The Left Posterior Superior Temporal Gyrus Participates Specifically in Accessing Lexical Phonology

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Abstract

■ Impairments in phonological processing have been associated with damage to the region of the left posterior superior temporal gyrus (pSTG), but the extent to which this area supports phonological processing, independent of semantic processing, is less clear. We used repetition priming and neural repetition suppression during functional magnetic resonance imaging (fMRI) in an auditory pseudoword repetition task as a semantics-free model of lexical (whole-word) phonological access. Across six repetitions, we observed repetition priming in terms of decreased reaction time and repetition suppression in terms of reduced neural activity. An additional analysis aimed at sublexical phonology did not show significant effects in the areas where repetition suppression was observed. To test if these areas were relevant to real word production, we performed a conjunction analysis with data from a separate fMRI experiment which manipulated word frequency (a putative index of lexical phonological access) in picture naming. The left pSTG demonstrated significant effects independently in both experiments, suggesting that this area participates specifically in accessing lexical phonology. ■

INTRODUCTION

Deficits in accessing the sound form of words (lexical phonology) are seen in various types of aphasia but are often difficult to cleanly separate from deficits in accessing word meanings (lexical semantics). For example, both repetition and comprehension deficits are seen in cases of Wernicke aphasia (Alexander, 2003; Binder, 2003; Saffran, 2000; Damasio, 1992). Conduction aphasia, by contrast, is also associated with impaired repetition, but comprehension is generally spared (Alexander, 2003; Saffran, 2000; Damasio, 1992; Damasio & Damasio, 1980). Both syndromes, however, arise from damage to brain areas that prominently include the left posterior superior temporal gyrus (pSTG) (Alexander, 2003; Saffran, 2000; Damasio, 1998; Damasio & Damasio, 1980). Here we refer to the pSTG as the posterior third of the STG, bordered posteriorly by the supramarginal gyrus (SMG).

Intracranial stimulation of the part of the arcuate fasciculus underlying the pSTG has been shown to produce phonemic, but not semantic, paraphasias (Mandonnet, Nouet, Gatignol, Capelle, & Duffau, 2007). Stimulation of the pSTG cortex proper (as opposed to the underlying white matter) has been shown to selectively impair verbal repetition (Quigg & Fountain, 1999). Functional neuroimaging data also suggest that the pSTG is involved in phonological access in general (Burton, LoCasto, Krebs-Noble, & Gullapalli, 2005; Démonet, Thierry, & Cardebat, 2005; Majerus et al., 2005; Hickok, Buchsbaum, Humphries, & Muftuler, 2003; Binder & Price, 2001; Buchsbaum, Hickok, & Humphries, 2001; Wise et al., 2001; Hickok et al., 2000; Price, 2000; Price et al., 1992).

Due presumably to the ambiguity of the parietal– temporal boundary, two prominent theories of pSTG function have variously referred to it as the area of the posterior Sylvian fissure at the parietal–temporal boundary (Spt) (Hickok & Poeppel, 2004), or the posterior superior temporal plane (STP) (Warren, Wise, & Warren, 2005). Both theories describe pSTG as serving as an auditory–motor interface, where an auditory sensory template is matched to a motor template for speech (Warren et al., 2005; Hickok & Poeppel, 2004). These theories do not specify whether this template matching is best described in terms of lexical (whole-word) or sublexical representations.

By contrast, other theories hold that the pSTG may subserve lexical phonological access in particular (Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004; Indefrey & Levelt, 2000, 2004). In a previous parametric functional magnetic resonance imaging (fMRI) study (Graves, Grabowski, Mehta, & Gordon, 2007), we used the word frequency effect (WFE) in picture naming to probe the neural regions participating in lexical phonological

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access. Pictures with names that occur less often in the lexicon (lower frequency words) take longer to initiate a naming response compared to those with higher frequency words (Jescheniak & Levelt, 1994; Oldfield & Wingfield, 1965). Evidence that word frequency modulates lexical phonology separately from lexical semantics comes largely from the frequency inheritance effect. When a homophone refers to both a high- and low-frequency concept (e.g., NONE and NUN), the low-frequency word inherits the fast access speed (Jescheniak, Meyer, & Levelt, 2003; Jescheniak & Levelt, 1994) and lesser vulnerability to error (Dell, 1990) of its high-frequency counterpart. Additionally, evidence that the WFE arises in processes separate from articulatory processes comes from studies in which the naming response has been delayed in order to allow time for lexical access to take place. The WFE generally disappears under these conditions (Jescheniak & Levelt, 1994; Monsell, 1990). Effects of word frequency have also been shown to be separate from those of phonotactic complexity in intact (Santiago, MacKay, Palma, & Rho, 2000) and brain-damaged subjects (Goldrick & Rapp, 2007). Based on this and other evidence, a leading model of lexical access holds that the WFE arises at the level of lexical phonological access (Levelt, Roelofs, & Meyer, 1999).

In our previously published fMRI study, we made the bridging assumption that because lower-frequency words take longer to access, there would be increased recruitment of neural resources (more neural activity integrated over time). We therefore expected blood oxygenation level-dependent (BOLD) signal increases for regions participating in retrieval of lower-frequency words. In light of the cognitive model, we interpreted this activation as reflecting lexical phonological access.

However, all the responses the subjects produced were real words which, by definition, have semantic content. To try to further separate lexical phonological from lexical semantic access, we analyzed the responses in terms of rated concept familiarity. When compared to the WFE activations, spatially overlapping activity was seen in the following left-sided areas: the inferior frontal gyrus (IFG) and the ventral occipito-temporal cortex (OT). WFE-related activation occurred alone in pSTG, suggesting that this area is specifically involved in accessing lexical phonology.

