, p < .01$, and that word targets primed with homophones showed more errors than did word targets primed with orthographic controls, $F(1, 22) = 25.66, p < .01$. The difference between orthographic and unrelated primes to target words was non-significant. In addition, there were no significant differences in accuracy between the priming conditions for the pseudoword targets

Behavioural: regularity effects

The mean RTs for regular and irregular targets are illustrated in Figure 1(c). Effects of regularity on phonological priming were investigated by a 2 (regularity: regular vs. irregular) \times 2 (priming: homophonic vs. unrelated) ANOVA. The main effect of prime type for reaction times was significant, $F(1, 11) = 5.65, p < .05$, reflecting slower reaction time for homophone pairs than for unrelated pairs. Both the main effect of regularity and the interaction between priming and regularity were non-significant for reaction times.

The mean error rates are illustrated in Figure 1(d). A two way ANOVA of error rates showed a significant main effect of prime type, $F(1, 11) =$

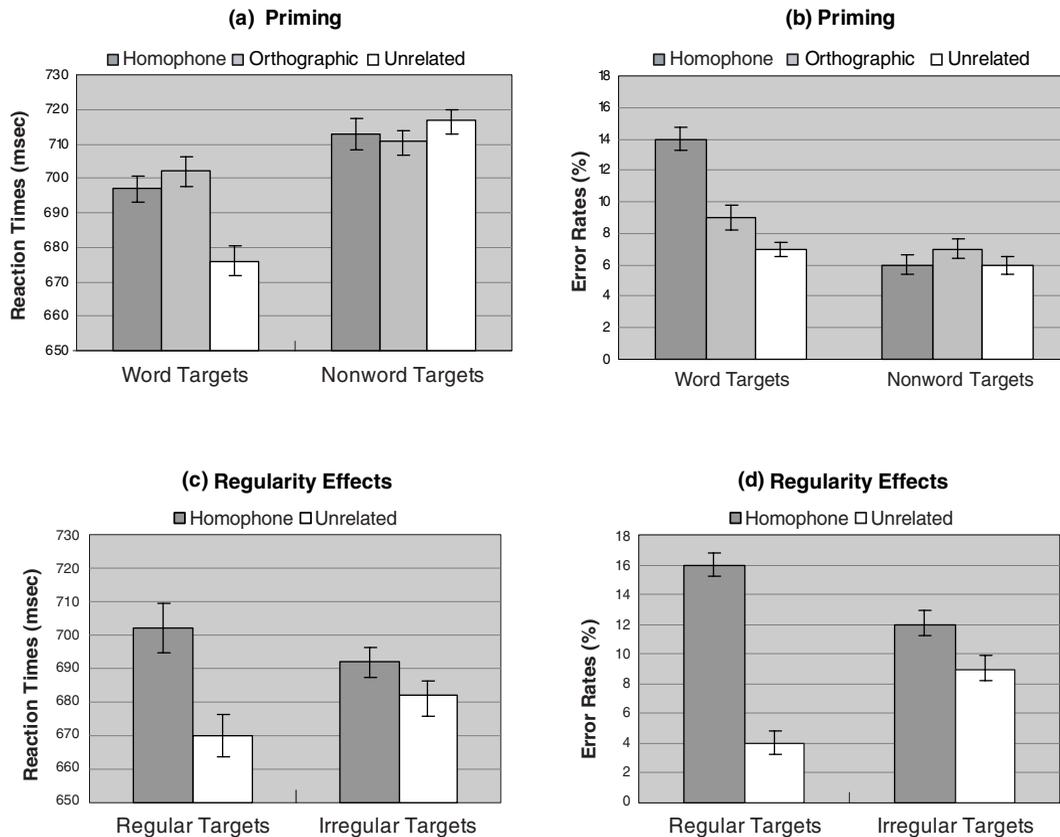


Figure 1. Behavioural results. (a) homophone, orthographic, and unrelated primes with word and pseudoword targets for reaction times, (b) same as (a) but for error rates; (c) homophone and unrelated primes with regular and irregular targets for reaction times, and (d) same as (c) but for error rates. Error bars indicate the standard error of the mean after between-subject variability has been removed, which is appropriate for repeated-measures comparisons (Loftus & Masson, 1994).

