

Published in final edited form as:

Neuroimage. 2011 March 15; 55(2): 724–731. doi:10.1016/j.neuroimage.2010.12.019.

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 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.

Keywords

fMRI; phonology; priming; implicit memory; superior temporal gyrus; supramarginal gyrus; default-mode network

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1. 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; Kouider et al., 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 left lateralized IFC and superior temporal sulcus (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 task involved. However, direct comparisons across 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 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.

2. Methods

2.1 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 informed consent to participate in the study consistent with the guidelines of the Colorado Multiple Institution Review Board.

2.2 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 in order 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 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 (Figure 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 minutes. 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, 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/nonword pairs intermixed with two pairs randomly chosen from the other three conditions. Rest blocks were of equal duration to trial blocks (i.e., series of plus signs presented for the trial length of 2000 ms repeated eight times). Within blocks, stimuli were pseudorandomized (Figure 1B). Stimulus order was the same for all participants.

Statistical analyses of stimuli parameters and behavioral data were performed using SPSS version 11 (SPSS Inc., Chicago, IL) with a two-tailed alpha criterion of 0.05. To examine matching of stimuli, all measured linguistic parameters for word stimuli, as well as length and number of syllables for all stimuli (i.e., including pseudohomophone primes and nonword targets), were separately entered into one-way ANOVAs (e.g., frequency by condition, bigram sum by condition, etc.). For behavioral data, accuracy was examined by entering the percentage of each condition correctly identified into a one-way ANOVA. A' scores were also calculated for each subject in order to obtain a nonparametric measure of signal detection (Stanislaw and Todorov, 1999). Reaction times were examined by entering the mean reaction times of all accurate trials for the homophone, pseudohomophone, unrelated, and word/nonword conditions into a one-way ANOVA. For all ANOVAs, assumptions of sphericity were confirmed via Mauchly's test with degrees of freedom corrected using Greenhouse-Geisser estimates of sphericity as needed. Post hoc comparisons

were conducted using the least significant difference (LSD) pairwise multiple comparison test.

2.3 MRI Data Acquisition and Analyses

Imaging data were acquired with at 3T GE whole-body MR scanner with an Excite upgrade using an 8-channel head coil. A high-resolution, T1-weighted 3D anatomical scan was acquired for coregistration to functional data (inversion recovery-spoiled gradient-recall acquisition IR-SPGR, TR = 9 ms, TE = 1.9 ms, TI = 500 ms, flip angle = 10°, matrix = 256², FOV = 220 mm², 124 1.7-mm-thick coronal slices). Functional images were acquired with a gradient-echo T2* Blood Oxygenation Level Dependent (BOLD) contrast technique with TR = 2000 ms, TE = 30 ms, FOV = 220 mm², 64² matrix, 32 slices, 3.5 mm thick, 0.5 gap, angled parallel to the planum sphenoidale. Additionally, one IR-EPI (TI = 505 ms) volume was acquired from each subject to improve the spatial normalization of EPIs.

Data were analyzed using SPM8 (Wellcome Department of Imaging Neuroscience, London). The first four image volumes were excluded for saturation effects. Functional data from each subject were realigned to the first volume. The realigned images were then normalized to Montreal Neurological Institute space using the unified segmentation algorithm (Ashburner and Friston, 2005) on the IR-EPI images and applying the resultant estimated warp parameters to the EPI data. Finally, functional images were smoothed with an 8-mm FWHM Gaussian kernel. All trials belonging to each of the five conditions (i.e., homophone, pseudohomophone, unrelated, word/nonword, and rest) were separately convolved with the canonical hemodynamic response function using the general linear model (e.g., homophone trials within homophone blocks as well as homophone trials within word/nonword blocks, word/nonword trials within word/nonword blocks as well as word/nonword trials within homophone blocks, etc.). Response accuracy within a window of 300 to 1440 ms of target onset was included as an additional regressor at the first level to model and remove variance associated with task performance. A 182-second high-pass filter was applied to remove low-frequency fluctuation in the BOLD signal, and a one-lag autoregression (AR(1)) model was used to correct for serial (i.e., temporal) autocorrelations.

