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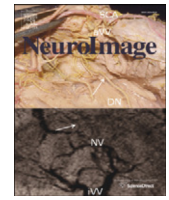

Implicit phonological priming during visual word recognition

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ABSTRACT

Phonology is a lower-level structural aspect of language involving the sounds of a language and their organization in that language. Numerous behavioral studies utilizing priming, which refers to an increased sensitivity to a stimulus following prior experience with that or a related stimulus, have provided evidence for the role of phonology in visual word recognition. However, most language studies utilizing priming in conjunction with functional magnetic resonance imaging (fMRI) have focused on lexical–semantic aspects of language processing. The aim of the present study was to investigate the neurobiological substrates of the automatic, implicit stages of phonological processing. While undergoing fMRI, eighteen individuals performed a lexical decision task (LDT) on prime-target pairs including word–word homophone and pseudoword-word pseudohomophone pairs with a prime presentation below perceptual threshold. Whole-brain analyses revealed several cortical regions exhibiting hemodynamic response suppression due to phonological priming including bilateral superior temporal gyri (STG), middle temporal gyri (MTG), and angular gyri (AG) with additional region of interest (ROI) analyses revealing response suppression in the left lateralized supramarginal gyrus (SMG). Homophone and pseudohomophone priming also resulted in different patterns of hemodynamic responses relative to one another. These results suggest that phonological processing plays a key role in visual word recognition. Furthermore, enhanced hemodynamic responses for unrelated stimuli relative to primed stimuli were observed in midline cortical regions corresponding to the default-mode network (DMN) suggesting that DMN activity can be modulated by task requirements within the context of an implicit task.

Introduction

Phonological processing involves recognizing, manipulating, and producing the elemental sounds of language. Evidence for the role of phonology in visual word recognition has been provided by numerous behavioral studies utilizing priming (e.g., Berent, 1997; Grainger and Ferrand, 1994; Lukatela et al., 1990; Lukatela and Turvey, 1994a,b). Priming refers to a form of implicit memory that results in a change in the speed, bias, or accuracy of processing a stimulus (i.e., the target), following a prior presentation of the same or a related stimulus (i.e., the prime). In conjunction with functional magnetic resonance imaging (fMRI), priming has been used as a tool to identify brain regions associated with the processing of linguistic stimuli. However, these studies have generally focused on lexical–semantic aspects of language. Few have investigated phonological processing (e.g., Chou et al., 2006; Graves et al., 2008; Haist et al., 2001; Kouider et al., 2010, 2007; Vaden et al., 2010); and, of these, only three have investigated visual (as opposed to auditory) word recognition (Chou et al., 2006; Haist et al., 2001; Kouider et al., 2007).

The most consistent finding in fMRI priming studies is decreased hemodynamic response for primed relative to unprimed stimuli in cortical regions typically involved in processing the type of stimuli or the aspect of the stimuli manipulated between primed and unprimed trials. However, response enhancements have also been observed (for a review see Henson, 2003). In priming studies investigating phonological processing, priming effects have been observed in regions consistently implicated by previous imaging studies to be involved in phonological processing, including bilateral superior temporal gyri (STG), largely left lateralized supramarginal gyrus (SMG), and left lateralized inferior frontal cortex (IFC) (e.g., Bles and Jansma, 2008; Booth et al., 2002; Burton et al., 2005; Hickok et al., 2000; Hickok and Poeppel, 2007; Jobard et al., 2003; Price, 2000; Shalom and Poeppel, 2008; Stoeckel et al., 2009; Vigneau et al., 2006). However, the direction of the priming-induced hemodynamic responses has varied with both response suppression and enhancement reported across and within studies.

Vaden et al. (2010), for example, observed repetition suppression and enhancement in an equal number of cortical regions in response to phonological repetition of aurally presented words. These included suppression in the left lateralized IFC and the superior temporal sulcus

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(STS), with enhancement observed in the left SMG. Using pseudowords in auditory priming tasks, Graves et al. (2008) observed hemodynamic response suppression in the left STG, whereas Kouider et al. (2010) observed STG response enhancement. These differences, however, were most likely due to differences in study design and task requirements across these two studies. Graves et al. (2008) utilized supraliminally presented single pseudoword trials, which subjects repeated aloud. Kouider et al. (2010), on the other hand, utilized prime-target pairs with subliminally presented primes in combination with a lexical decision task (LDT).

Both types of priming effects have also been observed in the three previous phonological priming studies involving visual stimuli. However, similar to studies utilizing aurally presented words, direct comparisons between studies are complicated by several methodological differences, including differences in task and stimuli design. Haist et al. (2001) used single word, pseudohomophone, and nonword trials to examine repetition priming effects within a LDT and an orthographic decision task. They observed both response suppression and enhancement within the left STG, SMG, inferior temporal cortex (ITC), and IFC depending on the stimuli type and the task involved. However, direct comparisons across the tasks, stimuli, or relative to an unrelated baseline were not made. In the other two visual studies, prime-target pairs were utilized. Chou et al. (2006) reported response suppression in the left SMG, but response enhancement in the left middle temporal gyrus (MTG) and the left fusiform gyrus (FG). Kouider et al. (2007), who examined both subliminal and supraliminal phonological priming, reported response enhancement in the left IFC and anterior insular cortex (AIC) for supraliminal phonological priming with no phonological priming effects observed in the subliminal condition. However, comparisons between these two studies are also difficult to make due to methodological differences. Chou et al. (2006) utilized a LDT, and Kouider et al. (2007) a semantic classification task. Differences in task demands have been suggested to affect the linguistic processes that are engaged during priming. Categorization tasks are thought to require or at least be more sensitive to early semantic processing, whereas LDTs may be more sensitive to presemantic interlexical relationships (e.g., Bueno and Frenck-Mestre, 2008; Van den Bussche et al., 2009). Furthermore, while both studies utilized homophonic stimuli, Chou et al. (2006) included word–word homophone prime-target pairs, whereas Kouider et al. (2007) included pseudoword–word prime-target pairs.