55.00, $p < .01$, indicative of increased error rates for targets following homophone primes as compared to unrelated controls. The interaction between priming and regularity was significant, $F(1, 11) = 10.47$, $p < .01$. A simple main effects analysis showed a significant difference between the homophone and unrelated primes for regular targets, $F(1, 22) = 49.73$, $p < .01$; and was close to significance for the irregular targets, $F(1, 22) = 3.56$, $p = .06$.

Imaging: phonological priming

In order to examine phonological priming effects, we directly compared all three conditions (homophone, orthographic and unrelated) for the

word targets (see Table 2). The left MTG (BA 21) and fusiform gyrus (BA 37) activation was significant ($p < .05$ corrected for multiple comparisons) for the contrast of homophone versus unrelated word pairs (see Figure 2a). The haemodynamic responses (mean percentage signal change from rest) of the MTG and fusiform gyrus regions of interest are plotted for the three word conditions at the peak voxel (Figure 3a). t -tests revealed that homophone priming in the MTG produced significantly more activation than the orthographic or unrelated primes [$t(11) = 2.24$, $p < .05$; $t(11) = 4.67$, $p < .01$, respectively], and that the orthographic and unrelated pairs were not significantly different. Likewise, homophone priming in the fusiform gyrus produced significantly more activa-

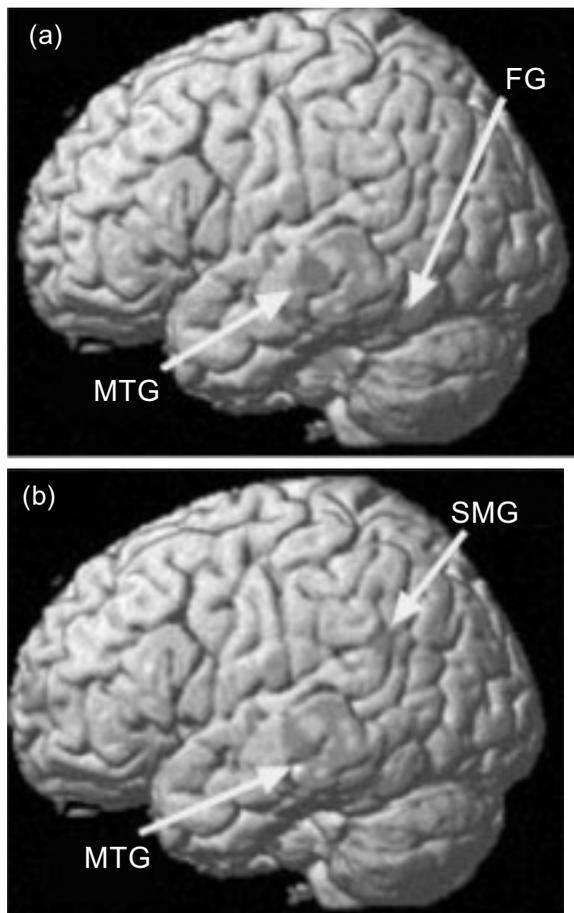


Figure 2. Brain maps. (a) Activation in the left middle temporal gyrus (MTG, BA 21) and fusiform gyrus (FG, BA 37) for word targets was greater for homophone than for unrelated primes (b) The interaction between regularity and priming in the left supramarginal gyrus (SMG, BA 40) and the left MTG. The left SMG showed a significant reduction for regular targets for homophone compared to unrelated primes and left MTG showed greater activation for irregular target words for the homophone compared to the unrelated primes.

tion than the orthographic or unrelated primes [$t(11) = 2.35, p < .05$; $t(11) = 2.19, p < .05$, respectively], and that the orthographic and unrelated pairs were not significantly different. The orthographic pairs activated the medial frontal gyrus as compared to the unrelated condition (see Table 2).

