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An fMRI examination of the effects of acoustic-phonetic and lexical competition on access to the lexical-semantic network

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Abstract

The current study explored how factors of acoustic-phonetic and lexical competition affect access to the lexical-semantic network during spoken word recognition. An auditory semantic priming lexical decision task was presented to subjects while in the MR scanner. Prime-target pairs consisted of prime words with the initial voiceless stop consonants /p/, /t/, and /k/ followed by word and nonword targets. To examine the neural consequences of lexical and sound structure competition, primes either had voiced minimal pair competitors or they did not, and they were either acoustically modified to be poorer exemplars of the voiceless phonetic category or not. Neural activation associated with semantic priming (Unrelated–Related conditions) revealed a bilateral fronto-temporo-parietal network. Within this network, clusters in the left insula/inferior frontal gyrus (IFG), left superior temporal gyrus (STG), and left posterior middle temporal gyrus (pMTG) showed sensitivity to lexical competition. The pMTG also demonstrated sensitivity to acoustic modification, and the insula/IFG showed an interaction between lexical competition and acoustic modification. These findings suggest the posterior lexical-semantic network is modulated by both acoustic-phonetic and lexical structure, and that the resolution of these two sources of competition recruits frontal structures.

Keywords

Semantic priming; Lexical competition; Acoustic-phonetic competition; FMRI; Middle temporal gyrus

1. Introduction

Our unique ability for verbal communication requires mapping highly variable speech signals onto semantic representations, allowing us to express and exchange ideas. In most contemporary models of spoken word recognition (e.g. TRACE: McClelland & Elman, 1986; DCM: Gaskell & Marslen-Wilson, 1997, 1999), the acoustic information is mapped onto increasing levels of abstraction, eventually culminating in activation of the word-form and retrieval of meaning. Nonetheless, the presentation of an auditory input does not result in accessing *only* the intended lexical representations; instead, hearing a word appears to activate a neighborhood of similar acoustic-phonetic representations that compete for selection (Luce & Pisoni, 1998). The appropriate representation must be selected at each

level of linguistic processing (e.g. phonological, lexical). Correctly interpreting the word 'time', for instance, requires resolving not only competition between the voiceless stop consonant [t] and its voiced counterpart [d], but also requires resolving competition at the lexical level, wherein the target stimulus 'time' competes with the partially activated representation of the phonologically similar word 'dime'.

Although early 'encapsulated' views of word recognition proposed that such competition was resolved before reaching subsequent levels of processing (e.g. Forster, 1981; Tanenhaus, Carlson, & Seidenberg, 1985), findings from behavioral studies have shown that both acoustic-phonetic and lexical competition impact access to the meaning/conceptual properties of a word (e.g. Andruski, Blumstein, & Burton, 1994; McMurray, Tanenhaus, & Aslin, 2002). For example, using the visual world eye tracking paradigm, McMurray et al. (2002) showed that eye movements to a target picture from an array of four, for example, target (bear), phonological competitor (pear), and two other distractors, were influenced in a graded fashion by fine-grained voicing differences in the auditorily presented target word. Thus, there were more looks to the competitor as the voicing of the initial consonant of the target word approached the acoustic-phonetic (e. g. [b-p]) boundary. In another study, Apfelbaum, Blumstein, and McMurray (2011) showed that the number of looks to a semantic associate of a target word was influenced by the number of phonological competitors the target word had. There were fewer looks to the semantic associate for target words that had a lot of phonological neighbors compared to target words that had few phonological neighbors. Taken together, the results of these two studies indicate that both the 'goodness' of the acoustic-phonetic input of a word and its phonological similarity to other words in the lexicon influence access to the conceptual/semantic representation of a word.

Neuroimaging studies have shown that accessing a word recruits a neural system including temporal, parietal and frontal areas. In particular, modulation of activation has been shown in the posterior superior temporal cortex and supramarginal/angular gyri (SMG/AG) as a function of lexical density and phonological competition (Okada & Hickok, 2006; Prabhakaran, Blumstein, Myers, Hutchison, & Britton, 2006; Righi, Blumstein, Mertus, & Worden, 2010). Additionally, the IFG is recruited in the resolution of lexical competition. Righi et al. (2010) found more activation in the left IFG, as well as the left temporo-parietal region, for words with onset lexical competitors (e.g. hammer vs. hammock) compared to words without. Neural activation also increases in the IFG when participants must retrieve subordinate meanings of ambiguous words (e.g. bank-river vs. bank-money), or nondominant properties of the meaning of a word (e.g. banana-slip vs. banana-peel) (Bedny, McGill, & Thompson-Schill, 2008; Bilenko, Grindrod, & Blumstein, 2008; Gennari, MacDonald, Postle, & Seidenberg, 2007; Grindrod, Bilenko, Myers, & Blumstein, 2007; Whitney, Jeffries, & Kirchner, 2011; Zempleni, Renken, Hoeks, Hoogduin, & Stowe, 2007).

