

The Neural Bases of the Lexical Effect: An fMRI Investigation

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The lexical effect is a phenomenon whereby lexical information influences the perception of the phonetic category boundary for stimuli from word-nonword continua. At issue is whether this effect is due to “top-down” influence of upper levels of processing on perceptual processing, or instead is due to decision-stage processes. In this study, brain activity was monitored using functional magnetic resonance imaging as subjects performed a phonetic categorization task on items taken from 2 continua in which one end of the continuum was a real word and the other was not (gift-kift and giss-kiss). If the lexical effect has a perceptual basis, modulation of activation should be seen as a function of the lexical effect in areas such as the superior temporal gyri (STG) which have previously been implicated in perceptual processing. In contrast, if the effect is purely due to decision-related factors, such modulation would be expected *only* in areas which have been linked to executive processes, such as frontal and midline structures. Modulation of activation as a function of the lexically biased shift in phonetic category boundary was observed in the STG bilaterally as well as in frontal and midline structures. This activation pattern suggests that the lexical effect has at minimum a perceptual component, in addition to an executive decision-related component. These results challenge the view that lexical effects on phonetic boundary placement are due solely to postperceptual, decision-stage processes, and support those models of language processing which allow for higher-level lexical information to directly influence the perception of incoming speech.

Keywords: Ganong effect, lexical processing, neuroimaging, superior temporal gyrus, top-down processes

Introduction

Communication often takes place in a noisy environment. Acoustic masking of parts of words or variation in speakers' productions can result in local perceptual indeterminacies which require listeners to use available information to resolve the incoming acoustic stream. Evidence from phoneme restoration studies (e.g., Warren 1970), results showing a lexical frequency bias for perception of speech in noise (Broadbent 1967), and evidence showing an advantage for grammatical versus ungrammatical speech in noise (Miller et al. 1951) indicate that lexical, syntactic, and semantic information are brought to bear as listeners resolve indeterminacies when listening conditions are imperfect. What is less clear is at what stage or stages of processing this information comes into play. Does “top-down” information from higher-level information sources influence lower-level basic perceptual mechanisms? Does it play a role during decision stages of processing? Or is top-down information used at both of these stages of processing?

Of particular interest is the effect of knowledge of the lexicon on the perception and identification of phonetic contrasts. One example of this sort of top-down effect is the “lexical effect.” Ganong (1980) presented subjects with acoustic-phonetic continua varying in voice-onset time (VOT), an acoustic cue to the perception of the phonetic feature of voicing in stop consonants. In half of the trials, the voiceless end of the continuum was a real word, and the voiced end of the continuum was a nonword (e.g., *peace-beace*). In the other half of the trials, the voiceless end of the continuum was a nonword and the voiced end of the continuum was a word (e.g., *peef-beef*). The presence of a meaningful lexical item at one end of the continuum shifted the phonetic boundary of the continuum such that there were greater voiced responses to stimuli in the boundary range when the real word endpoint stimulus began with a voiced stop, and there were greater voiceless responses when the real word endpoint stimulus began with a voiceless stop. This lexically biased shift in the locus of the phonetic boundary or “lexical effect” was taken by Ganong and others (see Pitt 1995 for review) as evidence that lexical status influences the basic perceptual analysis of acoustic-phonetic properties of speech. This hypothesis has not gone unchallenged, however. Others (e.g., Fox 1984) have argued that the lexical effect is due to decision-related processes that result when subjects are forced to categorize ambiguous stimuli. This debate is, as of yet, unresolved in the literature (Connine and Clifton 1987; Burton et al. 1989; McQueen 1991; Pitt and Samuel 1993).

The inability to determine whether the lexical effect is perceptual or decision related in nature may in part be due to the limitations of the experimental methodology. The measures that experimenters have had at their disposal with regards to this question, that is, perceptual decision and response latency, are almost certainly influenced by both perceptual and decision-stage factors. Neuroimaging techniques, particularly event-related functional magnetic resonance imaging (fMRI), offer an opportunity to address the question of the basis of lexical effects on phonetic categorization (PC). Specifically, it may be the case that activation patterns due to lexical effects emerge in those brain areas that have been previously implicated in lower-level speech processing such as the superior temporal gyrus (STG). Such a result may be taken as evidence that lexical status influences perception in a direct way. Alternatively, it may be the case that lexically modulated activation patterns emerge *only* in frontal or midline areas that have been associated with executive processes. This pattern of results would lend credence to the argument that lexical effects operate uniquely on decision-stage processes. Previous work (Blumstein et al. 2005)

has shown sensitivity to phonetic category structure and in particular to within-phonetic category VOT differences in perceptual areas such as the STG as well as in areas linked to executive components of language comprehension, such as the left inferior frontal gyrus (LIFG), and those linked to decision making in general, such as the anterior cingulate cortex (ACC). This sensitivity was exploited in the current study to determine whether lexically biased shifts in the locus of the phonetic category boundary are perceptual or decision related in nature.

Both neuroimaging data and lesion studies commonly implicate the bilateral STG and the LIFG in speech processing. The proximity of the STG to primary auditory cortex makes it a prime candidate for early acoustic and phonetic processing. Patients with bilateral lesions to the STG often suffer from pure word deafness, a disorder characterized by a dense auditory comprehension deficit in the presence of relatively intact production (Poeppel 2001). STG activation also tends to increase as stimuli become more speech-like (Belin et al. 2000; Binder et al. 2000; Giraud and Price 2001; Zatorre and Belin 2001). In addition, the STG is sensitive to the acoustic and acoustic-phonetic properties of the stimulus (Giraud and Price 2001; Binder et al. 2004; Blumstein et al. 2005) with greater activation as stimuli approach a phonetic category boundary (Blumstein et al. 2005). However, activation in these areas does not correlate with reaction time performance (Binder et al. 2004; Blumstein et al. 2005), and hence does not appear to be sensitive to task difficulty as subjects make phonetic decisions. The relative insensitivity of the STG to task demands and its sensitivity to speech sounds support a role for the STG in acoustic-phonetic processing.

In contrast, activation in inferior frontal areas appears to be related to executive decision-related processes. These areas are significantly affected by task demands. Studies have shown that activation in the LIFG correlates with reaction time in a phonetic decision task, and may be tightly linked to difficulty (Binder et al. 2004; Blumstein et al. 2005). Moreover, the activation of the LIFG in meta-linguistic tasks such as phoneme identification and phoneme monitoring (Burton 2001) as well as its activation under conditions of competition and stimulus uncertainty (Blumstein et al. 2005) supports a role for these areas in phonetic decision-stage processes.

A final area which appears to be recruited generally in decision-stage processing is the ACC (Gehring and Knight 2000). The ACC is activated when subjects are engaged in tasks which involve competition between responses (Carter et al. 1998) and for experimental trials on which subjects make errors (e.g., Rissman et al. 2003), independent of the stimulus modality. The ACC has also shown modulation of activation as a function of phonetic category structure, with increasing activation as stimuli approach the phonetic boundary in a PC task, consistent with its proposed role in resolving response competition (Blumstein et al. 2005). Thus, the anterior cingulate appears to be involved in decision-stage processing in language tasks as well as other experimental tasks.