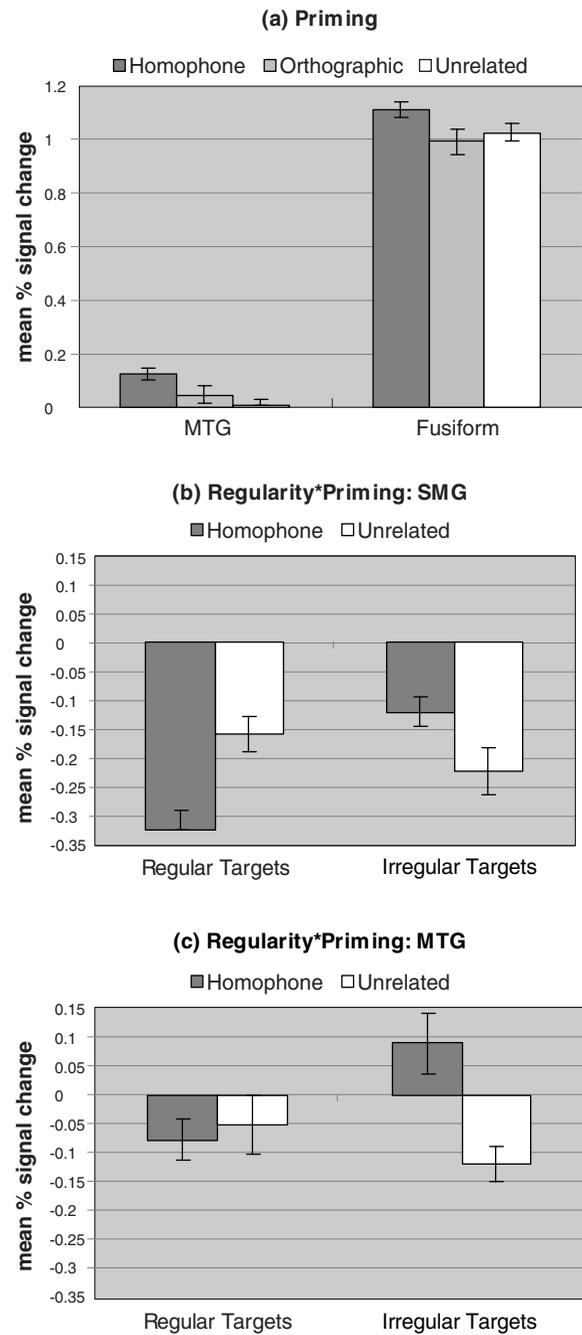


Figure 3. Signal change of peak voxels. (a) the main effect of priming conditions on word targets in the left MTG and fusiform gyrus (b) the interaction of regularity and priming on word targets in the left SMG, and (c) the same interaction in the left MTG. Error bars indicate the standard error of the mean after between-subject variability has been removed, which is appropriate for repeated-measures comparisons (Loftus & Masson, 1994).

Table 2
fMRI activations.