Here we ask how phonetic category goodness and lexical competition influence access not only to a word but also to its lexical-semantic network. That is, to what extent does acoustic-phonetic goodness and phonological-lexical competition influence access to words that are part of the lexical-semantic network of a target word? One approach to this question is to examine the influence of these factors on the magnitude of semantic priming in a lexical decision task. Early behavioral studies found that subjects respond faster when making a lexical decision (word or nonword) to a target (e.g. 'doctor') preceded by a semantically related (e.g. 'nurse') compared to a semantically unrelated word (e.g. 'bread') (e.g. Meyer & Schvaneveldt, 1971). It is generally assumed that this priming effect reflects the functional architecture of the semantic system. In particular, it has been proposed that the presentation of a prime stimulus activates not only the target word but also partially activates its lexical semantic network and hence words that are semantically or associatively related to it, and it

is this partial activation of the semantically related word that accounts for the shorter reaction time (RT) latencies in the lexical decision task.

Neuroimaging studies examining the neural correlates of semantic priming have shown activation in frontal and temporal areas, demonstrating reduced neural activity for related versus unrelated pairs in the middle temporal gyrus (MTG), superior temporal gyrus (STG), and inferior frontal gyrus (IFG), although no one study found activation in all three of these regions (Copland et al., 2003; Copland, de Zubicaray, McMahon, & Eastburn, 2007; Giesbrecht, Camblin, & Swaab, 2004; Gold et al., 2006; Kotz, Cappa, von Cramon, & Friederici, 2002; Matsumoto, Iidaka, Haneda, Okada, & Sadato, 2005; Rissman, Eliassen, & Blumstein, 2003; Rossell, Bullmore, Williams, & David, 2001; Rossell, Price, & Nobre, 2003; Wible et al., 2006). The question we are asking in the current study is what the effects are on this system when a semantically related prime is either a poorer acoustic-phonetic exemplar and/or has a phonological competitor.

Prior behavioral work has shown that both acoustic-phonetic category goodness and phonological competition influence the magnitude of semantic priming in a lexical decision task. Results show that there is less semantic priming when the prime stimulus is acoustically modified or has a lexical competitor (Andruski et al., 1994; Misiurski, Blumstein, Rissman, & Berman, 2005; Utman, Blumstein, & Sullivan, 2001). Andruski et al. (1994) examined the magnitude of semantic priming in a lexical decision task when the prime stimuli had a reduction in the duration of voice-onset time (VOT) of the initial voiceless stop consonant, effectively making them poorer exemplars of the voiceless phonetic category. Significantly less priming was seen for pairs with modified primes (henceforth denoted by an asterisk, e.g. t*ime-clock) than for pairs with unmodified primes, even though subjects still perceived the initial stop consonants as members of the voiceless phonetic category (t*ime was heard as 'time' and not 'dime').

The current study sought to identify the neural consequences of acoustic-phonetic and lexical competition on accessing the lexical-semantic network by using a semantically primed lexical decision task performed during fMRI. In order to examine the effects of acoustic-phonetic and lexical competition, prime words either had a lexical competitor or they did not, and their initial consonants were either reduced in an acoustic parameter of voicing, voice-onset time (VOT) or not. As described above, the neural areas activated in semantic priming include the MTG (Copland et al., 2003; Giesbrecht et al., 2004; Gold et al., 2006; Rissman et al., 2003; Rossell et al., 2003; Wible et al., 2006), the STG (Kotz et al., 2002; Matsumoto et al., 2005; Rissman et al., 2003; Wible et al., 2006), the middle frontal gyrus (MFG) (Rissman et al., 2003; Kotz et al., 2002), and the IFG (Copland et al., 2003, 2007; Giesbrecht et al., 2004; Kotz et al., 2002; Matsumoto et al., 2005), although often activation of the IFG was attributed to retrieval of a dominant over subordinate meaning or other increased executive demands (Copland et al., 2003, 2007; Kotz et al., 2002; Whitney et al., 2011). It is possible that the effects of phonetic category goodness and lexical competition on semantic priming will have similar effects on these areas. However, it has generally been proposed that these areas have different functional properties. Access to stored semantic representations is hypothesized to recruit temporal structures (Binder, Desai, Graves, & Conant, 2009; Hickok & Poeppel, 2004; Indefrey & Levelt, 2004; Vigneau et al., 2006), whereas executive processes for resolving competition or selecting among meaning alternatives are hypothesized to recruit frontal structures (Badre, 2008; Bookheimer, 2002; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001). Based on these considerations, we hypothesize that both acoustic-phonetic manipulations and lexical competition in semantically related prime stimuli will influence access to and activation of the semantic network and hence will result in modulation of activation in temporal lobe structures. We predict that the presence of lexical competition

will result in increased activation in the MTG, presumably reflecting activation of a greater number of lexical candidates or more generally increased lexical-semantic processing demands.