In the current study, we sought to more decisively verify the specificity of the neural areas thought to be involved in lexical phonological access. Here we constructed a WFE de novo in an auditory pseudoword repetition task by exposing the subjects to some pseudowords more than others. The use of pseudowords (pronounceable nonwords) in this manipulation was motivated by two factors: (1) stimuli would be equally novel for all subjects, allowing tight control over experience with the phonological form, and (2) by definition, pseudowords do not have corresponding semantic representations, thereby providing confidence that changes

in activity would not be confounded with semantic-level effects. In this repetition priming task, pseudowords that have been heard and repeated more often should elicit progressively lower levels of neural activity (neural repetition suppression), and a corresponding reduction in reaction time [RT] (repetition priming) (for a discussion of the relationship between repetition priming and suppression, see Grill-Spector, Henson, & Martin, 2006).

Perhaps the most encouraging evidence for the detectability of repetition suppression with short-term exposure to pseudowords comes from a positron emission tomography study by Majerus et al. (2005). Both their study and the current one utilized auditory presentation of pseudowords and manipulated amount of exposure to the stimuli. Their stimuli were composed of combinations of syllables exhibiting either high or low phonotactic frequency (i.e., the probability that any combinatorial pair of syllables would appear together in a real word for a given language). The primary relevant finding was an interaction showing that the repetition suppression in the bilateral superior temporal sulcus (STS) was significantly smaller for pseudowords of low phonotactic frequency relative to those of high phonotactic frequency. This activity also correlated with the repetition priming response for repetition of low phonotactic frequency pseudowords.

The current study differs from that of Majerus et al. (2005), however, in that we are concerned with whole (pseudo)word phonological access rather than the sublexical assembly presumably indexed by their manipulation of phonotactic frequency. To this end, we examine the effect of number of repetitions separately from phonotactic frequency. This approach should reveal areas that respond to repetition of whole pseudowords as potentially separate from those responding to different levels of phonotactic frequency.

Specifically, we expect to observe priming in terms of decreased latencies with repeated production of pseudoword stimuli. We hypothesize that concurrently acquired imaging data will show repetition suppression in left-lateralized areas including the pSTG. That is, we expect that some brain areas (or at least the pSTG) will demonstrate tuning to the phonological form as a whole. The advantage of such tuning would presumably be that less neural effort would be required to retrieve the form of a previously encountered pseudoword, compared to that required for assembling the pseudoword from its sublexical constituents. Such "from scratch" assembly would presumably be reserved for production of the novel pseudowords, or possibly those with constituents of particularly low phonotactic frequency. Hence, "lexical" is used here not to indicate a cognitive pointer to word meanings, but rather to emphasize access to a stored whole phonological form, as opposed to "sublexical" phonological assembly.

Some evidence for the assumption that a pseudoword may become lexically stored comes from a study

by van Turennout, Wagensveld, and Zwitserlood (2005) in an fMRI experiment comparing spoken responses to pseudowords consisting of either trained or untrained syllables. A preferential response to pseudowords with trained syllables was seen in the left pSTG, which the authors interpreted as reflecting comparatively automatic retrieval of a stored phonological code.

There is also the question of whether findings from this study will be relevant to how phonological forms for real words are accessed. This concern is addressed by performing a conjunction analysis of the present results with the word frequency-related findings from our previously reported picture naming study (Graves et al., 2007). Findings are expected to be consistent across these two studies to the extent that (1) lexical phonology is accessed separately from lexical semantics, and (2) mechanisms for lexical phonological access are shared for words and pseudowords (for evidence of this, see Glosser, Kohn, Friedman, Sands, & Grugan, 1997; Martin, 1996).

METHODS

Subjects

Subjects were recruited for fMRI scanning from the University of Iowa community and paid $50 for participation in the 2-hr scanning session, in compliance with local institutional review board guidelines. Inclusion criteria required that all subjects be right handed (a score of at least +85 on the Oldfield–Geschwind handedness questionnaire), have no history of neurological or psychiatric disease, and be able to undergo a magnetic resonance imaging scan. Included were 12 subjects (9 women, 3 men), mean age was 29.2 years (min = 20, max = 54, SD = 11.5). The mean number of years of education across all subjects was 15.2 years (min = 12, max = 19, SD = 1.8). The North American Adult Reading Test (NART-R; Blair & Spreen, 1989) was administered to obtain estimated verbal intelligence quotient scores. These were available for 11 of the 12 subjects, with an overall mean of 107.9 (min = 91, max = 122, SD = 8.0).

Stimulus Material

Stimuli consisted of 250 pseudowords obtained from a stimulus set developed by Gupta et al. (2004). Equal numbers of two- and four-syllable pseudowords were included. Two-syllable pseudowords were included to try to ensure that subjects could easily perform the task, and four-syllable pseudowords were included to try to ensure that the task would be difficult enough to keep the subjects engaged. These pseudowords were comprised of consonant (C)–vowel (V) nonfinal syllables and a CVC final syllable. All stimuli were audio recordings, digitally sampled at a rate of 44.1 kHz, from a single native speaker of American English. Quantitative char-acteristics for the subset of stimuli we used from the Gupta et al. (2004) set are provided as supplementary material.

Repetition latencies were measured from stimulus onset time to response onset time. These latencies were analyzed using a multiple linear regression model which consisted of terms for number of trials for each pseudoword, number of syllables for each word, and one of two possible measures of mean positional biphone frequency (mpbf). Number of syllables was included to account for differences in duration among pseudowords, as suggested for analyzing pseudoword repetition latencies by Lipinski and Gupta (2005).

In addition to the number of repetitions analysis, RT (i.e., time to initiate repetition) and imaging data were also analyzed in terms of phonotactic frequency. Phonotactic frequency was calculated for these stimuli in two ways. One measure was calculated using the phonotactic probability calculator made available on the Internet by Vitevitch and Luce (2004). This tool calculates summed positional biphone probabilities as follows: All instances in which a biphone in a specific position occurs in a word are counted. The log-transformed frequencies of the words in which the position-specific biphones occurred are then summed and divided by the summed log-frequencies for all the words in the Kučera and Francis (1967) corpus that contained a biphone in that position (for further details and examples, see Vitevitch & Luce, 2004). The second method used for calculating phonotactic frequency differed from the first in that it used CELEX-based log-transformed word frequencies (Baayen, Piepenbrock, & Gulikers, 1995). Also, the denominator consists only of words with the same number of biphones, whereas the first method compares the pseudoword biphones to their occurrence in words of any length that contain a biphone in the same position. Hence, the second method can be considered a more length-constrained measure than the first. Summed positional biphone frequencies based on these two methods were then divided by the total number of biphones to yield two mpbf values, one unconstrained by length and one constrained, for each pseudoword.