	Location		MNI Coordinates					Z-test	Voxels
	Area	H	BA	X	Y	Z			
Phonological Priming									
(HP - UP)word	Middle Temporal Gyrus*	L	21	-58	-24	-4	3.21	78	
	Lingual/Middle Occipital Gyrus	L	19,18	-6	-48	-2	4.25	544	
	Parahippocampal Gyrus/Culmen	L	28,37	-26	-22	-16	3.52	275	
	Fusiform Gyrus*	L	37	-40	-58	-18	3.02	27	
(OP - UP)word	Medial Frontal Gyrus/Anterior Cingulate	R	11,25	8	28	-12	3.7	317	
(HP - OP)word	Uncus	L	20	-30	-2	-36	3.4	59	
Regularity Effects									
(UP-HP)reg - (UP-HP)irreg	Supramarginal Gyrus*	L	40	-62	-52	28	3.62	37	
	Precuneus	L	7	-8	-60	40	3.44	167	
	Medial Frontal Gyrus/Anterior Cingulate	L	10,32	-6	52	6	3.12	301	
	Middle Temporal Gyrus*	L	21	-56	-30	-10	2.96	34	
(UP - HP)reg	Supramarginal Gyrus*	L	40	-56	-54	26	3.76	159	
	Middle Temporal Gyrus	R	21	52	2	-32	3.38	60	
	Middle Frontal Gyrus	L	9,10	-6	46	20	2.91	68	
(HP - UP)irreg	Middle Temporal Gyrus*	L	21	-56	-24	-8	3.55	138	
	Middle Occipital Gyrus	R	19	38	-86	18	2.96	30	
(UP-HP)irreg - (UP-HP)reg	Superior Parietal Lobule	R	7	26	-64	50	3.65	153	
	Insula	R	13	38	6	18	2.9	33	
Lexicality Effects									
Nonword - Word	Middle Occipital Gyrus	R	19	36	-78	16	3.58	144	
	Fusiform Gyrus	R	37	24	-52	-14	3.38	77	
	Cuneus	L	18	-28	-68	18	3.17	35	
	Superior Temporal Gyrus	L	22	-34	-44	12	3.16	28	
	Insula	R	13	30	-30	16	3.11	36	
	Parahippocampal/Fusiform Gyrus [^]	L	37	-34	-38	-4	2.89	62	
	Superior Temporal Gyrus	R	22	64	-50	8	2.84	35	

Note. Coordinates of activation peaks are given in the MNI stereotactic space. HP, homophone pairs; OP, orthographic pairs; UP, unrelated pairs; reg, regular; irreg, irregular; L, left; R, right; BA, Brodmann area. Regions marked * reach small volume correction at $p = .05$; marked [^] reach small volume correction at $p = .07$.

We also conducted an analysis of the correlation between behavioural performance and brain activity for all contrasts. This showed that longer reaction times were associated with greater activation in the MTG for the contrast of homophone versus unrelated word pairs (MNI coordinates [-60, -18, -12], $Z = 2.70$, $p < .005$ uncorrected). The correlations of behavioural performance and sig-

nal intensity were not significant for other contrasts.

We furthermore examined the correlation of the continuous variable of prime frequency and peak signal strength across all event-related responses for the word pairs (as in Chou et al., 2006a; Chou et al., 2006b). No significant correlation was found for this analysis. Thus, prime

frequency was not responsible for the observed MTG, STG, or FG activations.

Imaging: regularity effects

We examined the interaction between regularity (regular and irregular) and condition (homophone and unrelated) for the word targets with an exclusive mask from the contrast of orthographic versus unrelated word pairs to exclude activation attributable to form-priming (see Table 2 and Figure 2b). The left SMG (BA 40) and left MTG (BA 21) showed a significant interaction ($p < .05$ corrected for multiple comparisons). To unpack this interaction, we compared the homophone and unrelated conditions separately for the regular and irregular targets. There was a significant reduction in the left SMG for regular targets for homophone compared to unrelated primes ($p < .05$ corrected for multiple comparisons) and greater activation for homophone than unrelated primes for irregular targets in the left MTG ($p < .05$ corrected for multiple comparisons). Two plots of the peak response in each condition in the left SMG and the MTG are illustrated in Figure 3b and 3c. Finally, the direct comparisons of the regular and irregular targets within prime type showed that the contrast of regular versus irregular targets had a significant reduction in the left SMG for homophone primes (MNI coordinates [-60, -54, 26], $Z = 3.33$, $p < .05$ corrected for multiple comparisons).

A further analysis of the correlation between behavioural performance and brain activity showed that longer reaction times were associated with greater activation in the MTG for the contrast of homophone versus unrelated word pairs for irregular targets (MNI coordinates [-52, -22, -4], $Z = 3.32$, $p < .05$ corrected for multiple comparisons). Moreover, greater activation was correlated with longer reaction times in the SMG for the contrast of unrelated versus homophone word pairs for regular targets (MNI coordinates [-56, -48, 34], $Z = 2.87$, $p < .005$ uncorrected).