We also expect modulation of activation for both acoustic-phonetic modification and lexical competition in frontal structures. In an extension of Andruski et al. (1994) described above, Utman et al. (2001) examined the effects of acoustic modification and lexical competition on semantic priming in Broca's aphasics who had left frontal lesions (four of the eight aphasics for whom there was lesion information had damage that included the IFG). They found that although the aphasics performed similar to normals with reduced semantic priming for semantically related pairs that had acoustically modified primes (e.g. the magnitude of semantic priming was greater for cat-dog than for c*at-dog), in contrast to normals, they lost priming for semantically related pairs that had primes which had both a reduced VOT and a voiced lexical competitor (e.g. t*time-clock, time has a lexical competitor, dime). Based on these findings, we expect modulatory effects in frontal areas of both acoustic modification and lexical competition on semantic priming.

2. Materials and methods

2.1. Pretests

Two pretests were conducted. The first pretest was designed to examine how strongly a potential set of stimuli primed their semantic associates, ensuring that all of the unmodified stimulus pairs for the fMRI experiment would show semantic priming. The second pretest was designed to assure that when the prime stimulus was phonetically altered by shortening the VOT of the initial voiceless stop consonant, subjects still perceived the stimulus as beginning with a voiceless stop consonant.

2.1.1. Priming pretest

2.1.1.1. Subjects: Eight healthy participants who reported normal hearing and no history of neurological disorders were recruited from the Brown University community on a voluntary basis. Subjects gave written informed consent in accordance with the Human Subjects Policies of Brown University and the Helsinki Declaration of 1975, as revised in 1983, and were paid for their participation.

2.1.1.2. Stimuli: Stimuli for the priming pretest consisted of 97 primes paired with either a semantically related, semantically unrelated, or nonword target. Primes for the semantically related condition were English words beginning with the voiceless stops /p/, /t/, or /k/, either with (48—Competitor condition) or without (49—No competitor condition) a minimal pair competitor (e.g. pear–bear vs. pot–bot). Primes and targets for both conditions were controlled for duration as well as lexical frequency (Kucera & Francis, 1967). To obtain these materials, a male speaker of American English read each word and nonword aloud three times, and the best tokens were selected as stimuli as deemed by the experimenter (DM) to be the clearest production.

2.1.1.3. Behavioral procedure: In order to determine whether the related and unrelated stimulus pairs showed semantic priming, participants were presented a lexical decision task in which they were asked to listen to each prime-target pair through Sony (MDR-V6) headphones and to press a button indicating whether the target was a word or nonword. Each of the 97 primes appeared four times, totaling 392 pairs: once with a semantically related target, once with a semantically unrelated target, and twice with a nonword target. Prime stimulus presentation was blocked across conditions such that no prime appeared more than once per block. There was an interstimulus interval of 50 ms between the offset of the prime

and the onset of the target and a 3 s intertrial interval. Performance and response times (RTs) were recorded.

2.1.1.4. Results: The magnitude of semantic priming was calculated for both conditions by subtracting the RTs for the semantically related pairs from the RTs for the unrelated pairs. Stimuli in the no competitor condition had an average magnitude of priming of 136 ms, while stimuli in the competitor condition had an average magnitude of priming of 181 ms. The 30 pairs showing the greatest magnitude of priming from each of the two conditions were selected for use in the scanner (These stimuli are shown in the list of stimuli used in the fMRI scanner in the Appendix).

2.1.2. Acoustic modification pretest

2.1.2.1. Subjects: Ten healthy volunteers who reported normal hearing and no history of neurological disorders were recruited from the Brown University community. Subjects gave written informed consent in accordance with the Human Subjects Policies of Brown University and the Helsinki Declaration of 1975, as revised in 1983.

2.1.2.2. Stimuli: Acoustically modified versions of the primes were created using the BLISS software system (Mertus, 2002) by measuring the voice-onset time of each stimulus (average VOT=63 ms, SD = 1.0) and excising the middle one third. The acoustic modification of the stimulus made it a poorer exemplar of the voiceless stop consonant category, and also made it closer in acoustic-phonetic space to the voiced stop consonant.

2.1.2.3. Behavioral procedure: Participants were presented the 97 acoustically modified primes, as well as 23 unmodified words and 23 nonwords, one at a time in a pseudo-randomized order via Sony (MDR-V6) headphones and asked to repeat back exactly what they heard. The examiner listened to and identified any incorrect responses.

2.1.2.4. Results: Any acoustically modified stimulus that was misperceived more than 30% was identified. The acoustically modified k*ing was the only such stimulus. Because 'king'–'queen' showed a large magnitude of semantic priming in the first pretest, a new acoustically modified k*ing was created. A second auditory pretest with the new k*ing (otherwise identical to the first) was given to three participants. The new k*ing was correctly repeated by all three participants, and thus this stimulus was used in the experiment proper.

2.2. fMRI experiment

2.2.1. Subjects—Seventeen volunteers (9 females, mean age 21.4) were recruited from the Brown University community. All 17 participants were native speakers of English and were confirmed to be strongly right-handed by the Edinburgh Handedness Inventory (Oldfield, 1971). fMRI subjects were screened for MR compatibility prior to scanning. Subjects gave informed consent in accordance with the Human Subjects policies of Brown University and the Helsinki Declaration of 1975, as revised in 1983, and received modest monetary compensation for their participation.