Task and Scanning Session

Subjects were told that they would see a series of fixation crosses each immediately followed by a speech sound (pseudoword). They were instructed to repeat each pseudoword aloud as quickly and accurately as possible. The auditory stimuli were delivered through MRI-compatible pneumatic, noise dampening headphones (Avotec, Stuart, FL). Visual (fixation cross) stimuli were delivered through a video projector aimed at a rear projection screen secured to the end of the scanner bed near the subject's feet. Subjects viewed the projected stimuli through mirrors attached to the head coil.

All data acquisition and stimulus delivery events were time stamped with submillisecond resolution using the Input/Output time-aWare Architecture (I/OWA) system (Smyser, Grabowski, Frank, Haller, & Bolinger, 2001). Use of the I/OWA system obviates the need for explicitly synchronizing stimulus delivery and scanner TR, eliminates the need for slice-timing correction, and facilitates extraction of response latencies from stimulus and speech onset times (Grabowski et al., 2006; Mehta, Grabowski, Razavi, Eaton, & Bolinger, 2006).

The experiment consisted of six runs lasting approximately 6.5 min each. Stimuli in each run were completely randomized with a variable ISI (mean = 4.54 sec, min = 3.01 sec, max = 6.30 sec). Seventy-five pseudoword stimuli were presented in each run. For the first run, all pseudowords were novel. For each subsequent run, 40 of the pseudowords were repeated from the previous runs, and the rest were novel. Thus, by the end of the six-run scanning session, subjects had heard and repeated 40 of the pseudowords a total of six times.

Images were acquired with a General Electric LX CV/i scanner at a field strength of 1.5 T using a transmit-and-receive quadrature head coil. T2*-weighted time-series images were acquired using a spiral-in/spiral-out pulse sequence (Glover & Law, 2001) (TE = 40 msec, TR = 2 sec, FOV = 24 cm, matrix 64 × 64). This pulse sequence is less susceptible than standard echo-planar imaging (EPI) to signal dropout in areas such as the inferotemporal and orbito-frontal cortices. For each run, 190 time-series image volumes composed of 24 contiguous oblique axial slices (5 mm thick) were acquired parallel to the intercommissural plane and covering the whole brain.

Structural scans

A high-resolution 3-D anatomical scan (SPGR, flip angle = 30°, TR = 24 msec, TE = 7 msec, 256 × 192 × 124), a T1-weighted series (SPGR, flip angle = 30°, TR = 24 sec, TE = 7 msec, FOV 24 cm, matrix 256 × 192), and an eight-shot echo-planar T2*-weighted series (matrix 128 × 128) were acquired. The latter two scans were acquired in the same oblique axial orientation as the time-series data and were used as intermediaries for registration to the subject's anatomical scan (for a more complete description, see Mehta et al., 2006).

Data Processing and Analysis

Image registration was performed using Automated Image Registration, AIR 5.2.3 (Woods, Grafton, Holmes, Cherry, & Mazziotta, 1998; Woods, Grafton, Watson, Sicotte, & Mazziotta, 1998). The first three images in the time series were discarded to avoid saturation effects. Images within a run were aligned to the fourth image of the time series using a 3-D six-parameter rigid-body model. Data from all runs were then aligned to the average image of the first run and later analyzed in this orientation after smoothing with a Gaussian kernel (7.5 × 7.5 × 10 mm full width at half maximum). Each subject's structural scan was registered to a Talairach-compatible atlas (Woods, Dapretto, Sicotte, Toga, & Mazziotta, 1999; Talairach & Tournoux, 1988) using a low-order nonlinear warp. The derived transformations were later applied to the statistical images to allow for group analyses.

Speech processing was performed using custom software implementing a time-aware spectral subtraction algorithm, which removed noise due to scanner activity while leaving the speech signal intact (Mehta et al., 2006). Overt responses were automatically paired with stimulus presentation times and checked manually for accuracy of assignments before final calculation of speech onset latencies. Speech responses were judged to be errors only if (1) the response contained an incorrect number of syllables, (2) the subject noticeably stumbled over or paused during part of a response, (3) the subject repeated part or all of a response, (4) the response was preceded by a delay such that it overlapped with presentation of the next stimulus, or (5) the subject failed to give any response.

The fMRI time-series data were analyzed voxelwise using tal_regress, a custom software module that implements the general linear model (Frank, Damasio, & Grabowski, 1997). The regression model included nuisance covariables for slicewise global (mean) signal intensity (per time point), a constant, and four truncated Fourier series pairs with a cutoff of 1/110 Hz to model noise due to low-frequency drifts. Boxcar regressors, spanning the duration of the speech event, were also included to model systematic speech artifacts (Mehta et al., 2006). The remainder of the covariables included in the regression model were each convolved with a canonical hemodynamic response function (Cohen, 1997) and consisted of (1) successful trials; (2) unsuccessful trials; (3) total number of exposures to a pseudoword presented in a given trial, nested within successful trials; (4) number of syllables in the pseudoword presented in each trial, nested within successful trials; (5) constrained mpbf (choice of the constrained measure was based on the behavioral results described below); and (6) a term for the interaction of number of exposures with mpbf, derived by multiplying the two response functions. By nesting number of exposures within successful trials, the exposures variable is modeled as an incremental decrease in BOLD signal relative to the novel pseudowords for each run. For example, in Run 1, each pseudoword is presented for the first time, so the "successful trials" variable and the "number of exposures" variable are identical. For Run 2, half the pseudowords are being presented for the second time, and that additional exposure is modeled by multiplying the expected BOLD signal for successful execution upon initial exposures in that run by −1. Likewise for Run 3, half the pseudowords are now being

experienced for the third time, and the expected decrease in BOLD signal is modeled by multiplying the unit BOLD signal for those repeat trials which are successfully executed by −2, and so on through Run 6. In this way, responses to successful repeated exposures are always being modeled as decreases in activation compared to successful initial trials within the same run. This approach was used to avoid the possible confound of a decrease in overall signal across runs.