To account for both within-group and within-subject variance, a whole-brain random-effects analysis was implemented. Parameter estimates for each individual's first level analysis (SPM contrast images) were entered into second-level one-sample t tests. Contrasts of interest included: 1) primed (i.e., homophone + pseudohomophone) vs. unrelated and 2) homophone prime vs. pseudohomophone prime. Analyses were conducted with the initial feature-inducing threshold set at $p < 0.001$ to define local maxima and clusters, with all reported regions meeting the cluster-wise false discovery rate (FDR) corrected threshold of $q < 0.05$ (Chumbley and Friston, 2009). Anatomic localization of all reported clusters was established using the Automated Anatomical Labeling (AAL) atlas supplemented with visual inspection and based on the labeled region containing the local maximum voxel of each cluster (Tzourio-Mazoyer et al., 2002).

In addition to whole-brain analyses, region of interest (ROI) analyses were conducted wherein the initial feature-inducing threshold was again set at $p < 0.001$ across the whole-brain. A small volume correction (SVC) (Worsley et al., 1996) was then applied within individual ROIs, which were anatomically defined using the AAL atlas. Based on previous imaging studies of phonological processing, the following ROIs were included in the analyses: left lateralized STG, SMG, MTG, FG, IFC, and insular cortex (IC). All reported regions met a SVC corrected threshold of $p < 0.05$.

Since not all of our participants were right-handed, we investigated the effect of handedness by computing a regression between Annett Handedness Scale scores and our functional SPM contrasts of interest.

3. Results

3.1 Stimulus Parameters

ANOVAs performed to examine matching of stimuli revealed no significant differences between conditions for any of the measured parameters ($p = 1.00$ for all measures).

3.2 Behavioral Data

No differences in percentage accuracy were found between conditions ($F(1.23, 20.95) = 2.12$, $p = 0.16$). Furthermore, the A' scores for all conditions were greater than 0.8, suggesting the absence of systematic response bias in the subjects. Examination of reaction times revealed a significant main effect of condition ($F(1.29, 21.96) = 26.96$, $p < 0.001$). Post-hoc comparisons indicated reaction times for the word/nonword condition were significantly slower than each of the three other conditions ($p < 0.001$). In addition, reaction times for the pseudohomophone condition were significantly faster than the unrelated condition ($p = 0.03$) with a trend of being significantly faster than the homophone condition ($p = 0.06$). Mean accuracy and reaction time data are listed in Table 2.

3.3 fMRI

Whole-brain cluster-level FDR corrected fMRI results are listed in Table 3. Whole-brain regions that exhibited decreased hemodynamic responses for primed relative to the unrelated stimuli included bilateral MTG, bilateral STG, the left angular gyrus (AG), right precuneus, and right superior frontal gyrus (SFG). The right lateralized hemodynamic response suppression observed in the cluster containing the MTG, STG, and precuneus extended into right lateralized SMG, AG, and inferior parietal lobule (IPL). In contrast, greater responses for primed stimuli relative to unrelated stimuli were only observed in bilateral anterior cingulate (AC) gyri, extending into the orbital portions of the right SFG and middle frontal gyrus (MFG).

In addition, whole-brain analyses revealed several regions that exhibited response enhancement for homophone priming relative to pseudohomophone priming. These included the left post- and precentral gyri, right cerebellar lobules IV/V, the cerebellar vermis, and right MFG. Enhancement in the left post- and precentral gyri extended into the left MFG and SFG. Enhancement in the right cerebellar lobules IV/V extended into the corresponding left lateralized cerebellar lobules as well as bilateral cerebellar lobule VI, cerebellar Crus I, and FG. Enhancement in the right MFG extended into the orbital portions of the SFG as well as bilateral AC. Relative to homophone priming, enhancement for pseudohomophone priming was observed in the left IPC and AG.