2.2.2. Stimuli and procedure—While in the scanner, each subject was presented with a total of 360 stimulus pairs, 180 real word target trials and 180 nonword target trials. The real word targets were preceded by real word primes in 3 priming conditions (related, acoustically modified related, unrelated). For the related real word pairs, there were 60 prime-target pairs, all beginning with a voiceless stop consonant, 30 had a voiceless competitor and 30 did not. Each of these prime stimuli appeared twice, once with no acoustic manipulation and once with a one third reduction in the VOT of the initial voiceless stop consonant (cf. Andruski et al., 1994 for details). The 60 word targets used in the

competitor and no-competitor conditions were also paired with a prime that was semantically and phonologically unrelated to the prime stimulus.

There were 60 nonword target pairs which consisted of 60 nonwords preceded by the prime stimulus from the unrelated condition (due to experimenter error, one of the nonword targets was incorrectly paired with the wrong real word prime). Each of these prime-target pairs occurred three times. Word stimuli were matched for word frequency and duration across conditions (see Table 1). The Appendix shows the stimuli used in the experiment.

All 360 stimulus pairs were divided evenly between four runs (90 pairs each) and three trial onset asynchronies (3.7, 7.4, 11.1 with a mean of 7.4 s) (120 pairs each). The presentation of the unmodified or modified prime stimulus was counterbalanced across the 4 runs. Each trial began with 2 s of scanning, followed by a 1700 ms silent gap during which the prime-target stimulus pair was presented. There was a 50 ms ISI between the offset of the prime and the onset of the target. Fig. 1 shows the design of the experiment. Participants were instructed to indicate whether the target word was an English word by pressing one of two response keys, one for word and the other for nonword responses. The position of the appropriate response key was counterbalanced across subjects. Mean reaction times were calculated for each subject and across subjects for each of the seven conditions (competitor related, competitor modified, competitor unrelated, no competitor related, no competitor modified, no competitor unrelated, and nonword).

2.2.3. Data acquisition—Scanning was done on a 3T Siemens Trio scanner with a standard 8-channel head coil at the Magnetic Resonance Facility at Brown University. Prior to entering the MR bore, each participant laid supine on the automated gurney as their head was roughly centered in the magnetic field by aligning their nasion with a laser cross-hair projection. Participants were instructed to refrain from moving their head during MR imaging, and were reminded to keep their eyes closed and remain as still as possible.

High-resolution anatomical images were collected using a 3D T1-weighted magnetization prepared rapid acquisition gradient echo sequence (TR = 2.25 s, TE = 2.98 ms, 1 mm³ isotropic voxel size). The functional scans were acquired in a transverse plane using blood-oxygenation-level-dependent (BOLD) imaging, arranged in a multi-slice, ascending, interleaved (EPI) sequence with 30 axial slices (3 mm thickness, 3 mm² axial in-plane resolution, 64 × 64 matrix, 192 mm² FOV, TE = 28 ms, TR = 3700 ms). Prior to acquiring the EPI images, the center of the imaged slab was aligned to each participant's corpus callosum using a sagittal localizer image, which allowed for the collection of functional data from bilateral peri-sylvian cortex. Each EPI volume acquisition was obtained in 2 s (~67 ms per slice) followed by 1700 ms silence, during which the auditory stimulus was presented, yielding an effective volume repetition time of 3700 ms (see Fig. 1). Each of the four runs consisted of 185 echo-planar volumes acquired over 11.47 mins. Including the volumes taken for localization, the EPI test, and the MPAGE, the experiment lasted approximately 51.37 min. One participant's behavioral and fMRI data were eliminated due to excessive movement in the scanner (greater than 3 mm in any given direction).

3. Results

3.1. fMRI behavioral

Reaction times greater than 2 standard deviations from their respective subject and condition means were excluded. One run for one of the subjects was excluded from the behavioral analysis because the position of their fingers on the button box shifted midway through the experiment.

Fig. 2 shows the RT latencies for correct responses to real word targets (RT latency for the nonword targets was 986 (SEM = 37)). All subjects ($n = 16$) demonstrated a semantic priming effect defined as faster reaction time latencies for related compared to unrelated prime-target pairs. RT latencies were subjected to a 3×2 analysis of variance (ANOVA) with the three-way factor Relatedness (semantically related, modified related, unrelated) and the two-way factor Competition (minimal pair competitor, no minimal pair competitor). Results showed a main effect of Relatedness, $F(2,30) = 96.4$, $p < .001$. Post-hoc tests revealed semantic priming in both the unmodified and modified conditions, i.e. there were faster RT latencies for each of the semantically related conditions compared to the unrelated condition (competitor related, $t(15) = 11.98$, $p < .001$, competitor related modified, $t(15) = 8.41$, $p < .001$, no competitor related, $t(15) = 5.18$, $p < .001$, no competitor related modified, $t(15) = 8.52$, $p < .001$). Neither the main effect of competition nor the interaction between relatedness and competition reached significance (competition $F(1,15) = 1.11$; interaction $F(2,30) = 1.99$). Nonetheless, analysis of simple effects showed a significant difference between the modified and unmodified related word pairs in the competitor condition, $t(15) = 2.37$, $p = .032$, with increased RT latencies for the modified word pairs. In contrast, there was no difference between the modified and unmodified related word pairs in the no competitor condition, $t(15) = 0.98$, $p = .345$. Thus, the magnitude of priming was significantly reduced only when the prime stimulus had both a voiced competitor and its initial voiceless stop was acoustically modified to be closer to the voiced phonetic boundary (see Fig. 2).