All task covariables were generated from events defined to occur at stimulus *offset* times. Playback time for several of the four-syllable pseudowords is approximately a full second, introducing the possibility that image data would contain an unwanted amount of influence from simple auditory perception.

The model described above was used to analyze the data with voxelwise multiple linear regression, and the resulting coefficient images were transferred to a Talairach-compatible atlas space for group-level analysis. *t*-Statistic images were generated from the group regression images and thresholded at $p < .001$, before correcting for multiple comparisons. A spatial extent threshold of at least 11 contiguous voxels was subsequently applied to the uncorrected results in order to arrive at a corrected threshold of $p < .05$. This combination of uncorrected p value and spatial extent threshold is one we have used previously (Graves et al., 2007). It is based on a technique employed by McDermott, Petersen, Watson, and Ojemann (2003), who used Monte Carlo simulations on random noise following a method described by Forman et al. (1995).

The thresholded results of the current experiment were then used as input to a conjunction analysis (Nichols, Brett, Andersson, Wager, & Poline, 2005) to test for areas of overlap with results from a related experiment (Graves et al., 2007). The conjunction analysis was performed as follows: (1) group-level results for the effect of pseudoword repetition were thresholded as described above and a binary value of 1 assigned to significant voxels, 0 otherwise; (2) thresholded group-level results for the word-frequency manipulation reported in Graves et al. for a separate group of subjects producing real words as part of a naming task were also obtained, and binary values were assigned to the voxels; (3) binarized images from the two sets of results were multiplied, leaving nonzero values only for those areas showing significance in both images. Note that this method requires independent corrected significance in both groups, and that intergroup differences in neuroanatomy are effectively discounted by the smoothing kernel applied in both studies.

RESULTS

Behavior

Amount of experience with each pseudoword, measured by the number of trials for each, explained a significant amount of variance in RT ($\beta = -0.12$, $p < .0001$), separate from that explained by duration (number of syllables) ($\beta = 0.71$, $p < .0001$). The negative β-weight for number of trials indicates that the effect was in the expected direction, with repetition latency decreasing as number of trials increased. That is, there was a significant priming effect. The resulting regression equation was as follows: RT $= 0.2559$ (X_{length}) $+ -0.0247$ (X_{trial}) $+ 1.0727$. This equation shows a linear relationship in which overall RT decreased 24.7 msec for each repetition of a pseudoword. In Figure 1, this relationship is displayed separately for two- and four-syllable pseudowords, overlaid onto a plot of the mean RT ($\pm$ standard error) for each exposure. Note that the β-weights reported above have different values than the coefficients in the regression equation. Here, β indicates standardized regression weights, whereas the terms in the regression equation given above are nonstandardized regression coefficients used to graph the raw RT data in Figure 1.

Figure 1. Behavioral results: Mean RT is plotted against number of exposures (repetitions) to the same pseudowords, separately for those containing either two (left) or four (right) syllables. Bars above and below the mean represent standard error. The broken line on each graph is the regression plot.
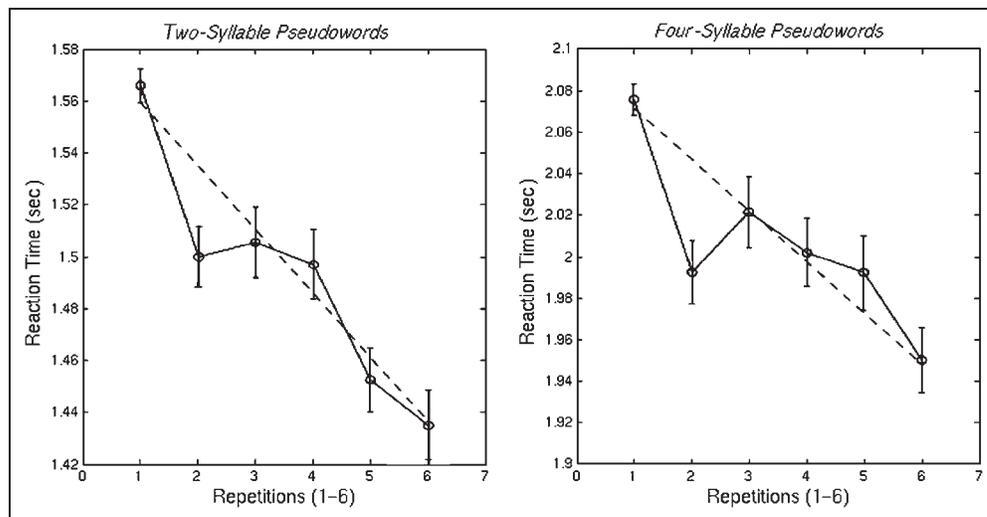
As a check to ensure that this effect was not being driven by acclimation to the task, or the wearing off of its initial novelty after the first experimental run, we analyzed Runs 2 through 6 alone. The rationale here being that subjects should have acclimated to the task and at least most of the initial novelty effects should have worn off by the end of the first run. A regression analysis for this restricted dataset revealed that amount of repeat experience with pseudowords continued to explain a significant amount of variance in response latencies ($\beta = -0.06$, $p < .0001$), separate from that explained by duration (number of syllables) ($\beta = 0.75$, $p < .0001$). A simple correlation of response latency with number of repetitions revealed a linear relationship in which overall response latency decreased 13.5 msec for each pseudoword repetition. As indicated by the somewhat attenuated slope of this relationship, initial novelty of the task does seem to account for some of the relationship between number of repetitions and response latency. However, even without the first run, where the majority of the novelty effects would presumably have occurred, there remains a clearly significant overall pattern of priming in which increased experience repeating each pseudoword corresponds to decreased response onset latencies to those pseudowords.