ROI fMRI results are listed in Table 4. For the selected regions of interest, the only additional significant response suppression or enhancement for all contrasts of interest that was not observed in whole-brain analyses was a region of suppression in the left SMG for primed stimuli relative to unrelated stimuli.

No significant correlations were found between Annett Handedness Scale scores and any of the regions of significant activation for all contrast of interest at a whole-brain FDR corrected threshold of $q < 0.05$ or at the more liberal uncorrected threshold of $p < 0.05$. Therefore, handedness was not considered further as a covariate in any of the main analyses.

4. Discussion

4.1 Priming effects on language-related brain networks

We observed priming-related response suppression, which is regarded as the most common finding in fMRI priming studies, in a network of regions known to be involved in language processing. This included, as hypothesized, significant bilateral STG response suppression. The STG has consistently been associated with prelexical aspects of phonological processing although the laterality and region of the STG involved in phonological processing is still debated (Binder, 2000; Hickok and Poeppel, 2007; Obleser and Eisner, 2009; Turkeltaub and Coslett, 2010). In the present study, STG response suppression was clearly bilateral, but the present design does not allow a differentiation between acoustic and phonetic or phonological processes. However, observed left lateralized mid-STG response suppression corresponds to the region of the STG reported by Turkeltaub and Coslett (2010) in a meta-analysis of neuroimaging studies of sublexical speech perception to be most closely associated with performing phonetic and prelexical phonological processing.

In addition to STG response suppression, we hypothesized response suppression in largely left lateralized SMG for phonological priming across conditions. While not observed in our whole-brain analyses, significant response suppression in left lateralized SMG was observed in our ROI analyses with response suppression observed in right lateralized SMG in our whole-brain analyses. Bilateral SMG regions have been implicated in previous studies of phonological processing (e.g., Booth et al., 2002; Lee et al., 2007; Vaden et al., 2010), with bilateral SMG suggested to be involved in conversion between orthography and phonology (Booth et al., 2002) and bilateral posterior regions suggested to bind phonological and semantic information (Lee et al., 2007). Right lateralized SMG regions have also been shown to be sensitive to the phonetic complexity of stimuli (Benson et al., 2001). In the present study, response suppression was also observed in bilateral AG. In their meta-analysis, Turkeltaub and Coslett (2010) reported that left lateralized SMG and AG performed categorical phoneme perception, although they noted that caution was warranted regarding these results since only two experiments in their analyses drove this effect. Furthermore, the AG has generally been regarded to be involved in semantic processing (Binder et al., 2005; Humphries et al., 2006, 2007; Mummery et al., 1998). Therefore, rather than resulting from facilitated phonological processing, the observed response suppression observed in bilateral AG may be due to a greater reliance on semantic processing in the unrelated condition. This interpretation may be debated, however, given the implicit nature of our paradigm and our use of a LDT, which is more commonly considered to measure presemantic stages of lexical processing (e.g., Bueno and Frenck-Mestre, 2008; Van den Bussche et al., 2009). As noted in the introduction, the direction of phonological priming effects has been inconsistent across previous studies. The use of a subliminal prime duration in the present study and the observed response suppression suggest that bilateral STG, SMG, and possibly bilateral AG are involved in automatic, implicit aspects of phonological processing.

Our results contrast somewhat with those of Kouider et al. (2007), who did not observe phonological priming effects in their subliminal condition (i.e., a 43 ms prime duration combined with forward and backward masking). Unlike Kouider et al. (2007), we used a shorter prime duration and excluded the backward mask to investigate if subliminal phonological priming would be observed under less strict masking conditions. It has been suggested that severe masking may reduce the amount of subliminal priming (Van den Bussche et al., 2009), and the present results are consistent with this suggestion. It is possible that the lack of backward masking allowed the prime to be perceptible to participants despite its very short duration. Related to this, perception of the prime could have resulted in order effects if participants became aware of the manipulation of the prime-