In the present study, activation was measured using fMRI in an event-related design as subjects performed a PC task on items from 2, 7-point voicing continua. In one continuum (*gift-kift*) the voiced end of the continuum was a real word, and in the other (*giss-kiss*) the voiceless end of the continuum was a real word. A clustered acquisition design was used so that the stimuli could be presented in the relative silence between echo planar imaging (EPI) acquisitions (Edmister et al. 1999; Talavage

et al. 1999). Statistical comparisons were made between items of the same VOT value which fell on the phonetic category boundary in one continuum, but did not fall on the boundary in the other continuum due to the lexically biased shift in category boundary. This comparison allowed for examination of the shift in phonetic category structure as a function of the lexical effect while controlling for the absolute VOT of the stimulus.

If the lexical effect reflects early use of lexical information in guiding speech perception, it is expected that the lexical effect will influence basic perceptual mechanisms (STG) as well as decision mechanisms (IFG and ACC). Modulation of activation is expected to emerge within executive regions such as the left IFG and the ACC whether the lexical effect is perceptual or decision related in nature, due to the inescapable fact that the PC task involves an executive decision. Nonetheless, task difficulty is expected to vary as a function of the ambiguity of the stimulus. As such, more activation should emerge in the LIFG and ACC for stimuli which fall on the category boundary, and are therefore more ambiguous phonetically, than for those stimuli which do not. In particular, when comparing items across continua with the same VOT value, it should be the case that a stimulus which falls on the phonetic category boundary in its continuum will show greater activation than its partner stimulus in the other continuum which does not fall on the boundary.

If changes in activation emerge in the STG due to the biasing presence of a lexical item, these findings may be taken as evidence that the lexical effect operates at the perceptual level. In particular, if the lexical effect indeed alters the perception of a given VOT value such that the perception of a stimulus on the phonetic category is altered as a function of its potential lexical status, then differences should emerge in the activation patterns for the same VOT value when it is perceived as a boundary value stimulus versus when it is not, with greater activation seen in the former than in the latter.

In sum, it is hypothesized that more activation will emerge in frontal areas such as the LIFG and ACC for boundary value stimuli when compared with their VOT-matched counterparts in the opposing continuum due to the executive demands involved in resolving the identity of boundary value tokens. A similar pattern of activation in the STG would provide support for the hypothesis that the lexical effect has a perceptual component to it.

Materials and Methods

Pilot Study: Evaluating the Lexical Effect

In the literature, evidence of a lexical effect is demonstrated through a comparison of the phonetic category boundary between 2 continua, a word to nonword continuum versus a nonword to word continuum. A difference in the locus of the category boundary between continua is interpreted as the occurrence of the lexical effect. What is not known from these studies is whether the demonstrated difference in boundary between continua biased toward opposite ends of the phonetic continuum is due to the shift of one or of both continua. The hypotheses generated for this experiment suppose that both continua are subject to lexical influences on categorization which result in a boundary shift. To assure that this is the case, it is necessary to show that the boundary values for the *gift-kift* and *giss-kiss* continua are significantly different from each other, but also that these continua separately each show movement of the phonetic boundary due to biasing lexical factors with respect to a neutral (unbiased) baseline. To this end, a pilot study was run in the lab in which subjects performed a PC task on items from these continua. Boundary values for the 2 lexical effect continua were

compared in order to determine whether any lexically biased boundary shift occurred. In addition, a separate group of subjects performed the same task on items from a nonword to nonword, *gisb-kish* continuum. This continuum served as a baseline for finding the locus of the phonetic boundary for the VOT continuum in the absence of biasing lexical factors. In order to determine whether a significant lexical shift occurred, boundary values for each of the lexical effect continua were separately compared with those for the nonword control continuum.

Materials

Two sets of word/nonword pairs, *gift-kift* and *giss-kiss*, were selected that met the following criteria: they were one-syllable [StopVCC] stimuli that shared the same vowel, and the same manner of articulation in final consonant(s); to the extent possible, word endpoints were matched for frequency (Kucera and Francis 1967), and word and nonword members of each pair were matched for both neighborhood density (Luce and Pisoni 1998), and phonotactic probability (Vitevitch et al. 1999) (see Table 1 for a list of the lexical properties of these stimuli). In order to establish a neutral baseline against which lexically shifted identification functions could be compared, a nonword to nonword continuum, *gisb-kish*, was also chosen, matched as close as possible to the word/nonword pairs in terms of density and phonotactic probability.

The stimulus set was digitally recorded in list intonation by a male native speaker of American English. These recordings were digitized and resampled to 22.050 kHz. Stimuli were edited so that there was no silence at the beginning or end of each sound file. A 7-point VOT continuum was created for each stimulus pair using the BLISS speech editing program (Mertus 1989). The voiced end of the *giss-kiss* continuum was generated by splicing the initial/k/burst and first quasi-periodic pitch period from the naturally produced “kiss” token to the vowel plus coda portion of the naturally produced “giss” token. Successive points on the continuum were created by removing one pitch period from the onset of the vowel and splicing in the same length of aspiration from the “kiss” token. This yielded 7 stimuli with VOTs of 11, 18, 25, 33, 40, 47, and 54 ms, all with a total length of 528 ms. In order to create the other word-nonword continuum, *gift-kift*, and the nonword-nonword baseline continuum, *gisb-kish*, the initial stop plus vowel portion (135 ms) of each stimulus on the *giss-kiss* continuum was spliced to 393 ms of the/ft/offset from “gift,” or 393 ms of the/sh/offset from “gish.” All 3 continua thus shared the same set of onsets, and all stimuli were the same duration. Stimuli were checked for naturalness and waveforms were visually examined for acoustic discontinuities. The stimuli across the 2 continua were matched for overall amplitude; stimuli from the *gift-kift* continuum had an average root mean squared (RMS) energy of 2511, whereas those from the *giss-kiss* continuum had an average RMS energy of 2514.

Two sinewave tones were also created for use in a low-level sensory control task. Tones corresponding to the first and second formant frequencies of the steady-state portion of the vowel (457 and 1524 Hz) were created with the same duration (528 ms) as the experimental stimuli.

Participants

Nine subjects heard stimuli from the *gift-kift* and *giss-kiss* continua that ultimately composed the MR experiment. An additional 10 subjects heard stimuli from the nonword to nonword *gisb-kish* control

continuum. Subjects gave informed consent according to the Human Subjects Committees of Brown University.

Behavioral Procedure

Subjects performed a PC task on stimuli taken either from the *gisb-kish* nonword to nonword continuum or from the *giss-kiss* and *gift-kift* lexical effect continua. Subjects heard 20 tokens of each stimulus, presented in random order, and identified the onset of each stimulus as either a/g/ or a/k/ by pressing a button with their dominant hand to indicate their response. Subjects were instructed to respond as quickly as possible without sacrificing accuracy. Stimuli were blocked by continuum. Reaction time (RT) and accuracy data were collected, with RTs measured from stimulus onset.