3.2. fMRI analysis

Functional data were analyzed using AFNI (Cox & Jesmanowicz, 1999). Because the images were acquired in an interleaved, ascending manner, each run was corrected for slice acquisition time using the 3dTshift function. The runs were then concatenated, and head motion was corrected by aligning all volumes to the fourth collected volume using a 6-parameter rigid body transform. Data were then warped to Talairach and Tournoux (1988), resampled to 3-mm isotropic voxels, and spatially smoothed using a 6-mm full-width half maximum Gaussian kernel. Each subject's preprocessed EPI data for the seven experimental conditions (competitor related, competitor modified, competitor unrelated, no competitor related, no competitor modified, no competitor unrelated, and nonword) were modeled with the stereotypic gamma-variate hemodynamic response function provided by AFNI (Cox, 1996; Cox & Hyde, 1997). The hemodynamic response functions for each condition were included in a general linear model regression analysis along with the six output parameters from motion correction.

The raw fit coefficients for each voxel were then divided by the experiment-wise mean activation of that voxel, resulting in percent signal change values for each voxel by condition. Because we were interested in the effects of competition and modification on semantic priming, we focused our analyses on those neural areas showing a significant semantic priming effect. To that end, we conducted a mixed factor ANOVA contrasting activation patterns for the unmodified stimuli in the Unrelated and Related conditions for all 16 subjects. Using a voxel-wise threshold at $p < .05$, this analysis yielded a large semantic priming network (9085 voxels) with activation in bilateral (left-lateralized) fronto-temporo-parietal regions (see Fig. 3).

We then investigated the effects of acoustic modification and lexical competition on activation patterns within this semantic priming network. We focused our analyses on those participants who showed effects of acoustic modification under conditions of lexical competition; that is, these subjects had longer RTs for the modified related trials in the competitor condition compared to the modified related trials in the no competitor condition. Eleven subjects met this criterion. To identify potential clusters within the semantic

network, Monte Carlo simulations were conducted to determine the minimum cluster size at $p < .05$ with a voxel-wise threshold of $p < .025$. All reported clusters are greater than 37 contiguous voxels.

A two-way ANOVA (Acoustic modification $\times$ Lexical competition) revealed a significant main effect of competition with 3 clusters emerging in the left posterior portion of the middle temporal gyrus (pMTG), the left superior temporal gyrus (STG), and the left insula extending into the inferior frontal gyrus (IFG, BA45) (see Table 2 and Fig. 4). No other comparisons were significant.

We extracted percent signal change from the three clusters that showed the main effect of competition. In order to determine if there was a statistically reliable difference in the pattern of activation as a function of region, we conducted a $2 \times 2 \times 3$ MANOVA. Results showed a main effect of Region, $F(2,9) = 10.50$, $p = .004$ as well as a Region $\times$ Competition $\times$ Modification interaction that approached significance, $F(2,9) = 3.71$, $p = .067$. As expected based on the contrast used to identify these clusters, there was also a main effect of competition, $F(1,10) = 20.96$, $p = .001$. We then examined the patterns of activation within each cluster. Fig. 5 shows the results. Three two-way ANOVA (Competition $\times$ Modification) were conducted for each cluster. As expected, all three clusters showed a main effect of competition (pMTG: $F(1,10) = 19.56$, $p < .001$, STG: $F(1,10) = 14.70$, $p < .003$, insula/IFG: $F(1,10) = 16.57$, $p < .002$). However, only the pMTG demonstrated a significant main effect of modification (pMTG: $F(1,10) = 7.85$, $p < .02$, STG: $F(1,10) = .28$, $p = .608$, IFG: $F(1,10) = .07$, $p = .79$). There was also a significant interaction between modification and competition in the insula/IFG, $F(1,10) = 5.98$, $p = .035$.

4. Discussion

The goal of the current experiment was to examine how phonetic category goodness and lexical competition influence access to the semantic network of a word. To do so, we explored the neural consequences of acoustic-modification of voicing in stop consonants and phonological lexical competition on the magnitude of semantic priming. Our results identified a neural network sensitive to semantic priming. Namely, we found decreased activation for unmodified semantically related prime-target pairs compared to unmodified semantically unrelated prime-target pairs in fronto-temporo-parietal areas, replicating earlier fMRI semantic priming studies (Copland et al., 2003, 2007; Giesbrecht et al., 2004; Kotz, et al., 2002; Matsumoto, et al., 2005; Rissman et al., 2003; Rossell et al., 2001, 2003; Wible et al., 2006). Consistent with these findings are several review papers examining neural areas recruited in semantic processing (Binder et al., 2009; Cabeza & Nyberg, 2000; Vigneau et al., 2006).