In the present study, we developed a priming task involving both word–word homophone (e.g., PAUSE-paws) and pseudoword–word pseudohomophone (e.g., JURM-germ) pairs, in part to compare our findings with both prior visual modality phonological priming studies utilizing prime-target pairs. Behavioral studies involving homophones, which are pairs of words that sound the same but are spelled differently, have provided evidence for the role of phonological representations in silent reading. Homophones are particularly useful because the visual information of one member of the pair (e.g., pause) activates only one meaning (i.e., a break), whereas its phonological representation activates the meanings of both members of the pair (i.e., a break and an animal's feet). A number of behavioral studies have provided evidence that the phonological representation of a member of a homophone pair affects performance (for a review see Jared et al., 1999). Therefore, tasks involving homophones are presumably tapping into phonological processing skills. In addition to choosing homophonic stimuli for the present study, we chose a priming paradigm with a prime duration below perceptual threshold (i.e., 30 ms), because we wished to investigate the initial, automatic stages of visual word recognition and phonological processing.

For phonological priming across both homophones and pseudohomophone conditions, we hypothesized that the repetition of phonological information would facilitate phonological processing and result in response suppression in bilateral STG and largely left lateralized SMG. However, based on the results of Chou et al. (2006) and Kouider et al. (2007), we hypothesized that homophone and pseudohomophone priming would result in different patterns of hemodynamic responses relative to each other. For homophone priming, we expected to observe greater response enhancement in the MTG and FG due to greater demands in accessing semantic and orthographic information. In contrast, due to the greater phonological recoding demands for pseudoword primes, we hypothesized that pseudohomophone priming relative to homophone priming would result in repetition enhancement in the IFC and AIC.

Methods

Participants

The study included data from eighteen subjects (4 men, 14 women, mean age 43.3 ± 7.2 years). Data from one additional subject was excluded due to head motion greater than 3 mm during scanning. All subjects had English as their first language. Two were classified as left-handed, one was mixed dominant, and all others were right-handed as determined by the Annett Handedness Scale (Annett, 1985). To obtain a measure of cognitive ability, the four subtests of the Wechsler Abbreviated Scale of Intelligence (WASI) were administered to all subjects (Wechsler, 1999) (VIQ: 112.8 ± 11.3; PIQ: 114.1 ± 10.9; FSIQ: 115.1 ± 11.2). All subjects signed an informed consent to participate in the study consistent with the guidelines of the Colorado Multiple Institution Review Board.

Stimuli design, task procedure, and behavioral data analyses

A total of 192 prime-target pairs were developed for the current study. Stimuli were divided into four conditions: 40 homophone, 40 pseudohomophone, 40 unrelated, and 72 word/nonword pairs. All words were matched across conditions for written frequency, bigram sum, bigram mean, bigram frequency by position, number of phonemes, length, and number of syllables with ratings derived from the English Lexicon Project (ELP) Web Site (Balota et al., 2007). All nonwords were formed by rearrangement of the target words appearing in the other three conditions so that similar phonemes and syllable structures would be maintained across target conditions. All primes were presented in uppercase and all targets in lowercase so that the visual form of primes and targets differed. Examples and stimuli parameters are listed in Table 1.

Participants performed a LDT to ensure proper attention to the stimuli, which were presented using a projector and screen system. They indicated if each target was a real word or a nonword by pressing one of two buttons on an MR-compatible response pad. Participants were not informed of the presence of the uppercase prime, which was below perceptual threshold, but were told that they would see a series of number signs followed by a lowercase word to which they were to respond. Prior to the scan, all participants practiced the task on a set of additional trials not repeated in the scanner. A single trial proceeded as follows: 500 ms forward mask consisting of a series of number signs of equal length to the prime, 30 ms prime, 30 ms blank screen, 400 ms target, and 1040 ms blank screen during which participants responded (Fig. 1A). The preceding design resulted in an inter-stimulus interval of 60 ms and an inter-trial interval of 0 ms.

Stimuli were presented in one session of 30 16-second blocks, for a total time of 8 min. Each of the four conditions and a rest condition (i.e., fixation on a series of plus signs) were presented six times in the following order: homophone, pseudohomophone, unrelated and word/nonword. Each block of the homophone, pseudohomophone, and unrelated conditions consisted of six pseudorandomized word pairs within the given condition intermixed with two pairs from the word/nonword condition to minimize strategy use. Accordingly, each block of the word/nonword condition contained six pseudorandomized word/