Data Analysis

Identification functions were plotted for each subject and for each continuum. Boundary VOT values were calculated for each continuum in the following way. First, percent/g/scores for each point on the continuum were converted to z-scores. A critical range of VOT values was then selected which encompassed the minimum and maximum z-score values (for nearly all subjects, 5 to -5, or 100% consistent identification). In cases where a z-score value before the maximum or after the minimum deviated from that maximum or minimum, the score was only included if it deviated by more than 5%. The selected z-scores for each continuum were then submitted to a linear regression, which output slope and y-intercept values. The x-intercept, or 50% identification point, which corresponds to the phonetic category boundary, was then calculated. The stimulus number (1-7) which fell nearest to the calculated VOT boundary was determined for each continuum, and labeled as that subject’s “boundary” stimulus for that continuum. Analyses of variance (ANOVAs) were performed comparing boundary values for *gift-kift* to *giss-kiss*, and comparing boundary values for each of these continua with the nonword control, *gisb-kish* continuum, with Boundary VOT as the dependent variable and Continuum as the independent variable.

Results and Discussion

As expected, subjects in the pilot experiment perceived stimuli categorically, with near-ceiling consistency in categorization of the first 2 and final 2 members of each continuum (Fig. 1). Inspection of Figure 1A suggests that there are differences in the locus of the phonetic category boundary for the lexical effect continua; however, the locus of the phonetic boundary appears to be similar between the nonword-nonword continuum *gisb-kish* and the *giss-kiss* continuum. The ANOVAs confirmed these observations. There was a significant difference in the boundary VOT value between the *gift-kift* and *giss-kiss* continua ($F_{1,16} = 5.857$, $MSE = 87.164$, $P < 0.028$), indicating that one or both continua underwent a lexically biased shift in phonetic category boundary. One-way ANOVAs on individual subject category boundaries indicated that the boundary for *gisb-kish* was not significantly different from the *giss-kiss* boundary ($F_{1,18} = 0.879$, $MSE = 8.965$, $P < 0.362$), but was significantly different from the *gift-kift* boundary ($F_{1,18} = 17.808$, $MSE = 158.076$, $P < 0.001$). These results suggest that only the *gift-kift* continuum showed a lexical effect, that is, a significant shift away from the nonlexically biased baseline continuum.

The failure to show a boundary shift in the *giss-kiss* continuum is unlikely to be due to stimulus frequency or neighborhood density factors, as these values were controlled across the 2 continua and were within the range of values found in other studies which showed a significant lexical effect (c.f. Burton et al. 1989). One possibility for the lack of a lexical effect for the *giss-kiss* continuum is that there is an asymmetry in the perceptual shifts that emerge in a VOT continuum. In particular, the range of VOT values that characterizes voiced tokens in English is much smaller (-40 to 20-ms VOT) than is the range that characterizes voiceless tokens (about 30- to 170-ms VOT) (Lisker and Abramson 1964). As a consequence, movement of the phonetic boundary toward the voiced end of the continuum may be more difficult than movement toward the voiceless end of the continuum (Kessinger and Blumstein, unpublished data).

That said, in the MR experiment we still elected to compare the lexically shifted *gift-kift* continuum with the unshifted *giss-kiss*

Table 1
Properties of the stimulus set used in the fMRI experiment

Stimulus /phonology/	Frequency	FWND	Mean phoneme probability	Mean biphone probability
gift /glft/	33	9.531	0.058	0.002
kift /kft/	—	11.794	0.075	0.002
kiss /kls/	17	30.359	0.089	0.009
giss /gls/	—	26.366	0.067	0.009

“Frequency” indicates written frequency (Kucera and Francis 1967), FWND indicates frequency-weighted neighborhood density (Luce and Pisoni 1998), and mean phoneme and biphone probabilities are calculated after Vitevitch and Luce (2004).

continuum rather than with the nonword-nonword continuum. Our reasons are several. For the purposes of this study, we wanted to make the continua as "similar" as possible not only in their acoustic structure but also in their design. In particular, we wanted to ensure that for each continuum, there were members that could be perceived as either words or nonwords that word endpoints were matched in so far as possible for lexical frequency, and that the shape of the phonetic identification function was similar. In essence, the *giss-kiss* continuum shares all of the properties of the lexically shifted, *gift-kift* set, except that, due to the limitations imposed by phonetic category structure, it does not appear to undergo a lexically biased shift in category boundary. This being the case, the inclusion of the *giss-kiss* continuum allows us to directly assess whether the 2 continua show similar activation patterns despite the lack of a lexical effect in one continuum and the presence in the other as shown by the pilot behavioral data.

fMRI Study

Participants

Nineteen participants (11 females) took part in the MR version of the experiment and were paid for their participation. Participants ranged from 19 to 51 years of age (mean age = 27 years), and were all right handed, as indicated by the Oldfield handedness inventory (Oldfield 1971). Participants all reported having normal hearing, and had no known history of neurological disease. All participants gave written informed consent according to guidelines established and approved by the Human Subjects Committees of Brown University and Memorial Hospital of Rhode Island, and were screened for MR safety before entering the scanner room.

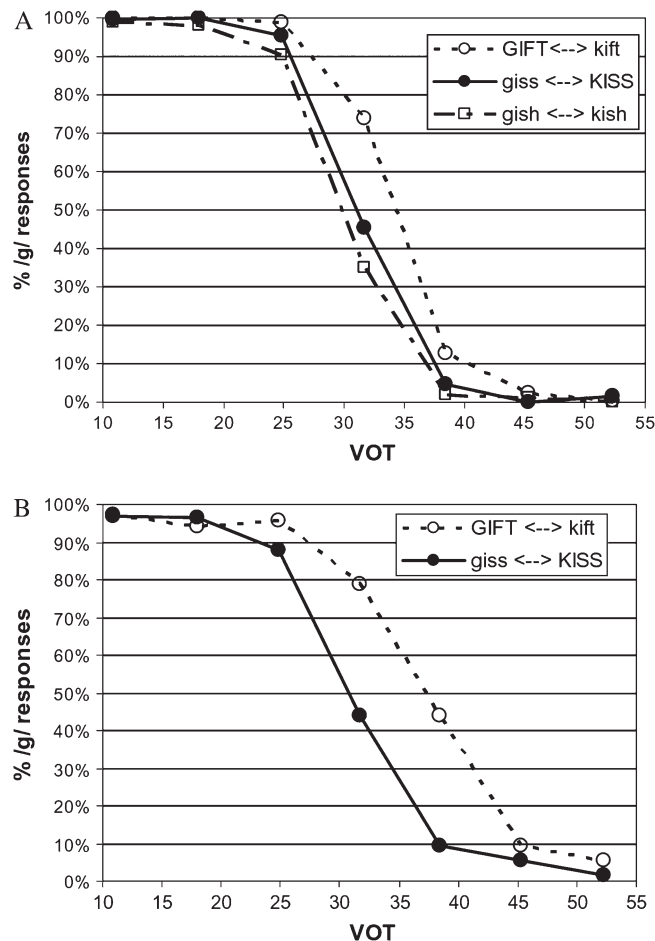


Figure 1. (A) Mean percent /g/ responses for pilot subjects ($n = 9$, circles), and for nonword control subjects ($n = 10$, squares). (B) Mean percent /g/ responses for fMRI subjects ($n = 17$).