Based on the criteria for judging erroneous responses outlined above, errors accounted for 2.5% of total responses. The breakdown for the majority of the errors is as follows: 50.8% were productions of the incorrect number of syllables, 11.2% were trials in which the subject's overt production overlapped with presentation of the subsequent stimulus, and 29.1% were from subjects stumbling over or pausing during a response.

Analyses were also performed to check for the presence of sublexical effects on RT, and any interaction with the number of repeat exposures. The mpbf measure, based on Vitevitch and Luce (2004), was used in a multiple regression analysis that included the same covariables as the analysis described above (number of trials and number of syllables), with the addition of the mpbf term. In this regression model, mpbf did not significantly predict RT beyond that of the other two variables in the model ($\beta = -0.01$, $p > .1$). However, mpbf values on the basis of the length-constrained calculation did significantly predict RT ($\beta = -0.03$, $p < .01$) beyond that explained by the other two variables in the model. The negative values for the β-weights reflect the pattern of lower mpbf values eliciting greater RTs, as expected. When an interaction term was included in the regression model (derived by multiplying the constrained mpbf term by the number of exposures term for each trial), constrained mpbf no longer reliably predicted RTs ($\beta = 0.01$, $p = .54$). The interaction, on the other hand, was a reliable predictor of RT ($\beta = -0.06$, $p < .001$). To examine the nature of this interaction, we performed a regression using a separate indicator variable for each level of exposure. This analysis revealed that the inter-

action effect was significant only for the first exposure ($p < .05$), which included both initial exposure to the 40 stimuli that were to be repeated as well as the 210 control stimuli that were never repeated. Indeed, when only responses to the 40 stimuli that were to be repeated were included in the regression, the effect of number of exposures remained significant ($\beta = -0.11$, $p < .0001$), but mpbf and its interaction with number of exposures did not ($\beta = -0.05$, $p = .07$, and $\beta = -0.02$, $p = .52$, respectively). Although the lack of a significant effect for either mpbf or its interaction with number of exposures in a regression model based only on the 40 repeated stimuli raises the question of detection power, we note that this regression model had an R^2 value of .56, indicating that the model accounted for 56% of the variance in RT.

In summary, repetition of whole pseudowords resulted in significant repetition priming as shown by decreases in RT. Sublexical effects, on the other hand, were comparatively weak and were not reliable for the 40 pseudowords that were repeated across runs.

Imaging

The parametric manipulation of number of pseudoword repetitions yielded a set of activated areas in parietal and temporal cortices (Table 1), prominent among which

Table 1. Results from the Parametric Analysis of Number of Repetitions (Top Rows) and Their Conjunction with Those of the Word Frequency Analysis in Picture Naming (Bottom Row)

Location	Size (Voxels)	Talairach Coordinates		
		x	y	z
Areas Showing Decreases with Number of Repetitions				
Parietal lobe				
Left postcent g	141	−36	−29	59
Left preCun/SPL	57	−5	−56	60
Right postcent s	31	28	−37	64
Temporal lobe				
Left pSTG	137	−51	−38	22
Cerebellum				
Left inferior cerebellum	18	−12	−44	−43
Conjunction of Repetition Suppression Effects with the WFE in Picture Naming				
Temporal lobe				
Left pSTG	116	−51	−38	22

Postcent g = postcentral gyrus; preCun/SPL = area at the juncture of the precuneus on the mesial surface and the superior parietal lobule on the lateral surface; postcent s = postcentral sulcus; pSTG = posterior superior temporal gyrus.

was an area in the left pSTG. This is the primary area we hypothesized to be involved in lexical phonological access. A conjunction analysis of these results with those of a previous study of WFEs in picture naming revealed overlapping effects in the pSTG (Table 1 and Figure 2). Although our previous study of picture naming showed effects of word frequency in the left IFG and OT, neither of these areas was modulated by number of pseudoword repetitions in the current study.

To address the possibility that activity modulation observed in the pSTG reflects sublexical phenomena, a term for constrained mpbf (the mpbf measure that significantly predicted RT) was included in the regression model for the image data. Because lower mpbf values correlated with greater RTs, we assumed that neural correlates of mpbf effects would appear as increased activity for pseudowords with lower mpbf values, whereas increasing mpbf values would be associated with reduced activity. That is, we hypothesized a negative correlation between neural activity and mpbf. Areas reliably showing this pattern are presented in Table 2, as are areas showing the opposite pattern (positive correlation of neural activity with mpbf). A term for the multiplicative interaction between number of exposures and constrained mpbf was also included in the image analysis, and areas of significant activation for this term are also reported in Table 2. Interactions reported as positive or negative refer to the sign of the regression coefficients, where positive indicates activity in the direction predicted by the regression model and negative in the opposite direction. Note that none of these centers of activation are in the area of the pSTG. This spatial separation was verified by a conjunction analysis, which showed no overlap between effects of the sublexical regressors (constrained mpbf and the interaction term) and those based on number of whole pseudoword repetitions.