target relationship between our conditions that were presented in a fixed sequence of blocks. However, participants were only instructed that the task consisted of a series of number signs followed by lowercase words to which they were to respond. None of the participants reported the presence of the prime when practicing the task prior to scanning or when asked of their general impression of the task post-scanning. The threshold duration of prime perception in the task could be quantified more systematically in future studies using signal detection strategies, but we believe that a 30 ms prime is below threshold for detection based on previous priming studies with longer prime durations (although with backward masking) in which the primes were not accurately identified by participants when explicitly requested to do so (e.g., Grainger et al., 2006; Wheat et al., 2010). In addition to differences in masking, Kouider et al. (2007) utilized only pseudoword primes and based phonological priming results relative to their orthographic condition in which partial phonological overlap existed between primes and targets. These are additional factors that could possibly account for the differences between the results of Kouider et al. (2007) and the present study.

Based on the two previous phonological priming studies utilizing visual prime-target stimuli, we hypothesized differential patterns of activation for homophone relative to pseudohomophone priming. While the hypothesized response enhancement in the MTG and FG for homophone relative to pseudohomophone priming was not observed, we did observe response enhancement in the left post- and precentral gyri, bilateral cerebellum, and right MFG for this contrast. There is growing evidence for the role of the cerebellum in language processing (Ghosh et al., 2008; Marien et al., 2001; Murdoch, 2010), including phonological processing (Bohland and Guenther, 2006; Chen and Desmond, 2005a, b; Fulbright et al., 1999; Ghosh et al., 2008). For example, superior portions of the cerebellum have been suggested to contribute to the articulatory component of the phonological loop as proposed by Baddeley (Baddeley, 1992; Chen and Desmond, 2005a, b). Superior cerebellar regions have also been suggested to be involved in phonologic assembly with more extensive regions including the vermis suggested to be involved in semantic processing (Fulbright et al., 1999). Given the implicit nature of the task, enhancement in cerebellar regions for homophone relative to pseudohomophone priming could reflect engagement of speech plan representations required to initiate the phonological loop that are not immediately available for pseudohomophone primes. In addition, Chen and Desmond (2005a,b) found that superior cerebellar regions activated in conjunction with frontal regions including the precentral gyrus and pars opercularis, thought to be involved in articulatory processes and rehearsal. In the present study, response enhancement for homophone priming was observed in both pre- and postcentral gyri, which could reflect engagement of the proposed cerebrocerebellar articulatory network, although the observed regions are more dorsal to those generally thought to be involved in articulatory processes. Lastly, it must be considered that homophone pairs were responded to slower than pseudohomophone pairs, so that the greater cerebellar, pre-, and postcentral gyri involvement could be due to motoric preparation and execution in the homophone condition.

Similar to homophone priming, we did not observe response enhancement for pseudohomophone relative to homophone priming in our hypothesized regions, but rather in the IPL and AG. The IPL as a whole has been implicated in numerous studies of verbal working memory and implicated in the phonological storage component of phonological working memory (e.g., Awh et al., 1996; Chen and Desmond, 2005a; Cornelissen et al., 2004). Enhanced IPL recruitment for pseudohomophone priming could, therefore, reflect more extensive recruitment of the phonological storage component of working memory due to the pseudohomophone primes, which lack addressed phonology (i.e., phonology activated on the basis of whole word representations in the orthographic lexicon as opposed to assembled phonology, which is phonology activated on the basis of direct grapheme-to-phoneme conversion). While the observed region of enhancement included the AG, it

straddled the posterior regions of the IPL, which by definition includes both the SMG and AG. Therefore, the observed priming effect could be ascribed to any of the functions thought to be performed by these two regions, and the specific involvement of the AG is difficult to interpret.