Within this semantic priming network, a smaller set of clusters emerged that were sensitive to lexical competition; these included the left posterior portion of the middle temporal gyrus, the left superior temporal gyrus, and the left insula extending into the inferior frontal gyrus (BA45). Within these areas, the left posterior middle temporal gyrus also showed sensitivity to acoustic modification and the insula/inferior frontal gyrus showed an interaction between acoustic modification and lexical competition.

Prior research has shown that middle temporal gyrus plays a critical role in accessing lexical-semantic information (Binder et al., 2009; Hickok & Poeppel, 2004, 2007; Indefrey & Levelt, 2004; Price, 2010; Vigneau et al., 2006). The results of the current experiment support these findings and extend them by showing that this area is sensitive to both the acoustic and lexical properties of words as they access the lexical-semantic network. Thus,

both the acoustic modification and the presence of a lexical competitor of a prime stimulus influenced the extent to which it primed a semantically related target.

That the middle temporal gyrus showed increased activation for semantically related prime-target pairs when the prime stimulus was acoustically modified or had a voiced lexical competitor is consistent with current models of auditory word recognition showing that the nature and quality of the sound structure of a word have a cascading effect on accessing the semantic representation of a word and its semantic network (Gaskell & Marslen-Wilson, 1997, 1999). Here, acoustic modification and lexical competition of the prime stimulus influence the activation of the prime word and this in turn affects the degree to which it activates its semantic properties and that of its semantic network. The acoustic modification of the initial voiceless stop of the prime stimulus rendered it a poorer exemplar of the voiceless phonetic category, e.g. good exemplar [p] of the word *pear* to a poorer exemplar [p*], *p*ear* (cf. Utman et al., 2001). Similarly, the presence of a voiced lexical competitor influenced the extent to which the prime word was activated, e.g. the presence of a lexical competitor *bear* influenced the activation of *pear*. Each of these properties has a cascading effect on access to the meaning of the prime word and its semantic network. In other words, the activation of the prime stimulus was sufficiently affected to influence the activation of a semantically related target, e.g. *fruit*.

The superior temporal gyrus also showed an influence of lexical competition on semantic priming. In particular, there was increased activation for prime-target pairs in which the prime stimulus had a voiced competitor compared to prime-target pairs which did not. These results are consistent with those of Okada and Hickok (2006) who found significantly more activation in the left superior temporal cortex in all 10 of their subjects for words that had many lexical competitors (i.e. high density neighbors) compared to words that had few lexical competitors (i.e. low density neighbors).

One question is why the main effect of Modification failed to show a significant cluster in the superior temporal gyrus. In the modified stimuli the voice-onset time of the initial voiceless stop consonant was reduced. Past research has shown that the STG is sensitive to voice-onset time as well as other acoustic-phonetic properties of speech (Blumstein, Myers, & Rissman, 2005; Chang et al., 2010; Desai, Liebenthal, Waldron, & Binder, 2008; Dewitt & Rauschecker, 2012; Hickok & Poeppel, 2000; Hickok & Poeppel, 2007; Joanisse, Zevin, & McCandliss, 2007; Liebenthal et al., 2010; Myers, Blumstein, Walsh, & Eliassen, 2009). In particular, the STG has shown sensitivity to within phonetic category manipulations similar to those used in the current experiment (Blumstein et al., 2005; Joanisse et al., 2007; Myers et al., 2009). There are two possibilities for this discrepancy. One is the 'depth' of analysis required across studies and the other is the weakness of behavioral effects of the acoustic-phonetic manipulation. In particular, sensitivity to within category manipulations such as voice-onset time emerged in the STG in studies using consonant-vowel (CV) stimuli. Thus, the 'level of analysis' in these stimuli was sound structure as the only differences in the stimulus set were the acoustic properties of these nonword CV stimuli. In contrast, in the current experiment, all of the prime stimuli, whether acoustically manipulated or not, were words and the task of the subject was to make a lexical decision on the target. Thus, the 'level of analysis' in these stimuli was word structure or the lexical status of the stimuli. The focus on the lexical properties of the stimulus in the current experiment likely reduced the perceptual salience of the VOT manipulations. Additionally, Andruski et al. (1994) also failed to show behavioral effects of a reduction in the magnitude of semantic priming when they reduced the VOT of initial stop consonants by one third (the reduction used in the current experiment), whereas the effect emerged for both competitor and non-competitor stimuli when the VOT was reduced even more by two thirds. Nonetheless, a modification effect did emerge in the current study when the acoustic

modification occurred in the presence of a phonological competitor. While the STG was not sensitive to our acoustic manipulation, it did show increased activation under conditions of lexical competition, supporting existing evidence that this area may store some phonological information (see Indefrey & Levelt, 2000, 2004).