Behavioral Procedure

Participants in the MR experiment performed 2 tasks while in the scanner, the PC and Tone Categorization (TC) tasks. For the PC task, subjects were asked to determine whether each presented utterance began with a [g] sound or a [k] sound, and to press one of 2 buttons indicating their response as quickly and accurately as possible with either their right index finger or middle finger. For the TC task, subjects were instructed to listen to each tone and decide whether it was the High tone (1524 Hz) or the Low tone (457 Hz), and to indicate their response with a similar button press. Responses were registered via an MR compatible button box secured under the right hand (Resonance Technologies, Northridge, CA), and the button mapping was counter-balanced across subjects.

The MR experiment consisted of 6 separate runs. There were 4 runs of the PC task, 2 for each continuum (*gift-kift* and *giss-kiss*), and 2 runs of the TC task. Eight of the final 17 subjects received the runs in the order: *gift-kift*, *giss-kiss*, tone, *gift-kift*, *giss-kiss*, tone, and the remaining 9 subjects received the runs in the order: *giss-kiss*, *gift-kift*, tone, *giss-kiss*, *gift-kift*, tone. Within each PC run, subjects heard 10 repetitions of each of the 7 stimuli along the selected continuum, for a total of 70 stimuli per run, and 20 total presentations of each stimulus in the entire experiment. Each tone run consisted of 10 repetitions of each of the 2 tones for 20 stimuli in each tone run, and 20 total repetitions of each tone stimulus.

Stimuli within each run were presented in a fixed, pseudorandomized order. Stimuli were presented using a laptop computer over noise-attenuating air-conduction headphones (Resonance Technologies $\text{\textcircled{R}}$). RT and accuracy data were collected as described in the Pilot Experiment. Subjects were familiarized with all stimuli during the anatomical scan, and were allowed to practice 14 trials of the PC task and 10 trials of the TC task. Behavioral data were analyzed as described in the pilot experiment. Reaction times greater than 2 s and those which were greater than 2 standard deviations from the mean in any condition were excluded from the behavioral analysis, but not from the analysis of the MRI data (6.73% of trials).

MR Imaging

MRI data were collected using a 1.5-T Symphony Magnetom MR system (Siemens Medical Systems, Erlangen, Germany) equipped with EPI capabilities. For anatomical coregistration, a 3D T_1 -weighted magnetization prepared rapid acquisition gradient echo sequence (time repetition [TR] = 1900 ms, time echo [TE] = 4.15 ms, time for inversion [TI] = 1100 ms, 1-mm³ isotropic voxel size, 256 \times 256 matrix) was acquired, and reconstructed into 160 slices. Functional scans consisted of a multislice, ascending, interleaved, EPI sequence with 15 axial slices (5 mm thickness, 3-mm² axial in-plane resolution, 64 \times 64 matrix, 192-mm² field of view, flip angle = 90 $^\circ$, TE = 38 ms, volume acquisition time = 1200 ms, TR = 2000 ms). EPI images were centered on each participant's thalamus using a reference sagittal scan so that the bilateral peri-sylvian cortex was imaged in every participant. Participants were instructed to refrain from moving the head during MR imaging, and were reminded to keep their eyes closed.

The acquisition of each slice in the EPI scans was clustered at the beginning of each TR (Edmister et al. 1999), leaving a silent gap in which to present auditory stimuli. Specifically, 15 slices were acquired in 1200 ms, followed by 800 ms of silence, yielding an effective volume repetition time of 2000 ms. Figure 2 shows the timing of the presentation of the stimuli relative to volume acquisition. As the figure shows, auditory stimulus presentation was timed such that the stimulus fell within the silent period. Stimulus presentation was jittered, such

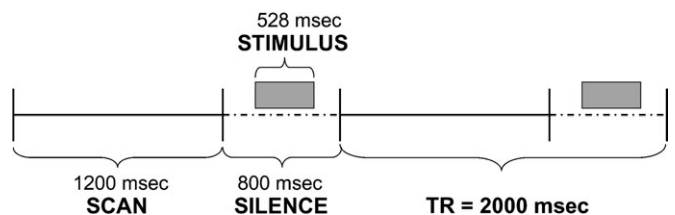


Figure 2. Scanning schematic.

that the 20 tokens of each stimulus type were distributed across the 6 trial onset asynchrony (TOA) bins (TOA = 2, 4, 6, 8, 10, or 12 s). There was a 4-volume offset between the start of EPI scanning and the onset of stimulus presentation in order to account for T_1 saturation effects. These 4 volumes were discarded from subsequent analysis. Each of the 4 PC runs consisted of 247 EPI volumes, and each of the 2 TC runs consisted of 72 EPI volumes, for a total of 1132 acquired volumes.

MR Analysis

Image preprocessing. Imaging data were analyzed using the Analysis of Functional NeuroImages software (AFNI) (Cox and Hyde 1997). EPI images were corrected for slice acquisition time on each run separately, and runs were concatenated (Paradis et al. 2001). The images were then corrected for head motion by aligning all volumes to the fourth collected volume using a 6-parameter rigid body transform (Cox and Jesmanowicz 1999), warped to Talairach and Tournoux space (Talairach and Tournoux 1988), and then resampled to 3-mm isotropic voxels using AFNI tools. Spatial smoothing was carried out using a 6-mm full width half maximum Gaussian kernel. Subsequent analysis was restricted to those voxels in which signal was recorded for all 17 subjects who showed the lexical effect, which excluded nonimaged voxels and those which fell outside the brain.

Statistical Analysis. In the behavioral literature, not all subjects show a lexical effect, and effect sizes are often small (e.g., 3–5 ms boundary shifts). Because our activation hypotheses rest on the assumption that a given subject actually shows a lexically biased shift in phonetic category, our primary analysis focused on those subjects who showed a shift in the expected direction (17 of 19 subjects, see behavioral results). However, to ensure that the overall results still emerged with the inclusion of these 2 participants, a secondary MR analysis was also conducted.

A regression analysis was carried out on each subject's preprocessed EPI data to estimate the individual hemodynamic response to each of the 16 stimulus types (7 each for *gift-kift* and *giss-kiss* continua, plus 2 tones). Vectors indicating the onset times of each stimulus type were convolved with a stereotypic gamma-variate hemodynamic response curve provided by AFNI (Cohen 1997). These reference waveforms served as the input to AFNI's 3dDeconvolve program, which output by-voxel raw fit coefficients for each subject and for each condition. Run-wise means and first-order trends were removed from each run, and the 6 motion parameters output from the motion correction process were included as regressors to remove motion artifacts. Fit coefficients for each subject and condition were then converted to percent change by dividing the coefficient from each voxel by the baseline for that voxel, which was calculated by computing an experiment-wise mean for that voxel.

Percent signal change data for all 16 stimulus conditions were entered into a mixed factor ANOVA with subject as a random factor and condition as a fixed factor. Three planned comparisons were carried out. The 2 critical comparisons were between the boundary stimulus in one continuum and the same stimulus in the other continuum. Specifically, stimulus 4, which was the boundary stimulus in the *giss-kiss* continuum, was compared with stimulus 4 in the *gift-kift* continuum, and stimulus 5, which was the boundary value in the *gift-kift* continuum, was compared with stimulus 5 in the *giss-kiss* continuum. Finally, the effect of lexical status (i.e., word vs. nonword) was examined by comparing the 2 continuum endpoints which were identified as words (stimulus 1 from the *gift-kift* vs. continuum and stimulus 7 from the *giss-kiss* continuum) to the 2 continuum endpoints which were identified as nonwords (stimulus 7 from the *gift-kift* continuum and stimulus 1 from the *giss-kiss* continuum). Statistical maps were corrected for multiple comparisons by including only clusters consisting of at least 62 contiguous voxels activated at a level of $P < 0.025$ or higher, yielding a corrected statistical threshold of $P < 0.05$, as determined by Monte Carlo simulations.