4.2 Priming effects on the default-mode network

Given the subliminal nature of the prime stimuli, an unexpected result of the present study was that subjects exhibited enhanced hemodynamic responses for unrelated stimuli relative to primed stimuli in cortical regions corresponding to the midline regions of the default-mode network (DMN) including the precuneus/posterior cingulate gyrus and superior frontal gyrus. As discussed above, enhanced responses for unrelated stimuli were also observed in bilateral AG, which are considered to be components of the DMN as well. Given the finding regarding DMN midline structures and the limitations of interpreting AG involvement within the context of an implicit phonological priming task, the observed AG response enhancement may be more relevant to DMN rather than language network processing. The present design, however, does not allow us to disentangle the AG contribution to each of these networks. The DMN refers to a set of brain regions that are spontaneously active during rest and internal modes of cognition. This network of regions has been found to exhibit less activation, often termed 'deactivation', during attention demanding or goal directed tasks (Buckner et al., 2008; Raichle et al., 2001). However, relatively greater activity within the DMN has been observed during a variety of tasks such as those engaging self-projection, implicit memory, and semantic retrieval (e.g., Binder et al., 1999; Buckner and Carroll, 2007; Greicius and Menon, 2004; Gusnard et al., 2001; Yang et al., 2010). Binder et al. (1999) have suggested that the DMN is involved in semantic processing. Therefore, it is possible that the increased DMN activation observed in the unrelated relative to the primed conditions may reflect a greater degree of semantic as opposed to phonological processing. Another explanation is suggested by the results of McKiernan et al. (2003) in which the magnitude of task-induced deactivations within the DMN increased with task difficulty. These deactivations were interpreted as a reallocation of resources from regions within to the DMN to regions involved in the processing of the relevant task. Findings of increased activation in the DMN for unrelated stimuli could also reflect the absence of the 'task' (i.e., priming) in the unrelated condition as opposed to both primed conditions, even though both conditions were otherwise active and well-matched tasks. Less activity within the DMN for the primed conditions could, therefore, be interpreted as a priming-induced deactivation of the network and a reallocation of resources to phonological processing.

Recent fMRI studies have provided evidence that a coupling exists between the default-mode and task-positive networks, such that activity between the two are strongly negatively correlated with increases in task-positive network activity accompanied by decreases in DMN activity and vice versa (Fox et al., 2005; Uddin et al., 2009). This inverse relationship between the default-mode and task-positive networks has been interpreted as reflecting a switch from internal to external modes of processing (McKiernan et al., 2003), as well as reflecting a switch from implicit to explicit memory processing (Yang et al., 2010). However, the present finding of modulation of default-mode and task-positive network activity within an implicit memory task suggests that even within the context of an implicit task DMN activity can be modulated by task requirements and that the distinction between implicit and explicit processes may not be entirely correct.

5. Conclusion

The present study provides evidence that subliminal phonological priming is attainable under less severe masking conditions and that phonological processing plays a key role in

visual word recognition. As such, our results add to previous fMRI findings of the role that phonology plays in visual word recognition as well as to recent studies using magnetoencephalography (MEG) and electroencephalography (EEG), which with their greater temporal resolution than fMRI, have provided evidence for the role of phonological processing in visual word recognition as early as 150 ms after stimulus onset (Braun et al., 2009; Wheat et al., 2010). Implicit phonological priming resulted in response suppression in cortical regions found in previous studies to be associated with phonological processing, including the STG, SMG, and AG. Within our task, priming-related suppression of activity in midline DMN structures suggests that it is possible that subliminal primes can effectively modulate activity between default-mode and task-positive networks in much the same manner as consciously perceived stimuli.

Acknowledgments

Role of funding sources

Funding for this study was provided by Autism Speaks Grant 2090, Autism Speaks Weatherstone Grant 6291, the National Institutes of Health (NIH) Grant PHS R01 MH082020, NIH/NCRR Colorado CTSI Grant TL1 RR025778, and the National Institute of Child Health and Human Development (NICHD) Grant HD041697. The funding sources had no further role in study design; in the collection, analysis, and interpretation of data; in the writing of the report; and in the decision to submit the paper for publication.