Imaging: lexicality effects

No significant behavioural priming effects were observed for pseudoword targets. We therefore collapsed over priming conditions and compared all pseudoword to all word targets. Pseudowords produced greater activation in the left fusiform gyrus (BA 37, $p = .07$ corrected for multiple comparisons). The contrast of word versus pseudoword targets did not produce significant activation.

Discussion

To the best of our knowledge, this is the first event-related fMRI study to use phonologically-primed lexical decisions to investigate the neural correlates of reading regular and irregularly-spelt words. This discussion will focus on neural activity in three regions of the left temporal lobe that showed distinct profiles of responses to the phonological priming manipulation; the left middle temporal gyrus (MTG, BA 21), left supramarginal gyrus (SMG, BA 40), and left fusiform gyrus (FG, BA 37).

Phonological priming

Imaging studies of priming have used reductions in neural activity produced by repeated stimuli to map the brain regions associated with different stages of processing (Henson, 2003; Schacter & Buckner, 1998). Previous studies using rhyme matching or phonological priming have identified brain regions involved in phonological processing, including the left SMG, left IFG, left MTG, and left inferior temporal gyrus (de Zubicaray et al., 2002; Haist et al., 2001; Poeppel, 1996; Price, 1997). However, in the current study, the left MTG showed an enhanced rather than a reduced response to stimuli that contained phonological repetitions. Such an enhanced response might reflect a neural correlate of the slower responses that we observed in our behavioural data and in other similar repetition priming studies using homophonic items

(Chou & Marslen-Wilson, 2001; Davelaar et al., 1978; Ferrand & Grainger, 1996, 2003; Grainger, Van Kang, & Segui, 2001; Pexman et al., 2001; Rubenstein et al., 1971). Computational models (Plaut & Booth, 2000) argue for the role of semantic representations in lexical decision and many neuroimaging studies show the involvement of the left MTG in semantic tasks (Booth et al., 2002b; Jernigan et al., 1998; Moore & Price, 1999; Price et al., 1996). Semantic involvement in lexical decision tasks is likely to increase due to the competition between multiple semantic representations from homophones. The fact that homophones involve one-to-many mappings between phonology and meaning should lead to increased settling time for semantic representations (see simulations in Rodd, Gaskell, & Marslen-Wilson, 2004; Pexman et al., 2001). We also found greater left MTG activation for irregular targets and longer reaction times to irregular targets were associated with greater activation in the left MTG. Irregular targets, especially those with slow reaction times, may place a greater demand on the lexical-semantic system because of the inconsistent mappings between orthography and phonology (Strain et al., 1995).

Another plausible explanation for slower responses during homophone priming is that demands on orthographic processing are greater when two different orthographic representations for the same sound are co-activated. This would create interference at the orthographic level. These orthographic processing demands are even greater when pseudo-homophones are included as pseudo-word targets (Davelaar et al., 1978; Ferrand & Grainger, 2003; Pexman et al., 2001). When two successive items have the same pronunciation, the second item can be either a real word (homophone) or a nonsense word (pseudo-homophone). The subject needs to check the second item carefully when the second item has the identical sound to the previous item. The process of the spelling or familiarity judgement for the second item (the target) should delay the subject's decision. A variation of the spelling check account is that when BEACH