Results

Behavioral Results

Categorization data for the MR participants are shown in Figure 1B. The magnitude of the boundary shift (*giss-kiss* boundary VOT minus *gift-kift* boundary VOT) was calculated for each

subject (see Methods for details). Of 19 subjects, 17 showed a lexically biased shift in phonetic category such that there were more "g" responses for the *gift-kift* continuum, and more "k" responses for the *giss-kiss* continuum. The mean size of this lexical effect was 6.72 ms (SD = 2.58), which was approximately equivalent to the size of the VOT step between points on the continuum.

Most subjects (11 of 17) had a category boundary which fell closest to stimulus #5 for the *gift-kift* continuum, and most (11 of 17) had a category boundary which was closest to stimulus #4 for the *giss-kiss* continuum. The distribution of boundary placement across the 2 continua is plotted in Figure 3A.

Phonetic category boundary VOT values were compared between continua in a one-way ANOVA. The difference in boundary value between the 2 continua was statistically reliable ($F_{1,18} = 52.550$, MSE = 6.261, $P < 0.001$) indicating that there was a significant lexical effect for the group of 19 MR participants. For the 17 subjects who individually showed a lexically biased shift, there was also a significant difference in boundary value between the 2 continua ($F_{1,16} = 115.784$, MSE = 3.319, $P < 0.001$). The remaining behavioral analyses report data from the 17 subjects who were included in the primary MR analysis.

Reaction time data from the 17 MR subjects is shown in Figure 3B. As is typical of PC experiments, subjects showed

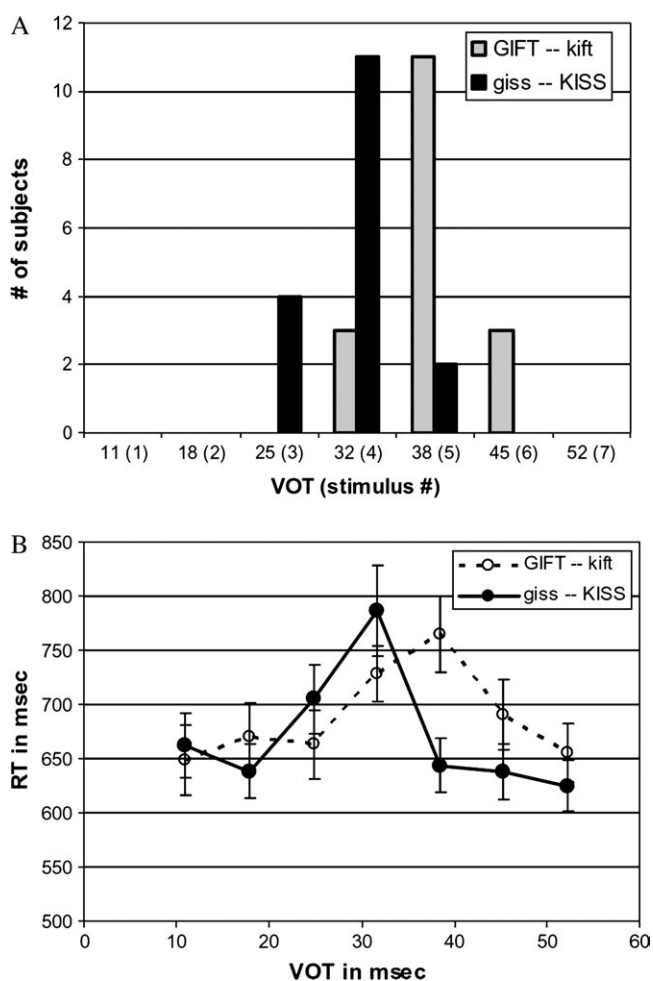


Figure 3. (A) Histogram of phonetic category boundary placement for fMRI subjects ($n = 17$). (B) Reaction time data from fMRI subjects ($n = 17$).

increased reaction times as stimuli approached the phonetic category boundary and were slowest to categorize the stimuli which fell on the phonetic category boundary for a given continuum. A 2-way continuum by VOT ANOVA confirmed these results. There was a significant main effect of VOT stimulus ($F_{6,96} = 15.432$, $MSE = 3566.0$, $P < 0.001$). The 2 continua did not differ significantly in overall RT ($F_{1,16} = 2.694$, $P > 0.120$), but there was a significant continuum by VOT interaction ($F_{6,96} = 14.176$, $MSE = 22,737$, $P < 0.001$). The reaction time peak for the *gift-kift* continuum was located at stimulus #5, and the RT peak for the *giss-kiss* continuum was located at stimulus #4 consistent with the view that the locus of the phonetic boundary differed between the 2 continua.

Imaging Results

Planned Comparisons

A summary of all clusters activated in the 3 planned comparisons, which were significant at a corrected $P < 0.05$ is shown in Table 2. The first 2 compared a boundary stimulus in one continuum with the same VOT value, nonboundary stimulus in the other continuum. Specifically, stimulus 5 was determined to fall on the phonetic category boundary in the *gift-kift* continuum, and was compared with stimulus 5 in the *giss-kiss* continuum (henceforth referred to as the *Gift-Kift* Boundary comparison). Comparably, stimulus 4 was determined to fall on the phonetic category boundary in the *giss-kiss* continuum, and this stimulus was compared with stimulus 4 in the *gift-kift* continuum (referred to as the *Giss-Kiss* Boundary comparison). The third comparison was designed to investigate potential differences in activation between words and nonwords.

Boundary Stimulus Comparisons

In every cluster activated in the *Giss-Kiss* and *Gift-Kift* Boundary comparisons, greater activation was observed for the VOT stimulus which fell on the phonetic category boundary than for its nonboundary counterpart in the opposite continuum (Table 2). Moreover, more clusters were observed in the comparison which involved the boundary token from the lexically shifted continuum (the *Gift-Kift* Boundary comparison, Table 2) than that involving the nonshifted boundary token (the *Giss-Kiss* Boundary comparison, Table 2).

Table 2

Areas of activation significant in planned comparisons for the 17 subjects who showed a behavioral lexical effect

Location of maximum intensity point	Coordinates			Number of activated voxels	t Value at maximum intensity point
	x	y	z		
<i>Giss-Kiss</i> Boundary comparison (<i>gift4</i> vs. <i>giss4</i>)					
L inferior parietal lobule	-47	-32	54	128	-3.338
R inferior parietal lobule	35	-68	48	83	-2.369
<i>Gift-Kift</i> Boundary comparison (<i>gift5</i> vs. <i>giss5</i>)					
L Cingulate	-5	11	36	960	4.507
L STG	-62	-8	6	374	2.735
R STG	62	-23	15	316	3.985
L precentral gyrus	-53	-2	42	85	3.102
L middle frontal gyrus	-29	50	30	78	3.170
L precuneus	-2	-56	51	76	3.037
<i>Word (gift1 and giss7) versus nonword (gift7 and giss1)</i>					
—No clusters found—					

Clusters thresholded at a voxel-level threshold of $P < 0.025$, cluster-level threshold of $P < 0.05$ (62 contiguous voxels). Coordinates indicate the maximum intensity voxel for that cluster. All coordinates are in Talairach and Tournoux space.