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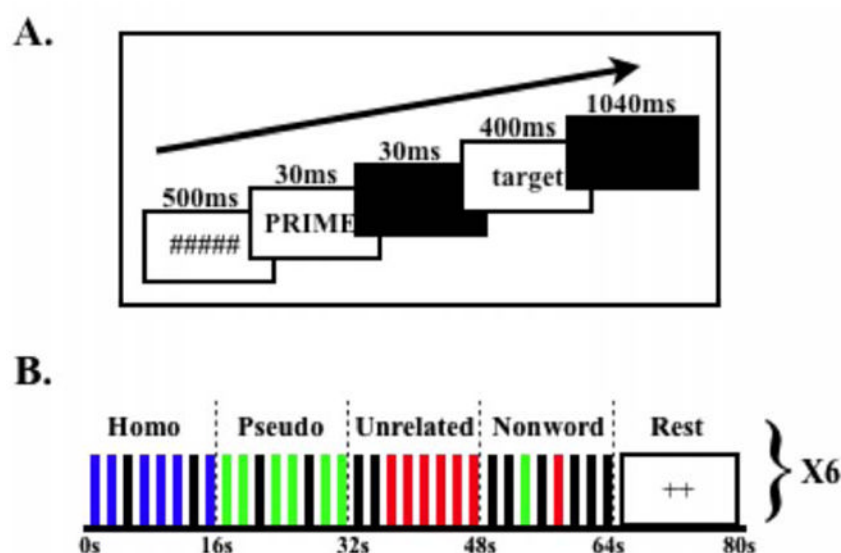


Figure 1.

(A) Individual trial procedure. (B) Schematic representation of trial order within the one run. Each bar represents a single prime-target pair with blue for homophone, green for pseudohomophone, red for unrelated, and black for word/nonword pairs. The order of the intermixed stimuli (e.g., word/nonword pairs within homophone, pseudohomophone, and unrelated blocks, as well as homophone, pseudohomophone, and unrelated pairs within word/nonword blocks) varied across the six repetitions of the five blocks.

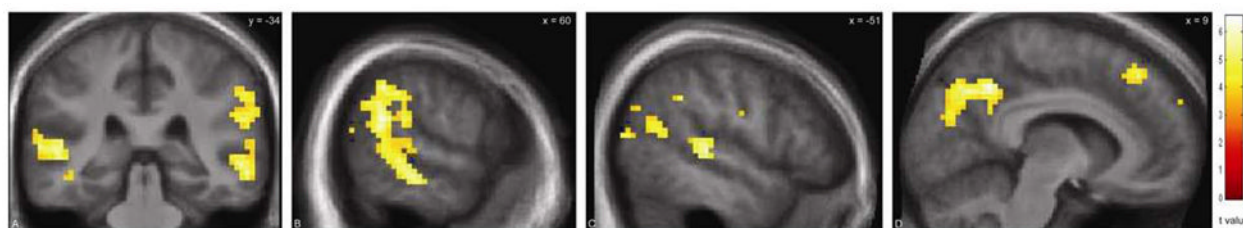


Figure 2.

Cortical regions exhibiting hemodynamic response suppression due to phonological priming. These included: (A) bilateral superior and middle temporal gyri, shown centered on the maximum voxel of the reported superior temporal gyrus cluster in the right (B) and left (C) hemisphere respectively; and (D) regions corresponding to the midline structures of the default-mode network including precuneus/posterior cingulate and superior frontal gyrus shown centered on maximum voxel of the reported precuneus/posterior cingulate cluster. Statistical maps are shown thresholded at $p < 0.001$ uncorrected, the cluster-defining threshold used in the study. Results are overlaid onto the average T1-weighted image from the study (N=18) and presented in neurological convention (left hemisphere on the left). Slice numbers (MNI coordinate) are shown in the upper right corner for each slice.