Of interest, similar to the current study, Clos et al. (2012) showed effects of degraded speech on processing only in the MTG and not the STG. In their study, stimuli were degraded such that only the prosodic (rhythmic) properties of the stimuli were retained; thus, there was no segmental information that could be perceived by the participants. The prior presentation of non-degraded matching sentences resulted in reduced activation in the left pMTG suggesting that prior speech and semantic information influenced and made easier the perceptual analysis of the degraded input. In contrast to Clos et al. (2012), in the current experiment, the degraded information in the prime stimuli preceded rather than followed the target. This preceding degraded information influenced access to the semantic information in the non-degraded target word, but in this case resulted in increased activation suggesting greater processing demands required for the non-degraded target stimuli.

A significant interaction emerged between competition and acoustic modification in the insula extending into the inferior frontal gyrus. That is, increased activation emerged as a consequence of acoustic modification but only under conditions of lexical competition. Previous fMRI findings have shown the inferior frontal gyrus to be sensitive to both acoustic modification and lexical competition. For example, the left IFG has shown graded activation for stimuli that varied in voice-onset time of the initial stop consonant with increased activation for within phonetic category and boundary value [d]–[t] stimuli compared to endpoint value stimuli, e.g. boundary > within-category > end-point (Blumstein et al., 2005). And the IFG also showed increased activation for words as a function of lexical competition. In particular, using an eyetracking paradigm, Righi et al. (2010) showed greater activation for words that had onset competitors (hammock/hammer) compared to words that did not. The current experiment is the first to show using fMRI that these two properties of language, lexical competition coupled with acoustic-phonetic manipulation, interact in a common area, in particular, in BA45 of the IFG.

Although acoustic modification and lexical competition affect access to the prime stimulus, it is worth noting that the participant did not have to attend to nor make any overt decision about its identity. Rather, the properties of the prime implicitly affected access to the semantic representation of the target influencing the magnitude of semantic priming. That the IFG was activated under such conditions indicates that these sound structure properties of words (acoustic-phonetic modification of category structure and phonological similarity of words in the lexicon) affect access to the semantic/conceptual meanings of words and hence selection among competing alternatives. Sensitivity to semantic competition has also been shown to recruit BA45. Thus, competition appears to be resolved in BA45 by multiple linguistic properties (Thompson-Schill et al., 1997).

The interaction effect shown in the IFG is also consistent with earlier findings in our lab showing that Broca's aphasics with frontal lesions lose semantic priming only when both the prime stimulus is acoustically modified and has a voiced lexical competitor (Utman et al., 2001). These same patients show, as do normals, a reduction in semantic priming when the prime stimulus was acoustically modified but did not have a lexical competitor. These results coupled with the fMRI results reported here provide further support that the IFG plays a 'necessary' role in the resolution of competition induced by the acoustic phonetic structure of phonetic categories and the phonological similarity of words (Price, Mummery, Moore, Frackowiak, & Friston, 1999).

It is not clear whether the increased activation for the acoustically modified stimuli in the competitor condition was a result of the poorer quality of the degraded stimuli or the result of increased competition between the [d] and [t] phonetic categories induced by the VOT manipulations. Although these two properties of the stimuli are confounded in the current experiment, some earlier research suggests that it is increased acoustic-phonetic competition and not stimulus quality that resulted in an increase in activation in the IFG. In particular, Myers (2007) investigated this question by examining neural activation patterns for a voice-onset time continuum in which the stimuli were good exemplars of the phonetic category, or they were phonetically modified such that they had extreme values of voicing that were further in acoustic-phonetic space from the competing phonetic category, or they had VOT values near the phonetic boundary that rendered them closer in acoustic-phonetic space to the competing phonetic category. Both acoustic-phonetic modification conditions influenced the phonetic quality of the stimuli. Results showed increased activation in the IFG only for the acoustically modified stimuli that were maximally competitive; that is, the VOT stimuli closer to the acoustic-phonetic boundary. In contrast, the STG showed increased activation for both acoustic modification conditions. These findings indicate that it was the increased competition and not stimulus quality that gave rise to increased activation in the IFG and are consistent with results showing that this area is recruited under conditions of response conflict (Gehring & Knight, 2000; MacDonald, Cohen, Stenger, & Carter, 2000).

In summary, the current findings show that access to word meaning is influenced by multiple sources of competition, and this competition has a modulatory effect throughout the lexical-semantic network. In particular, using semantic priming in an auditory lexical decision task as a window into accessing word meaning, three regions were identified that were sensitive to lexical competition. These included superior temporal gyrus, the middle temporal gyrus, and the inferior frontal gyrus. These regions have been implicated in prior studies examining access to word meaning and auditory processing of language. In the context of lexical competition, modification of the acoustic-phonetic structure has a modulatory effect on activation in the middle temporal gyrus and inferior frontal gyrus. Taken together, these results are consistent with models of lexical-semantic access identifying the role of the STG in phonological processing, the MTG in representing lexical-semantic information, and the IFG in selecting amongst competing lexical items.

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Appendix A

See Table A1.