In the *Gift-Kift* Boundary comparison, a cluster was found in the left STG posterior to Heschl's gyrus which extended into Heschl's gyrus and ventrally into the superior temporal sulcus (Fig. 4, left). A similar cluster was found in the right hemisphere, centered in the STG, and extending medially into the insula and into the right claustrum (Fig. 4, right). No clusters were found in the temporal lobes in the *Giss-Kiss* Boundary comparison. To confirm that no differences between the stimuli in the *Giss-Kiss* Boundary comparison (stimulus 4 in each continuum) existed within the STG, we looked within the functional ROI that was identified in the *Gift-Kift* Boundary analysis to see whether differences would emerge for the *Giss-Kiss* Boundary comparison as well. To this end, mean percent signal change was extracted from both STG clusters activated in the *Gift-Kift* Boundary comparison (Fig. 4, bottom). Results confirmed that, although differences emerge in both temporal areas in the *Gift-Kift* boundary comparison (stimulus 5), no such differences emerge between the *Giss-Kiss* Boundary comparison (stimulus 4).

In the *Gift-Kift* Boundary comparison, several clusters were activated in addition to those found in the STG. A very large cluster (960 voxels) was found in the left and right cingulate and anterior cingulate, which extended through left anterior white matter into the left insula (Fig. 5A). Frontal clusters were observed in the left precentral gyrus and insula, and again further dorsally in the left MFG and superior frontal gyrus (Fig. 5B,C). Finally, one midline cluster was observed in the precuneus. One cluster was found in this analysis in which the majority of activated voxels were located in a ventricle. Because of this it was determined to be an artifact, and is not included in Table 2.

In contrast, the *Giss-Kiss* Boundary comparison yielded only 2 significant clusters (Fig. 6). These clusters were in the bilateral inferior parietal lobules, with the right hemisphere cluster extending somewhat into the superior parietal lobule. Significantly, no differences in activation were found in this comparison in any of the areas previously shown to be sensitive to phonetic category structure, including left frontal areas, the STG areas, and midline areas. In order to determine whether one continuum in general produced greater activation than the other, each stimulus was compared with its VOT-matched counterpart in the opposite continuum. Overall, there was little difference in the magnitude of activation between the 2 continua. Of the clusters that emerged in this analysis, 7 were more active for the stimulus from the *giss-kiss* continuum and 10 were more active for the *gift-kift* continuum.

A secondary analysis of the data including the 2 subjects who did not show a behavioral lexical effect revealed fewer activated clusters. However, both the midline cluster centered in the cingulate and the left superior temporal cluster were still activated for the *Gift-Kift* Boundary comparison using the same statistical threshold as the data reported above. These clusters had the same maximum intensity coordinates as those reported in the 17 subject analysis (see Table 2), although they were smaller in size (556 voxels for the cingulate cluster, 177 voxels for the left STG cluster). No other clusters emerged in planned comparisons for the 19-subject analysis.

Effects of Lexical Status

It is important to confirm that any differences observed in the above-reported comparisons are due to processing differences inherent in phonetic category structure and not due to differences inherent in words versus nonwords such as

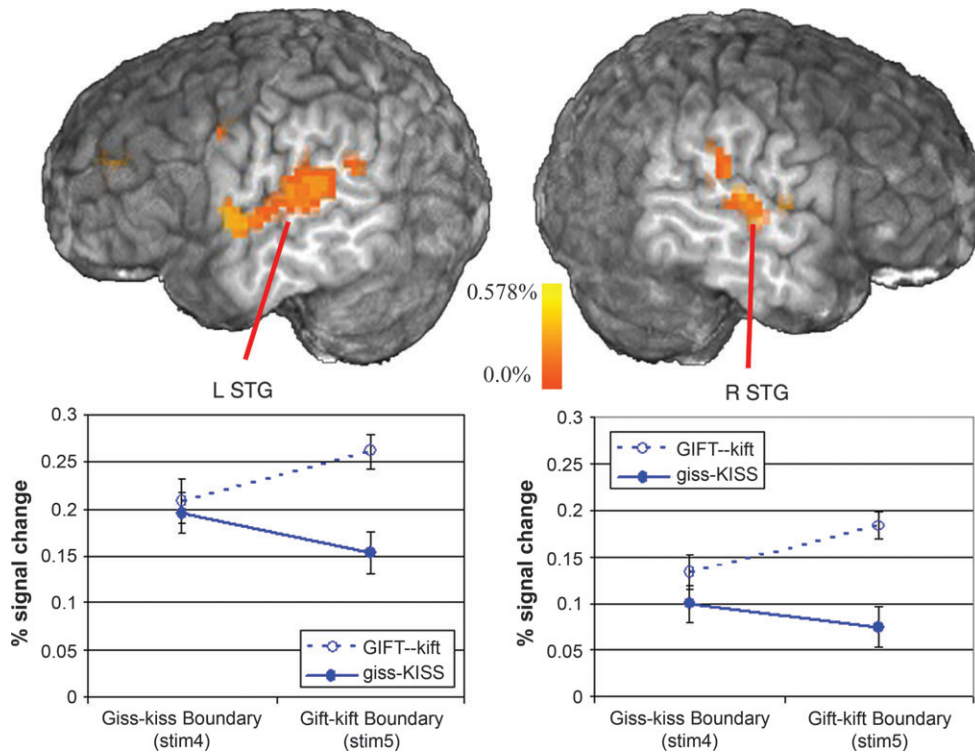


Figure 4. Clusters significant at a corrected threshold of $p < 0.05$ for the Gift Boundary Comparison (gift5–giss 5). All clusters are more active for stimulus 5 in the gift–kift continuum (boundary stimulus) than in the giss–kiss continuum (nonboundary stimulus). Activation displayed in percent signal change units. Left panel ($x = -58$) shows a cluster in the left STG (374 active voxels). Right panel ($x = 60$) shows a cluster in the right STG (316 active voxels). Graphs at bottom indicate the mean percent signal change within these clusters for stimuli 4 and 5 within both gift–kift and giss–kiss continua.