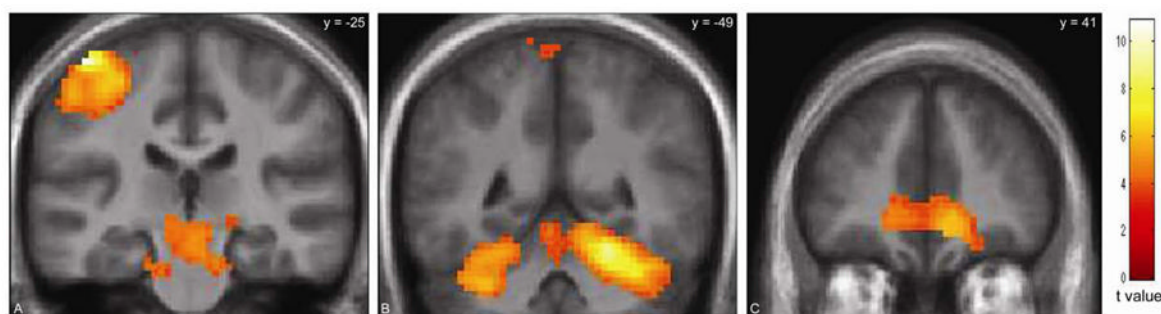


Figure 3.

Cortical regions exhibiting hemodynamic response enhancement for homophone relative to pseudohomophone priming. These included: (A) left lateralized postcentral gyrus, (B) right cerebellar lobule IV/V, and (C) right lateralized middle frontal gyrus. All figures centered on the maximum voxel of the reported significant clusters. Statistical maps are shown thresholded at $p < 0.001$ uncorrected, the cluster-defining threshold used in the study. Results are overlaid onto the average T1-weighted image from the study ($N=18$) and presented in neurological convention (left hemisphere on the left). Slice numbers (MNI coordinate) are shown in the upper right corner for each slice.

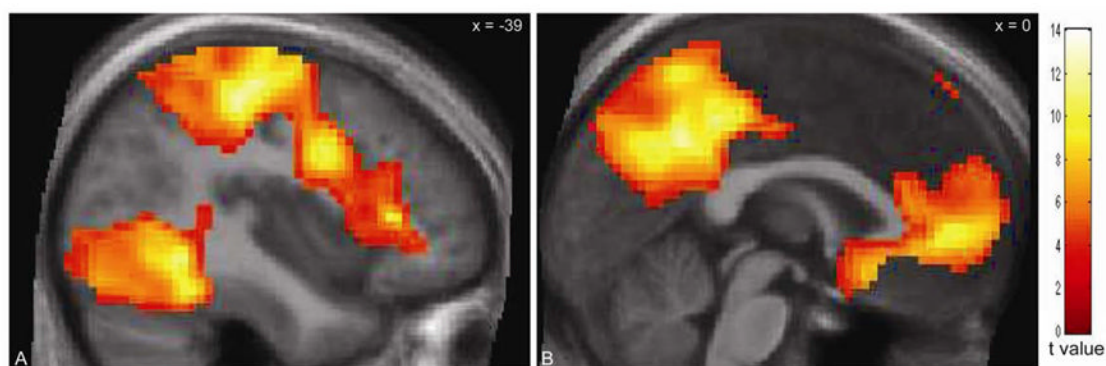


Figure 4.

Task-positive vs. default-mode network activity. (A) Cortical regions exhibiting enhanced hemodynamic responses for all task-related conditions (i.e., homophone, pseudohomophone, unrelated, word/nonword) relative to rest (i.e., fixation). These included left lateralized fusiform, inferior temporal, middle temporal, precentral, postcentral, and inferior frontal gyri. (B) Cortical regions exhibiting enhanced hemodynamic responses for rest relative to all task-related conditions. These included the precuneus/posterior cingulate and middle frontal gyrus. Statistical maps are shown thresholded at $p < 0.001$ uncorrected, the cluster-defining threshold used in the study. Results are overlaid onto the average T1-weighted image from the study ($N=18$) and presented in neurological convention (left hemisphere on the left). Slice numbers (MNI coordinate) are shown in the upper right corner for each slice.