DISCUSSION

The Model

A framework with which to interpret results from the current experiment and their conjunction with those from our previous picture naming experiment is shown in Figure 3. Processes thought to be specifically related to auditory pseudoword repetition are shown in red, those specifically related to picture naming in yellow, and shared processes in orange. Triangles represent input/output modalities, ovals are levels of representation, and rectangles with open-headed arrows represent levels at which each manipulated variable is thought to exert its greatest influence. Bidirectional solid arrows are used to reflect the neurally realistic assumption of interactive flow of information among the different levels of representation. This is in accord with both interactive spreading activation (e.g., Dell, Schwartz, Martin,

Table 2. Analysis of Sublexical Effects in Terms of Mean Positional Biphone Frequency (mpbf), and its Interaction with Number of Repetitions (Lower Rows)

Location	Size (Voxels)	Talairach Coordinates		
		x	y	Z
Areas Showing Negative Correlations of Activity with mpbf				
Parietal lobe				
Right postcent g	163	59	−10	17
Temporal lobe				
Right STS	51	61	−21	2
Areas Showing Positive Correlations of Activity with mpbf				
Frontal lobe				
Right MFG	112	37	43	25
Left SFG	15	−22	54	29
Area of Positive Interaction of mpbf with Number of Repetitions				
Frontal lobe				
Right gyrus rectus	34	8	32	−13
Area of Negative Interaction				
Frontal lobe				
Right IFG	28	44	31	−4

Talairach coordinates correspond to activation centers of mass. Note that none of these centers is in the vicinity of the left pSTG. Postcent g = postcentral gyrus; STS = superior temporal sulcus; MFG = middle frontal gyrus; SFG = superior frontal gyrus; IFG = inferior frontal gyrus.

Saffran, & Gagnon, 1997) and connectionist models (see review by Rohde & Plaut, 2003). In the spirit of these models, we conceive of the lexical-level representations enclosed in ovals as acting as whole words at the behavioral level, but being represented neurally in a distributed fashion. One neural mechanism for assembling unitary phenomena from distributed neural representations is described in the convergence zone framework (Damasio et al., 2004; Tranel, Damasio, & Damasio, 1998; Damasio & Damasio, 1994; Damasio, 1989a, 1989b). This is the neural framework for the model in Figure 3.

In the case of pseudoword repetition, the subject receives auditory input in the form of a recorded pseudoword, immediately followed by decoding of the basic phonetic structure of the sound. At this point, the signal could be translated directly into an articulatory–motor program for speech output. This step is thought to be modulated by phonotactic (sublexical) frequency (see Introduction and Goldrick & Rapp, 2007; Santiago et al., 2000). Alternatively, phonetic input could be mapped onto a learned lexical phonological representation, possibly increasing speed of access to the associated

Figure 2. Results of the conjunction analysis showing areas of decreased activity for increasing experience with repeating pseudowords in the current study with areas showing increased activity for producing increasingly low-frequency words during picture naming. The single area surviving this conjunction is located at Talairach coordinates −51, −38, 22 (highlighted with the yellow oval and listed in the last row of Table 1).
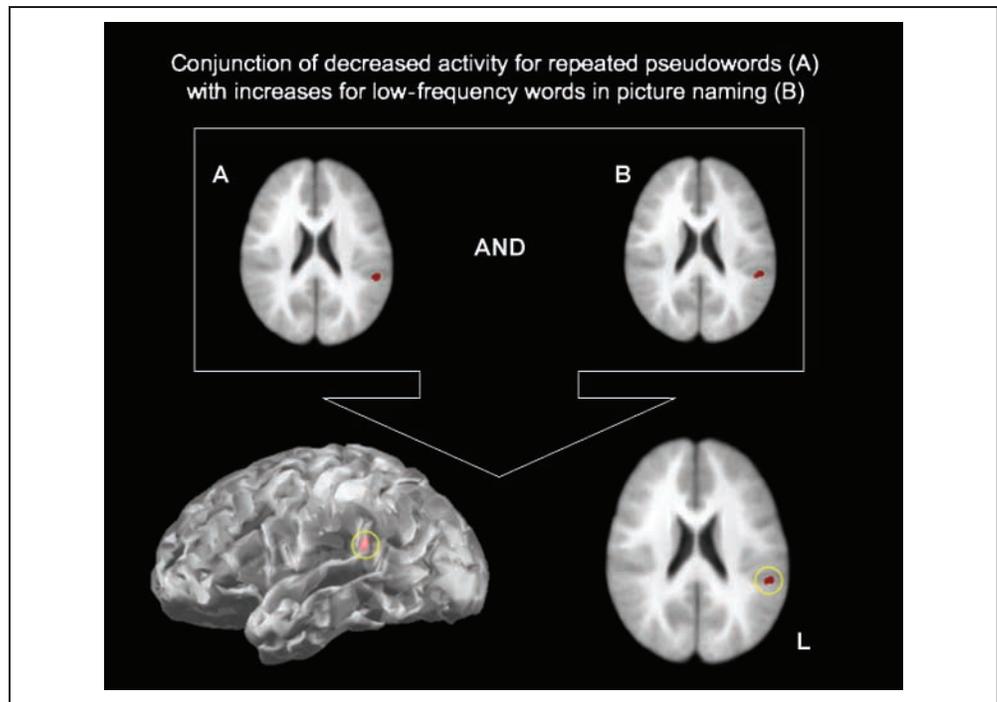
articulatory–motor program. In this experiment, subjects became more experienced with the form of some pseudowords more than others, leading to decreased RT for those items.
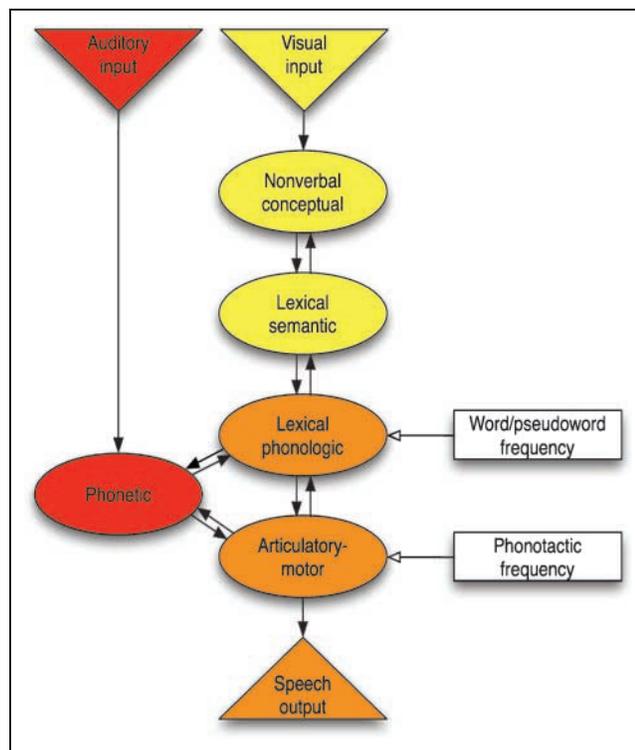

Figure 3. Processing model of pseudoword repetition (red) and picture naming (yellow). Highlighted in orange are the stages thought to be shared across the two tasks.