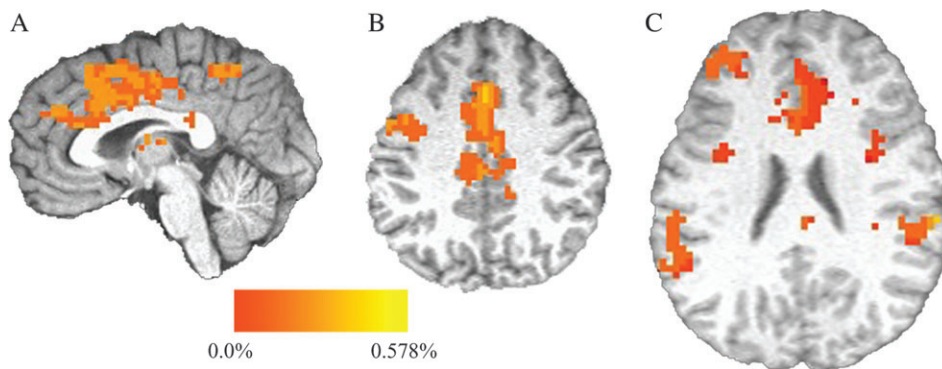


Figure 5. Clusters significant at a corrected threshold of $p < 0.05$ for the Gift–Kift Boundary comparison (gift5–giss 5). All clusters are more active for stimulus 5 in the gift–kift continuum (boundary stimulus) than stimulus 5 in this giss–kiss continuum (nonboundary stimulus). Activation displayed in percent signal change units. (A) Sagittal slice at $x = 1$, showing a large cluster centered on the cingulate gyrus. (B) Axial slice at $z = 39$, showing a left frontal cluster centered in the left precentral gyrus. Also visible is the large midline cluster shown in (A) (C) Axial slice at $z = 24$, showing a left frontal cluster centered in the left MFG. Also shows portions of midline and superior temporal clusters.

activation of semantic or lexical representations in the former and not in the latter. In particular, in the cross-continuum comparison of stimuli near the phonetic category boundary, one of the stimuli is a real word, whereas the other stimulus (being a boundary value stimulus) is equivocal in its lexical status. To investigate this issue, continuum endpoints which were unequivocally perceived as real words (endpoints perceived as “gift” and “kiss”) were compared with continuum endpoints which were unequivocally perceived as nonwords (endpoints perceived as “giss” and “kiff”). No clusters emerged in this comparison, suggesting that any differences which emerged in the previous analyses were not due to the lexical status per se of the stimuli.

Discussion

Behavioral Data

In general, subjects perceived both VOT continua in a categorical manner, and showed characteristic increases in RT as stimuli approached the phonetic category boundary. These results are consistent with the behavioral literature on categorical perception (Liberman et al. 1957; Pisoni and Tash 1974). Seventeen of 19 subjects showed shifts in the phonetic category boundary in a direction consistent with the lexical effect. Reaction time data also supported the presence of a lexical effect, with reaction time peaks at 32-ms VOT (stimulus #4) for the giss–kiss continuum, and at 38-ms VOT (stimulus #5) for the

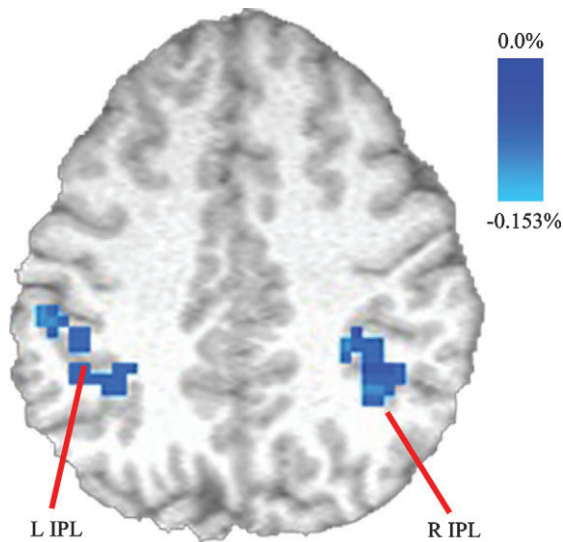


Figure 6. Clusters significant at a corrected threshold of $P < 0.05$ for the Giss-Kiss Boundary comparison (stimulus 4 in the gift-kift continuum vs. stimulus 4 in the giss-kiss continuum). All clusters are more active for stimulus 4 in the giss-kiss continuum (boundary stimulus) than stimulus 4 in the gift-kift continuum (nonboundary stimulus). Axial slice shown at $z = 40$, depicting clusters in the left and right IPL.

gift-*kift* continuum. The fact that boundary values for the 2 continua fell on different VOT values allowed for comparisons of activation patterns for stimuli with the same VOT value with one stimulus falling on the phonetic boundary and the other not falling on the boundary owing to the lexical effect.

Imaging Data

The Lexical Effect and the Temporal Lobes

In this study, lexically biased shifts in phonetic category boundary modulated activation in the STG bilaterally. Specifically, activation in the STG was greater for a stimulus which fell on the phonetic category boundary in the lexically shifted continuum than for its VOT-matched counterpart in the non-shifted continuum, which did not fall on the category boundary. Controlling for the VOT of the stimulus, this activation emerged in the shifted continuum (the Gift-*Kift* Boundary comparison, i.e., stimulus 5), but not when the stimulus had not undergone a lexical shift (the Giss-Kiss Boundary comparison, i.e., stimulus 4). The posterior left STG, often implicated in extracting speech-relevant properties of the stimulus (Binder et al. 2000; Poeppel et al. 2004; Scott and Wise 2004), lies in close proximity to the angular gyrus and supramarginal gyrus, areas that are commonly implicated in lexical and semantic processing. Thus, it is not surprising therefore that the STG might be sensitive to lexical as well as phonetic information.

Additionally, this pattern of activation in the STG does not seem to be attributable to the lexical status (i.e., word vs. nonword) of the stimuli, as suggested by the lack of activation differences found between unambiguous word and nonword endpoints of the continua. These findings suggest that PC decisions on good exemplar word and nonword stimuli invoke similar processing mechanisms.

Any involvement of the STG in the mediation of the lexical effect strongly suggests that this effect is not due solely to executive decision processes. If the lexical effect was purely decision related in nature, no modulation of activation would be

expected in the STG. Instead, the pattern of activation seen in temporal areas implicates perceptual, acoustic-phonetic processes in the mediation of the lexical effect. Nonetheless, at least 3 functional models might account for the pattern of results observed in this study (see Fig. 7). It should be noted that none of these models is intended to be a complete model of speech-language processing, but rather is intended to represent potential bases for modulation of activation in the STG owing to the lexical effect.

The most probable explanation in our view is that the STG itself subserves both acoustic-phonetic processing as well as access to lexical form (Model A, Fig. 7). Several studies (Giraud and Price 2001; Wise et al. 2001; Poeppel et al. 2004) have shown activation of the STG for word stimuli. If the neural substrates for phonetic categorization and for lexical processing coexist in the STG, it is not surprising that effects of lexical status on PC processes are seen in these areas. The second possibility (Model B, Fig. 7) is that modulation of activation in the STG is due to feedback to the STG from separate lexical-semantic areas such as the middle temporal gyrus, angular gyrus, or supramarginal gyrus (see Binder and Price 2001 for review).

Owing to the lack of difference in activation between word and nonword stimuli in either the STG or other candidate lexical processing areas, the present study cannot attribute access to lexical form to any area, and thus cannot distinguish between models A and B. This lack of difference may itself be due to the fact that, unlike many studies showing word versus nonword differences in activation patterns, words and nonwords were carefully matched along a number of dimensions, including neighborhood density and phonotactic probability (Prabhakaran et al. 2006).

A third possibility (model C, Fig. 7) is that activation patterns in the STG are influenced by feedback to the STG from decision-making areas such as the IFG or ACC. In this view, task-related processing in the frontal areas feeds back to the STG. If this were the case, we would expect the activation of the STG to be influenced by decision-related processes including the effects of task difficulty. Based on the results in the literature, frontal areas such as the IFG show increasing activation in proportion to difficulty in phonetic tasks as measured by reaction time. In contrast, activation in the STG does not show such a correlation (c.f. Binder et al. 2004; Blumstein et al. 2005).