Table 1

Stimuli examples and parameters.

Condition (PRIME-target)	Example	Frequency		Bigram Sum		Bigram Mean		Bigram Freq by Position		Number of Phonemes		Length		Number of Syllables	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Homophone	PAUSE	17.63	23.21	14750.83	6339.61	3749.67	1355.69	2770.08	1014.16	3.72	0.64	4.90	0.81	1.25	0.44
	paws	17.50	24.13	14782.40	6372.09	3799.23	1346.89	2777.15	1176.44	3.72	0.64	4.85	0.80	1.25	0.44
Pseudohomophone	JURM	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.83	0.75	1.25	0.44
	germ	17.63	23.89	14744.08	5666.48	3783.09	1371.33	2734.30	1150.06	3.73	0.68	4.92	0.69	1.25	0.44
Unrelated	CHECK	17.58	23.27	14771.38	6603.19	3726.03	1254.96	2727.75	1114.28	3.78	0.77	4.88	0.82	1.25	0.44
	slang	17.42	23.96	14747.65	6706.23	3776.24	1325.72	2717.73	1080.38	3.75	0.74	4.87	0.82	1.25	0.44
Word/Nonword	FISH	17.60	23.32	14765.07	6125.35	3729.93	1202.38	2789.15	1123.66	3.74	0.67	4.89	0.80	1.25	0.44
	nath	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.89	0.78	1.24	0.43

Table 2

Behavioral results (N=18).

Condition	Percentage Correct		Reaction Time - ms	
	Mean	SD	Mean	SD
Homophone	92.22	5.68	638.54	86.16
Pseudohomophone	95.97	4.13	624.02	72.84
Unrelated	95.83	4.62	638.58	87.72
Word/Nonword	90.66	13.21	745.68	72.94

Table 3

Whole-brain cluster-level FDR corrected fMRI results (N=18).

Brain region	q FDR	t	Cluster Size	MNI Coordinates
Unrelated > Primed				
Right middle temporal gyrus ^a	<0.001	6.56	944	48 -25 -14
Right precuneus/posterior cingulate gyrus	<0.001	6.31		9 -52 40
Right superior temporal gyrus	<0.001	6.28		60 -46 22
Left superior temporal gyrus	0.009	5.64	116	-51 -31 4
Right superior frontal gyrus	0.013	5.28	97	15 29 49
Left middle temporal gyrus ^a	0.009	4.80	111	-63 -58 19
Left angular gyrus ^a	0.009	4.62		-60 -58 37
Primed > Unrelated				
Right anterior cingulate gyrus ^a	<0.001	8.22	228	9 32 -8
Left anterior cingulate gyrus	<0.001	5.94		-9 32 -8
Homophone > Pseudohomophone				
Left postcentral gyrus	<0.001	10.89	680	-45 -25 64
Left precentral gyrus	<0.001	6.61		-30 -22 55
Right cerebellar lobule IV/V	<0.001	8.86	2640	24 -49 -20
Cerebellar vermis	<0.001	8.22		3 -67 -35
Right middle frontal gyrus, orbital part	<0.001	6.01	371	12 41 -8
Pseudohomophone > Homophone				
Left inferior parietal lobule ^a	0.020	6.32	99	-57 -55 46
Left angular gyrus ^a	0.020	5.19		-51 -79 28

Note. All labels are derived from the AAL atlas supplemented with visual inspection (see text). Where cluster size is not indicated, peak voxels represent sub-peaks within the above-labeled cluster.

^aThese peak voxels do not lie within the AAL atlas. Labels are derived from the nearest AAL labeled voxel.

Table 4

Region of interest (ROI) small volume corrected (SVC) fMRI results (N=18).

Brain region	t	Cluster Size	MNI Coordinates
Unrelated > Primed			
Left supramarginal gyrus	4.48	3	-51 -46 34

Note. Reported structure meets a SVC corrected threshold of $p < 0.05$. Structures reported in whole-brain analyses are not repeated in ROI results.