Interpretation and Previous Findings

This decrease in RT with increased pseudoword experience is unlikely to be due to changes at the lexical semantic level, as pseudowords, by definition, do not have semantic content. Constrained mpbf also influenced RT, although this was not the case when its interaction with number of repetitions was included in the regression analysis. Because mpbf is a measure of sublexical differences among the stimuli, this finding likely reflects small differences among the stimuli in terms of relative ease or difficulty of articulation. The interaction finding suggests that this effect varies with the number of exposures to the pseudowords. Neural correlates of the effect of mpbf and its interaction with number of repetitions were found (Table 2), but not in the pSTG. Hence, the repetition suppression of activity in the pSTG is unlikely to be due to lexical semantic or articulatory–motor effects. According to the model in Figure 3, the pSTG result most likely reflects increased efficiency at the level of lexical phonological access.

As mentioned in the Introduction, the Majerus et al. (2005) study is similar to this one, but with important differences. Most critically, theirs was a study in which items of different phonotactic frequency were presented in blocks, thereby confounding familiarization of the whole pseudoword with its phonotactic frequency. Hence, it was unclear whether their bilateral STS and left pSTG findings were related to phonotactic frequency, whole pseudoword repetition, or both. Our study, by utilizing event-related fMRI, has enabled the separation of lexical (whole pseudoword) and sublexical effects for the same items, thereby revealing neural systems that

respond preferentially to each factor. Specifically, our findings suggest that the repetition suppression found in the left pSTG is specifically related to more efficient access to whole phonological forms. Changes in phonotactic frequency, on the other hand, resulted in modulation of activity in the right STS. This is a replication of another of the Majerus et al. findings, which the current study suggests is related to processes of sublexical assembly. Hence, by examining the effect of number of repetitions separately from phonotactic frequency, we are able to show left pSTG responses to whole pseudowords separately from right STS responses to phonotactic frequency. This, combined with the confirmatory evidence from the conjunction analysis with lexical items, suggests that the left pSTG specifically supports access to whole-word phonological forms.

Task-related changes are also seen here in bilateral parietal cortices. To our knowledge, none of the major frameworks for word retrieval, such as those put forth by Damasio et al. (2004), Hickok and Poeppel (2004), Indefrey and Levelt (2004), or Price (2000), predict activity related to lexical, or even pseudoword, access in bilateral parietal cortices. This, combined with the observation that none of the parietal results seen here overlap with those seen in the picture naming study, and the fact that we do not have specific hypotheses regarding these areas, makes interpretation of this group of parietal lobe findings particularly challenging.

Some tentative interpretations of the bilateral parietal and cerebellar results can, however, be offered. Repetition suppression effects appeared in the more dorsal area of the postcentral gyrus in the current study, whereas activation modulated by word frequency appeared slightly posterior to that found in the dorsal aspect of the intraparietal sulcus in the study of Graves et al. (2007). Left cerebellar findings are also reported in these studies for both conditions. Part of the Indefrey and Levelt (2004) meta-analysis compared studies that used overt or covert responses and found a network of areas reliably associated with overt more than covert production that included the bilateral postcentral gyri and the left cerebellum. These areas were presumed to form a network which was interpreted as supporting phonetic encoding and articulation.

Another possible interpretation is that these areas form part of a neural network for word learning and/or phonological working memory. Evidence for the parietal component comes from a magneto-encephalography study by Cornelissen et al. (2004), in which subjects learned names of unfamiliar objects. The primary finding was an effect of learning on activity in the inferior parietal lobe, which the authors interpret as reflecting enhanced utilization of the phonological storage component of phonological working memory for the newly learned items. Those findings converged with results from their magneto-encephalography study of patients with anomia due to lesions involving part of the left

parietal lobe (Cornelissen et al., 2003). Areas of an intact parietal cortex near the lesion showed changes in activation that corresponded to improved performance due to training.

In addition to these studies implicating the parietal lobe in word learning, other work suggests that parietal and cerebellar cortices may act together to support word learning and verbal working memory. In a study of native French speakers learning English, Raboyeau et al. (2004) showed activity in the cerebellar and left parietal cortices corresponding to improved English performance at follow-up. Additionally, in a two-alternative forced-choice Sternberg paradigm (a verbal working memory task), Kirschen, Annabel Chen, Schraedley-Desmond, and Desmond (2005) found practice-related changes in both the cerebellar and left inferior parietal cortices. Subjects with cerebellar damage have been shown to have selective deficits in verbal working memory (Ravizza et al., 2006), and learning of a difficult second-language phonetic contrast has been shown to recruit parietal and cerebellar cortices (Callan et al., 2003). These studies, together with our results, suggest that areas of the left parietal cortex, perhaps together with cerebellar regions, may support verbal learning through the phonological storage component of verbal working memory. To the extent that this aspect of working memory may also support efficiency of articulatory–motor planning, these two views of our parietal and cerebellar findings may not be mutually exclusive. Investigations of the possibly distinct neural systems supporting these processes were beyond the scope of the current study and will require further experimentation.