primes BEECH, the subject may wonder whether the target BEECH is a misspelling of the prime BEACH. The process of a spelling check should delay the subject's judgement. Two elaborate models also try to explain a spelling check mechanism, one by incorporating response criteria (Norris, 1984), and the other by including feedback from the semantic system to the orthographic system (Harm & Seidenberg, 2004). In our follow-up behavioural experiment in which pseudo-homophones were taken out, the interference was greatly reduced (Chou & Marslen-Wilson, 2001). Several studies have suggested that the left fusiform gyrus is important for orthographic processing (Cohen et al., 2002; Fiebach et al., 2002). The hypothesis of increased orthographic interference is supported by our finding of greater activation in left fusiform gyrus (FG) for homophone primes. In contrast to elevated activity in the left MTG and FG for homophonic primes, we observed significant reductions in the left SMG (BA 40) for homophonic-primed regular targets. This priming-related decrease may be related to the usefulness of phonological information in word recognition (Naccache & Dehaene, 2001). The left SMG has previously been associated with mappings between orthography and phonology (Booth et al., 2002a, 2003; Jobard et al., 2003; Menard et al., 1996). For example, cross-modal conversion is required in spelling tasks with auditory input and rhyming tasks with written input; both of these tasks produce activation in this region (Booth et al., 2002a, 2003). A meta-analysis of imaging studies suggests that this region is involved in grapho-phonological conversion, allowing visually-presented words to be transformed into their spoken form (Jobard et al., 2003). Our results provide evidence consistent with this explanation because reduced activity in the left SMG for homophonic word pairs as compared to unrelated pairs was only observed for regularly spelt targets. This finding suggests that the role of left SMG in orthographic to phonological conversion will be more reliably observed for regularly spelt words - consistent with the functional separation between lexically- and sub-lexically mediated

reading that is present in most current models of reading aloud (Coltheart et al., 2001; Plaut et al., 1996). Whether this result implicates the SMG in computing grapheme-phoneme conversion rules (Coltheart et al., 2001) or in extracting statistical regularities between orthographic and phonological representations (Plaut et al., 1996) remains for future investigation. This study however was not designed to distinguish between regularity and consistency nor between the dual-route framework and the connectionist models. The motivation of this study was to evaluate the neural correlates of easy versus difficult spelling-to-sound correspondence as in Fiez et al. (1999).

Activation versus deactivation

One striking property of the neural priming effects (reduced activation) observed in the left SMG is that these accompany an inhibitory effect (longer RTs) on response times. This result suggests that while behavioural responses may reflect the net outcome of several processing stages, neural priming may provide a more transparent measure of underlying functional specialisation within specific brain regions. A possible explanation of our findings of phonological facilitation (reduced activation) in the SMG for homophone-primed trials may be that the prime activates phonological features that overlap with the target, and this pre-activation facilitates phonological processing of the target (Plaut & Booth, 2000). This preactivation may benefit regular targets more than irregular targets because of the consistent mapping between orthography and phonology. If this orthography to phonology conversion process were directly involved in producing lexical decision responses, then we might expect faster reaction times for the homophone pairs than for the unrelated pairs. However, this was not observed. Rather, the slower reaction times for the homophone pairs may reflect the involvement of different representational systems in the lexical decision task. Behavioural work has suggested that lexical decisions can involve a spelling check process when pseudohomophones

are used (Davelaar et al., 1978) or a greater involvement of semantics (Plaut & Booth, 2000). Slower reaction times for the homophone primed trials may therefore result from either of these additional processes. Our finding of greater activation in the left fusiform gyrus and in the left MTG for homophonic primed trials is consistent with both of these mechanisms, given prior evidence for left MTG involvement in semantic processing (Booth et al., 2002b; Price et al., 1996) and evidence for fusiform involvement in visual word form encoding (Cohen et al., 2002; Fiebach et al., 2002).

Inferior frontal gyrus

Neuroimaging studies looking for effects of regularity on reading aloud have shown greater activation in the left inferior gyrus for irregular compared to regular words (Fiez et al., 1999; Herbster et al., 1997; Pugh et al., 1997). However, in contrast to previous research, the present study failed to find activation in left inferior frontal gyrus (IFG) when comparing the experimental conditions. The absence of the IFG activation in the present study suggests that the activation of the IFG in the homophone condition is equivalent to that in the unrelated condition. To assess left IFG activation in these conditions separately, we conducted a further analysis of the homophone and unrelated conditions relative to the null event baseline. Significant IFG activation was found for homophone pairs (MNI coordinates [-46, 12, 24], $Z = 4.10$, 347 voxels, $p < .01$ corrected for multiple comparisons) and for unrelated pairs (MNI coordinates [-50, 12, 24], $Z = 3.75$, 335 voxels, $p < .01$ corrected for multiple comparisons). Further, a direct comparison of irregular versus regular targets collapsed over homophone and unrelated pairs produced activation in the left IFG at a more liberal threshold (MNI coordinates [-54, 14, 26], $Z = 2.55$, 9 voxels, $p < .005$ uncorrected). Therefore, our results are consistent with other studies which have found more activation in the inferior frontal gyrus for irregularly spelt words.