Table A1

<u>No competitor</u>		<u>Competitor</u>		<u>Nonword</u>
<u>Prime</u>	<u>Target</u>	<u>Prime</u>	<u>Target</u>	<u>Target</u>
Cake	Frosting	Cab	Taxi	Brill
Cart	Push	Cap	Hat	Cheav
Coin	Penny	Cash	Money	Clant

<u>No competitor</u>		<u>Competitor</u>		<u>Nonword</u>
Prime	Target	Prime	Target	Target
Comb	Hair	Cave	Den	Daucet
Cost	Price	Coat	Pants	Dend
Cow	Milk	Cold	Hot	Dup
Cup	Mug	Come	Go	Farle
Curve	Straight	Cut	Trim	Fet
Key	Door	Kill	Die	Folor
Kick	Boot	Pack	Bundle	Foncern
King	Queen	Pad	Pen	Frawl
Page	Book	Pain	Hurt	Frooth
Pave	Road	Palm	Hand	Gace
Peace	War	Park	Car	Gack
Pick	Choose	Peak	Top	Glab
Poach	Kill	Pear	Fruit	Gynk
Point	Sharp	Pig	Ham	Jarm
Poke	Annoy	Pill	Drug	Kague
Pub	Bar	Pond	Lake	Kaite
Pup	Dog	Pump	Water	Kank
Purse	Bag	Pun	Joke	Kautch
Tack	Stick	Push	Shove	Kawv
Take	Give	Tall	Short	Keln
Tar	Roof	Team	Coach	Kentce
Tax	Pay	Tent	Camp	Kerf
Test	Quiz	Time	Clock	Kighm
Toad	Frog	Toe	Foot	Klee
Tone	Noise	Ton	Weight	Kluse
Tooth	Brush	Tuck	Hide	Kriet
Top	Bottom	Tug	Pull	Kweete
Bad	Give	Bell	Ham	Loke
Bald	Dog	Blank	Weight	Mewb
Bell	Milk	Bull	Taxi	Mish
Bike	War	Chair	Water	Paife
Bound	Straight	First	Short	Parf
Cheese	Bar	Fit	Hand	Parnt
Chew	Road	Flake	Die	Peeb
Claw	Brush	Fork	Bundle	Pieth
Craze	Bottom	Fort	Top	Pilv
Deer	Bag	Hair	Den	Pindow
Fee	Door	Hog	Car	Pircle
Friend	Noise	Key	Money	Pive
Front	Choose	Law	Coach	Plun
Glum	Stick	Mate	Pants	Poaph

<u>No competitor</u>		<u>Competitor</u>		<u>Nonword</u>
<u>Prime</u>	<u>Target</u>	<u>Prime</u>	<u>Target</u>	<u>Target</u>
Goose	Book	Meat	Pull	Pooz
Hang	Penny	Nose	Pen	Poud
Heat	Pay	Note	Shove	Pumb
Jaw	Push	Part	Fruit	Pydd
Mess	Boot	Pen	Drug	Taum
Nut	Quiz	Rod	Hurt	Tav
Rib	Mug	Roll	Hide	Teff
Roll	Kill	Sack	Go	Tetter
Rust	Frosting	Seed	Joke	Teunde
Same	Annoy	Set	Lake	Tirp
Sit	Sharp	Ship	Hot	Toov
Small	Queen	Soil	Trim	Towde
Talk	Roof	Squeak	Hat	Tult
Tank	Hair	Wager	Foot	Turthe
Trunk	Frog	Wolf	Camp	Twave
Worst	Price	Worst	Clock	

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Fig. 1.
FMRI experimental design.

Fig. 2.
Reaction time latencies for real word targets across conditions.

Fig. 3. Activation map of the semantic priming network ($n = 16$). Sagittal views are of (A) left hemisphere at $x = -60$, (B) left hemisphere at $x = -40$, (C) right hemisphere at $x = 60$, and (D) right hemisphere at $x = 40$. The color scheme represents the t value threshold for the contrast (Unrelated-Related).

Fig. 4.

The three regions that showed a main effect of lexical competition ($n = 11$). The axial view is a slice at $z = 10$ showing the left IFG, STG, and MTG. The three sagittal views show the Insula/IFG at $x = -30$, the STG at $x = -55$, and the MTG at $x = -50$. The color scheme represents the t value threshold for the contrast (Competitor-no competitor).

Fig. 5. Percent signal change values plotted by condition for left IFG, STG, and MTG. Error bars represent standard error of the mean.

Table 1

Mean word frequency and stimulus duration of experimental stimuli.

	Competitor	No competitor
Word frequency		
<i>Prime</i>	115	83
<i>Target</i>	111	97
Mean duration (ms)		
<i>Prime</i>	456	466
<i>Target</i>	439	472

Areas of activation showing main effects of lexical competition and acoustic-phonetic modification on semantic priming that were significant in planned comparisons thresholded at voxel level $p < .025$, cluster level $p < .05$ (37 contiguous voxels).

Table 2

Region	Talairach coordinates			Cluster size (Number of voxels)	Maximum (<i>t</i> value)
	<i>x</i>	<i>y</i>	<i>z</i>		
<i>Competitor > No competitor</i>					
Left insula extending into IFG	-28	23	11	58	4.16
Left STG	-55	-34	11	42	4.69
Left MTG	-40	-52	8	41	5.19
<i>Modification > No Modification</i>					
No significant areas					