In contrast to the findings discussed so far, activity in some frontal lobe regions (Table 2) are positively associated with phonotactic frequency (left superior frontal gyrus, right middle frontal gyrus). Also, an interaction of pseudoword repetition with phonotactic frequency was found in the right inferior frontal gyrus. However, no relationship was found between frontal lobe activity and the main effect of pseudoword repetition. These frontal lobe findings point to a role in sublexical phonological assembly rather than whole pseudoword access. Such an interpretation is compatible with a role for the frontal lobe in phonetic encoding and articulation as described by Indefrey and Levelt (2004).

Returning to the left pSTG finding of the current study, both the pseudoword repetition task and the picture naming task from our previous experiment (Graves et al., 2007) involved overt verbal production where the experimental manipulation was in terms of amount of experience with the phonological form produced. That overlapping results were found at all across the two tasks, however, is striking given that they differed in terms of sensory modality (auditory compared to visual stimulation), material type (pseudowords compared to pictures), and time frame of experience presumably indexed by the independent variable (short-term experience for num-

ber of repeated trials with the pseudowords, long-term experience for word frequency). Given the broad nature of differences between these two experiments, and the comparative specificity of the processes they are thought to share (shown in orange in Figure 3), the conjunction of activity changes seen in the left pSTG strongly suggests that this area is specifically involved in lexical phonological access.

This functional imaging evidence for the role of the left pSTG in lexical phonological access is novel, and this finding gains added weight and significance from its consistency with previously published findings. In a landmark review and synthesis of evidence from studies of human lesions as well as relevant animal literature, Geschwind (1965) considers the pSTG to be the core of Wernicke's area and points out that, ''the loss of Wernicke's area can be regarded as the destruction of a memory store—as it was regarded classically. Presumably, it functions importantly as the 'storehouse' of auditory associations.'' Here we show that not only is this area more active for producing words of less frequent form, its activity is also reduced when subjects are given additional experience with production of the phonological forms. Importantly, the latter forms do not correspond to any semantic content, suggesting that the associations supported by the left pSTG, to which Geschwind refers, are indeed specifically auditory in nature.

Findings from functional imaging studies also indicate a role for the left pSTG in lexical phonological access, although few have done so with the specificity of the current analysis. For example, similar findings for real words were obtained by Katz et al. (2005) (their Experiment 3), who varied the number of repeated exposures to words during a single scanning session. Their subjects performed both lexical decision and word pronunciation in separate blocks. In light of the fact that the lexical decision task did not involve an overt verbal response, whereas the word pronunciation task did, it may be interesting to note that activity reductions were greater in the pSTG for word pronunciation than for lexical decision.

In addition to the studies just discussed showing learning-related activity changes in the left pSTG, imaging studies have also shown activity in this area across visual and auditory modalities. A study of cross-modality effects was performed by Price, Winterburn, Giraud, Moore, and Noppeney (2003) in the auditory and visual domains. They compared activation results across studies of auditory word repetition, reading, picture naming, and environmental sound naming. In all cases, responses were made covertly. Reading and auditory word repetition both activated the left-sided IFG, pSTG, and OT. Unfortunately, there was no direct comparison in this study between auditory word repetition and picture naming, as was performed in the current study. Regarding the possible sensory specificity of the pSTG,

this study suggests that there are modality-independent processes present in all four tasks to which the pSTG, as well as the IFG and the OT, are sensitive.

Alternate Possible Interpretations

Two possible alternative interpretations of the current results bear consideration, (1) that the left pSTG supports both lexical and sublexical phonological access, and (2) that the repetition suppression observed in the pSTG reflects decreased demands on phonological working memory. Regarding the first point, there are previous studies reporting responses in the posterior superior temporal cortex to both words and pseudowords. For example, in a positron emission tomography study of Fiez, Raichle, Balota, Tallal, and Petersen (1996), subjects were instructed to listen to the presented words or pseudowords. Compared to viewing a fixation dot, simply listening to words or pseudowords activated nearly identical areas of the left posterior temporal cortex. It may be important to note, however, the focus of that activation was 17 mm posterior to the pSTG activation reported here, in an area they describe as the ''temporo-parietal region.'' Additionally, Burton et al. (2005) performed an fMRI study comparing two phonological tasks (final consonant discrimination and rhyming) for words and pseudowords in visual and auditory modalities. The only two areas to show activity across all conditions relative to controls were the left-lateralized dorsal/posterior IFG (roughly BA 44) and the left pSTG. Although these studies are suggestive of a general role for the pSTG in lexical and sublexical processing, neither study explicitly attempted to disentangle these two processes, making firm conclusions about the nature of phonological processing in the pSTG difficult to draw from these studies.

The second possibility, that the left pSTG is involved in phonological working memory, relates to the point raised above that the parietal and cerebellar responses observed here may also reflect demands on phonological working memory. In fact, a previous study (Paulesu, Frith, & Frackowiak, 1993) using a series of tasks to isolate the effects of phonological memory load purported to locate the phonological storage component of verbal working memory in the left SMG. However, their location for the putative phonological memory store (−44, −32, 24) is anterior to ours, squarely in the parietal lobe within the SMG. The left inferior SMG has also been implicated in phonological aspects of verbal working memory in a study comparing verbal and nonverbal working memory tasks (Ravizza, Delgado, Chein, Becker, & Fiez, 2004). There is also preliminary evidence that patients with lesions in this area have deficits in verbal but not nonverbal working memory (Graves, Vianna, & Tranel, 2005). Although we see nothing in our results that is incompatible with a role for the left pSTG in phonological storage for verbal

working memory, these studies collectively suggest instead that it is the SMG that supports access to phonological information during verbal working memory tasks.

Conclusion

Results from the present study, along with others discussed here, indicate that activity changes in the left pSTG are observed under conditions which elicit phonological processing. The current results are also unique in demonstrating correspondence of left pSTG activity with parametric changes for variables thought to specifically relate to lexical phonological access. A common substrate for these changes was seen across tasks which required overt production but differed in terms of the lexical status of the stimuli and their presentation modality. As illustrated in Figure 3, a convergence of results across these tasks strongly suggests the presence of lexical phonological processing independent of influence from lexical semantics.

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