Lexicality effects: words versus pseudowords

We found that the left fusiform gyrus was more active for pseudowords when compared to words, collapsed across all priming conditions. Other studies have found this area active during lexical decisions to pseudowords (Rumsey et al., 1997) and when detecting a letter in pseudowords (Cappa et al., 1998). The left visual association region is thought to deal with orthographic processing, such as processing legal letter strings (Petersen, Fox, Snyder, & Raichle, 1990) or visually complex stimuli (Price et al., 1997). The greater activation for pseudowords in the left fusiform gyrus in our lexical decision task may be due to the application of a spelling check or familiarity judgment to the pseudowords. This interpretation is consistent with our finding that pseudowords produced longer decision times than words.

Conclusion

Priming between homophonic words was used to explore the brain regions involved in processing orthographic, phonological, and semantic information during visual word recognition. fMRI results suggest that the left supramarginal gyrus (BA 40) plays an important role in mapping orthographic input onto phonological representations, and that this mapping is facilitated (reduced neural activity) for phonologically-identical word pairs that have regular spelling to sound correspondences. The left middle temporal gyrus (BA 21) showed an elevated response to phonologically primed irregular targets consistent with behavioural evidence for greater semantic involvement in making lexical decisions to these stimuli. The left fusiform gyrus (BA 37) showed more activation for homophone word pairs and pseudoword pairs, implying additional orthographic processing in the presence of pseudohomophones. Thus, our work shows that phonological priming is associated with less activation in regions involved in mapping between orthography and phonology, but more activation in regions involved

in processing semantics and orthography. Elevated response times in phonological priming thus result from the complex interaction of several processing phases involved in visual word recognition.

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英文單字辨識的語音促發歷程： 功能性核磁共振造影的研究

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此篇研究採用功能性核磁共振 (fMRI) 來探討閱讀英文單字時，字形、字音、與字義如何交互影響閱讀的歷程。實驗的刺激嘗試是英文的字對，以促發的程序來安排，受試者閱讀連續出現的兩個刺激嘗試，並要判斷第二個刺激嘗試是否為一個合法的英文字。當兩個刺激嘗試為同音字對時，實驗者觀察第一個刺激嘗試如何去影響受試者對第二個刺激嘗試的判斷，並檢視其對應的神經機制。此外，第二個刺激嘗試並根據字的形音對應關係，分為規則字與不規則字，藉此探討在促發的實驗設計下，字的規則性如何去影響受試者對第二個刺激嘗試的判斷。三個主要的實驗的結果如下：第一，當英文字對包含不規則字時，由於字形與字音的轉換困難導致字義的涉入，在左腦半球的顳葉中區 (BA 21)

產生大腦神經活動增加的現象。第二，當英文字對包含規則字時，由於字形與字音的轉換容易，在左腦半球的頂葉下區 (BA 40) 產生大腦神經活動減少的現象。第三，同音字對與控制組字對相比較，因為對字形的檢查處理以判斷字的合法性，在左腦半球的視覺聯結區 (BA 37) 產生大腦神經活動增加的現象；同樣地，非合法的英文字對與合法的英文字對比較，在相同的區域產生大腦神經活動增加的現象。這些實驗結果建議，在行為資料中所產生的同音促發效果，是由數種的處理歷程所構成，並且反映在增加與減少的神經活動上。

關鍵詞：語言、促發、規則性、功能性核磁共振