Either model A or B stands in opposition to those models of language processing such as Merge (Norris et al. 2000) which disallow top-down influences or feedback from lexical stages of processing to acoustic-phonetic stages of processing. In contrast, both models A and B are consistent with those models which do allow for such feedback (e.g., McClelland and Elman 1986). Model C, however, allows for a bottom-up only flow of information from acoustic-phonetic to lexical processes, with feedback from executive (postaccess) processes back to acoustic-phonetic processes. Though the locus of the lexical effect in this model is a combination of the lexical status of the stimulus and the executive demands of the PC task, information from executive processes still contacts perceptual processing in the STG. This contrasts with models such as Merge in which postaccess, decision-stage processes guide the generated response, but do not recontact the perceptual processing system.

Evidence using MEG exists which supports the notion that the lexical effect arises due to reactivation of perceptual systems in the STG after lexical processing occurs (models A or B). Gow et al. (2005) report recent evidence in which the

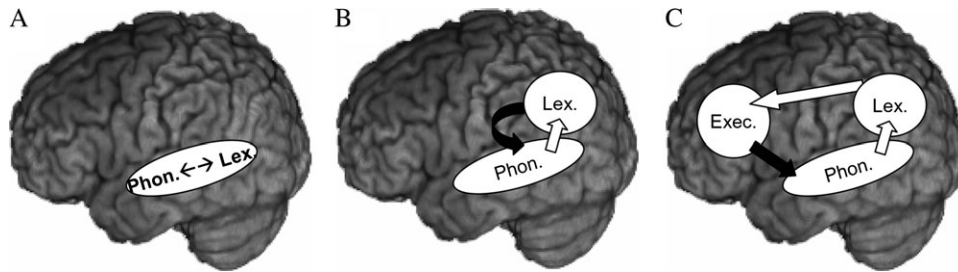


Figure 7. Models of possible explanations for STG modulation as a function of the lexical effect. Note that in all models, it is assumed that phonological, lexical, and executive processes will be engaged as a function of the executive decision on linguistic stimuli. These schemata are intended only to illustrate the source of the lexically biased STG modulation. In all models, acoustic-phonetic (Phon.) processing takes place in superior temporal areas. In model *A*, the STG subserves both acoustic-phonetic and lexical processing, and as such, activation in this area would reflect both types of processes. In models *B* and *C*, information spreads from temporal areas to lexical processing areas (Lex.) such as the angular gyrus, supramarginal gyrus, and/or middle temporal areas. However, in model *B*, lexical information feeds directly back to the STG, whereas in model *C*, lexical information then spreads from lexical processing to executive processing (Exec.) areas such as the IFG and ACC, at which point, activation feeds back to acoustic-phonetic processes in the STG.

STG shows initial activation 131 ms posttrial for both unambiguous words and midcontinuum words, and is then reactivated at 371 ms posttrial for only those stimuli affected by the lexical effect. This reactivation implies that the STG is involved in integrating lexical and phonetic information.

Data from aphasic populations also support the view that the lexical effect is mediated by posterior structures. Blumstein et al. (1994) showed that Broca's aphasics, who have damage to left anterior structures, showed a larger lexical effect than normals, whereas Wernicke's aphasics, who have damage to posterior temporal and parietal structures, showed no lexical effect. One possible interpretation of this data is that lexical effects arise due to interaction between the STG and adjacent areas including the middle temporal gyrus and supramarginal gyrus, areas which are thought to be involved in lexical processing (Binder and Price 2001). When these areas are damaged, as they typically are in Wernicke's aphasia, the lexicon may be unable to influence acoustic-phonetic processing. In contrast, when these areas are intact, but inferior frontal areas are damaged, as is typically the case in Broca's aphasia, lexical effects strongly influence perception.

Behavioral evidence (see Pilot data) demonstrated that only the gift-kift continuum showed a lexical effect, whereas the giss-kiss continuum did not. We suggested earlier that the reason for the asymmetry between the 2 continua was due to a corresponding asymmetry in the structure of the voicing distinction for stops in English. In particular, movement of the phonetic category boundary toward the voiced end of the continuum is blocked by properties of phonetic category structure, whereas movement toward the voiceless end of the continuum is not (see Results of Pilot I for further discussion). Taken together, both the behavioral and fMRI results suggest that there is an active interplay between available lexical and phonetic information which emerges when 2 conditions are met when 1) the stimuli are indeterminate with respect to their phonetic category status, and 2) the phonetic category structure permits movement of the phonetic category boundary. Consistent with this view, the STG show increased activation for stimuli which lie on the phonetic category boundary; additionally, activation for boundary tokens is boosted only when lexical information is brought to bear (see Fig. 4). These results suggest that the STG are more than just rote acoustic-phonetic analyzers of the incoming speech stream. Some information about the lexical properties of the stimuli must be available to neural structures involved in phonetic processing, but only when there is phonetic indeterminacy.

Modulation of Activation in Frontal and Midline Areas

Modulation of activation in left frontal areas and midline areas was demonstrated in the cross-continuum comparisons, with greater activation emerging for stimuli which fall on the phonetic category boundary. This pattern is consistent with previous research also showing increases in activation for stimuli close to the phonetic boundary (Blumstein et al. 2005; Myers 2007), suggesting a role for the left IFG in resolving acoustic-phonetic competition. Activation of these areas likely reflects the necessary executive demands placed on the participant by the explicit nature of the PC task. The fact that modulation of activation in temporal areas is observed *in addition to* that seen in frontal/midline areas lends credence to the proposal that the lexical effect has a perceptual component in addition to the necessary executive component.

Interactivity in Neural Models of Language Processing

The involvement of the STG in the lexical effect provides evidence that lexical information influences the perception of ambiguous phonetic tokens in a direct way. These findings are consistent with models of word recognition such as TRACE (McClelland and Elman 1986), which allow for immediate use of higher-level information as it becomes available for processing, and challenges models such as Merge (Norris et al. 2000) in which the lexical effect is due to decision-stage processes. The results presented here add to a growing body of evidence that suggest that higher levels of language processing may influence lower levels as processing unfolds online. Such effects have been shown in the influence of linguistic and nonlinguistic context in online sentence comprehension (Macdonald et al. 1994; Spivey and Tanenhaus 1998).

It is biologically sound for the speech processing system to have some degree of flexibility in adjusting the phonetic category boundary. Location of the phonetic boundary can be shown to be influenced not only by lexical status but also by lexical frequency (Connine et al. 1993), neighborhood density (Newman et al. 1997), and speech rate (Miller 1981), as well as other factors. An ability to accommodate early in the processing stream those factors which affect phonetic boundary placement would be advantageous for both the speed and economy of PC processes. As a neural site which is involved in acoustic-phonetic processing and which either processes lexical information or lies in close proximity to areas which do, the STG is a prime candidate for the locus of early integration of extra-phonetic factors in phonetic boundary placement. If the STG is universally sensitive to higher-level sources of information on

phonetic category structure, the STG bilaterally should show modulation of activity whenever any of the above biasing factors, including speech rate, neighborhood density, and lexical frequency shift the placement of the phonetic boundary. Further research is necessary to determine whether this is in fact the case.

Notes

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